MAMMALIAN HERBIVORES REINFORCE ECOLOGICAL STATE TRANSITIONS IN THE CHIHUAHUAN DESERT

BY

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THESIS

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ABSTRACT

Woody plant encroachment is a main driver of landscape change in drylands globally. In the Chihuahuan Desert, past livestock overgrazing interacted with prolonged drought to convert vast expanses of black grama (*Bouteloua eriopoda*) grasslands to honey mesquite (*Prosopis glandulosa*) shrublands. Such ecosystem state transitions have greatly reduced habitat for grassland wildlife species, increased soil erosion, and inhibited the delivery of ecosystem services to local communities. The potential for wild herbivores to trigger or reinforce shrubland states may be underappreciated, however, and few studies compare herbivory effects across multiple consumer taxa. Here, I address the roles of multiple mammalian herbivores in driving or reinforcing landscape change in the Chihuahuan Desert by examining their effects on plant communities over multiple spatial and temporal scales, as well as across plant life stages. Moreover, I studied these herbivore effects in the context of precipitation pulses, long-term climate influences, competitive interactions, and habitat structure. I used two long-term studies that hierarchically excluded herbivores by body size over 25 years (Herbivore Exclosure Study) and 21 years (Ecotone Study), and a perennial grass seedling herbivory experiment. Native rodents and lagomorphs were especially important in determining grass cover and plant community composition in wet periods and affected perennial grass persistence over multiple life stages. Conversely, during drought, climate drove declines in perennial grass cover, promoting shrub expansion across the landscape. In that shrub-encroached state, native small mammals reinforced grass loss in part because habitat structure provided cover from predators. This research advances our understanding of an underappreciated component of ecosystem change in drylands – small mammal herbivory – and highlights the need to incorporate positive feedbacks from native small mammals into conceptual models of grassland-shrubland transitions.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 SHRUB ENCROACHMENT

Drylands comprise 41% of the Earth's total land cover and are settled by approximately two billion people (MEA, 2005). Drylands provide a wealth of ecosystem services to their inhabitants and beyond including 50% of the world's livestock, 44% of all cultivated land, 35% of global Biodiversity Hotspot Areas, climate regulation locally via vegetation cover and globally via carbon sequestration, and habitat for game and non-game wildlife (MEA, 2005; Davies et al., 2012; Davies et al., 2016). Because dryland productivity is limited by precipitation, they are particularly vulnerable to global climate change and subsequent desertification, or the loss of biological productivity in drylands (Burrell et al., 2020). Sixty-five percent of drylands are classified as rangelands – grass-dominated arid ecosystems supporting livestock grazing (MEA, 2005). Pastoralism and cattle ranching of rangelands supports local economies and provides global markets with nutrient-dense foods (Sayre et al., 2013; Yahdjian et al., 2015). However, rangelands and other grass-dominated biomes are being lost to cropland conversion (Davies et al., 2012), desertification (Peters et al., 2015), biological invasions (Vasquez et al., 2010), and shrub encroachment (D'Odorico et al., 2011). In fact, six of the world's 14 terrestrial biomes are grass-dominated, and shrub encroachment has occurred in all six (Stanton et al., 2017).

Shrub encroachment is a global phenomenon that threatens the persistence of the world's arid grasslands. Such grassland-to-shrubland state transitions are noted by a drastic shift in plant community composition, typically generating subsequent shifts in ecosystem structure and function (Eldridge et al., 2011). Following drastic declines in grass and herbaceous cover, the establishment of alternative, stable shrubland states conveys increased cover of bare soil, soil erosion, increased sediment loads into watersheds, and edaphic droughts (D'Odorico et al., 2011; Ratajczak et al., 2012). Fundamental restructuring of semiarid and arid rangelands can produce strong, albeit variable, shifts in ecosystem services (Eldridge & Soliveres, 2015). The context in which shrub encroachment is considered affects whether ecosystem service shifts are interpreted as positive, negative, or neutral (Eldridge et al., 2011). For dryland communities dependent on livestock production, shrub encroachment into grasslands can impose negative stresses including loss of livelihoods and lost revenue for local economies from livestock raising (Sayre et al., 2013).

The drivers and feedbacks contributing to grassland-to-shrubland state transitions – overgrazing, dampened fire frequency, prolonged drought, increased atmospheric CO_2, increased climatic variability – operate and interact at multiple spatial and temporal scales to initiate, then reinforce, alternative shrubland states (D'Odorico et al., 2011; Bestelmeyer et al., 2018). To illustrate, a driver such as overgrazing by cattle amid drought conditions will reduce grass cover and fecundity, as well as fire fuel loads, allowing for the establishment of shrub seedlings. Continued pressure from these drivers will push the grassland ecosystem toward a critical threshold, after which a rapid succession from grassland to shrubland state will occur, which is difficult to reverse due to reinforcement by positive feedbacks.

1.2 SHRUB ENCROACHMENT IN THE SOUTHWESTERN US

In the Chihuahuan Desert of the southwestern United States, black grama (*Bouteloua eriopoda*) grasslands are undergoing ecological state transitions to honey mesquite (*Prosopis glandulosa*) shrublands. At the Jornada Basin Long Term Ecological Research (JRN LTER) site in southern New Mexico, cover of *B. eriopoda* grasslands diminished from 67% in 1858 to 3% in 1998, corresponding with the expansion of *P. glandulosa* shrublands from 15% to 59% (Peters et al., 2012). Grassland-to-shrubland state transitions at JRN LTER site were primarily triggered by historical livestock overgrazing amid periods of chronic drought, and reinforced by positive feedbacks in reduced fire frequency, increased atmospheric CO_2, and soil erosion (D'Odorico et al., 2011). Cattle grazing has been significantly reduced or removed from some pastures (Havstad & Bestelmeyer, 2019), but shrubland state-reversal to grassland remains uncommon and often requires intensive management intervention. Although cattle played an important role in triggering historical state transitions, researchers have emphasized the need to incorporate wild herbivore populations into current grassland-to-shrubland state transition models (Bestelmeyer et al., 2007).

1.3 HERBIVORY EFFECTS IN LANDSCAPES EXPERIENCING WOODY PLANT ENCROACHMENT

Herbivores interact with plant communities primarily through consumption of plant biomass (Belsky, 1986; Louda et al., 1990), but they can have profound influences on ecosystem dynamics secondarily through soil disturbance (e.g., trampling, digging, burrowing; Vavra et al., 2007), seed predation or dispersal (Brown & Archer, 1999; Archer, 1994), and diet selectivity (Venter et al., 2019). These direct effects of herbivory often initiate far-reaching indirect effects that can cascade through ecosystems. For instance, modification of elk (*Cervus elaphus*) habitat use and herbivory in response to wolf (*Canis lupus*) reintroduction in Yellowstone National Park, Wyoming increased canopy cover of willow (*Salix geyeriana*) and aspen (*Populus tremuloides*, Fortin et al., 2005). In turn, beaver (*Castor canadensis*) abundances increased, as did the recovery of desirable, biodiverse riparian ecosystems (Beschta & Ripple, 2018). Mammalian herbivores are a critical facet in trophic webs linking higher consumers with lower plant communities and thus determining the structure, function, and composition of ecosystems. Because of this, mammalian herbivore assemblages have been identified as a potentially key variable in understanding and managing landscape change (Pringle et al., 2007).

Van Auken (2000) proposed that the collective preference of an herbivore assemblage for either grasses or shrubs confers a disadvantage for that functional group, with consequences for ecosystem states. In Mozambique, for example, the reintroduction of an assemblage of large herbivores actually reversed long-term shrub encroachment because these species displayed a dietary preference for shrubs, thus limiting shrub survival, recruitment, and cover (Guyton et al., 2020). In contrast, the Jornada Basin herbivore assemblage favors grasses (Brown & Heske, 1990; Smith et al., 1998; Bestelmeyer et al., 2007), which should promote shrubland states. Moreover, a meta-analysis of plant responses to herbivory revealed that shrubs and forbs are more resistant than grasses to herbivory in low-resource environments (Hawkes & Sullivan, 2001), conferring a disadvantage to grasses where herbivory pressure is high. At the JRN LTER site, then, we would expect shrubland states to be favored both because native herbivores prefer grasses and because these grasses will respond poorly to herbivory in this low-resource landscape.

1.4 NATIVE HERBIVORES

Research on native rodents and lagomorphs in the Chihuahuan Desert has found their effects on grasses to be either strong or weak. Among rodents, kangaroo rats (*Dipodomys* spp.) have been recognized for their keystone status, functioning as ecosystem engineers that can reinforce shrub-encroached grasslands through grass seed predation and soil disturbance created by burrowing behavior (Brown & Heske, 1990). Kerley et al. (1997) also demonstrated, through rodent exclusion, that rodent effects on grassland dynamics can be driven by graminivory – the consumption of grass structural and photosynthetic tissues (Kerley & Whitford, 2009). Further, rodents can alter plant community composition through preferential harvest of species with larger seeds (Maron et al., 2021). Parallel research into lagomorphs of the Chihuahuan Desert, including black-tailed jackrabbit (*Lepus californicus*) and desert cottontail (*Sylvilagus audubonii*), established similar herbivory effects. Bestelmeyer et al. (2007) found that lagomorphs can reinforce grass loss in shrub-encroached rangelands of New Mexico through grass seedling predation in shrublands and in ecotones between shrublands and grasslands. These results were supported by a recent study that identified herbivory of grasses by lagomorphs, *S. audubonii* in particular, as an important mechanism for driving and reinforcing shrubland states (Abercrombie et al., 2019). Hence, evidence exists that small-bodied mammalian herbivores in southwestern rangelands can contribute to grassland-to-shrubland state transitions through numerous pathways.

Conversely, similar research has demonstrated only weak herbivory effects from native small mammals. Through experimental exclosures and shrub removal, Havstad et al. (1999) tested for effective methods of grassland restoration and found that lagomorphs imposed only weak effects on grass recruitment, whereas physical removal of shrubs elicited stronger responses. Svejcar et al. (2019) also found no rodent or lagomorph graminivory effects on *B. eriopoda* recovery following disturbance in either grasslands or shrublands, while both taxa showed greater abundances in shrublands. Baez et al. (2006) attributed the weak effects of rodents to bottom-up regulation whereby periods of low net primary production regulate rodent abundances, in turn reducing the potential for top-down effects of rodents on perennial grasses. Net primary production in the Chihuahuan Desert fluctuates widely in response to precipitation and may indeed play a strong role in the outcomes of studies focusing on top-down pressures exerted by small mammals (Schooley et al., 2018).

Thus, herbivory by rodents and lagomorphs may exert either strong or weak effects on biomass, composition, and recruitment of plant communities and these varied outcomes may depend on climate (Schooley et al., 2018), local predator-prey dynamics (Wagnon et al., 2020), density-dependent controls (e.g., rabbit hemorrhagic disease; *see* Asin et al., 2021), and spatiotemporal scale of studies. In southwestern drylands, the influence native herbivores impose on ecosystem states appears to be highly context-dependent and requires further investigation.

1.5 INVASIVE UNGULATE HERBIVORY

Native large-bodied herbivores, mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*), are rare within the JRN LTER site (Schooley et al., 2024). However, the introduction of exotic African oryx (*Oryx gazella*), a generalist ungulate species (≥200 kg), has created a novel herbivore assemblage in the Jornada Basin and surrounding rangelands. Ninety-five African oryx were originally released between 1969 and 1977 into the adjacent White Sands Missile Range as part of a state management plan to increase revenue through exotic game hunts (Reid & Patrick, 1983). Native to the Kalahari Desert of southern Africa, oryx are well-adapted to aridity (e.g., carotid rete; Maloney et al., 2002), display dietary plasticity in periods of drought (Lehmann et al., 2013), and predator release in low elevation areas of New Mexico (Prude & Cain, 2021). Since their initial release, White Sands populations have reached an estimated >3,400 individuals (Bender et al., 2019). Little is known about oryx interactions with native wildlife and landscapes, but an exotic generalist ungulate in this low-productivity landscape likely poses consequences for diminishing *B. eriopoda* grasslands imperiled by ongoing grassland-to-shrubland transitions.

Invasive ungulates can exert numerous direct and indirect effects on grassland and shrubland ecosystems through grazing and browsing (Maron & Vila, 2001; Vavra et al., 2007) with consequences for native biodiversity (Spear & Chown, 2009). In other systems, the effects of invading ungulates have been dramatic. White-tailed deer (*Odocoileus virginianus*), for example, are invasive in northern Canadian boreal forests and have altered ecosystem composition, structure, and function. Cascading, indirect consequences have been documented for the composition and abundance of native insect, bird, and mammal communities, nutrient cycling, economic viability of forestry and agriculture, and the establishment of alternative stable states (Côté et al., 2004; Fisher et al., 2020). Invasive pigs (*Sus scrofa*), Asiatic water buffalo (*Bubalis bubalis*), and European cattle breeds (*Bos taurus, B. indicus*) established in vast northern Australian savannas have disturbed expanses of continuous grass cover, increased soil erosion and nutrient input in watersheds, facilitated the spread of invasive grasses, and dampened fire regimes (Mihailou & Massaro, 2021). Further, their populations are thought to exist at higher densities in Australia because of lack of predators (Freeland, 1990). Such far-reaching effects of invasive ungulates have been reported globally.

Recent evidence suggests oryx in the Jornada Basin prefer grassland habitats, especially during dry years, thus implicating oryx in a potential coupled herbivore-climate trigger of shrub encroachment (Andreoni et al., 2021). In fact, all previous diet research on exotic oryx in New Mexico has reported grasses to constitute ≥50% of their diets (Smith et al., 1998; Marquez &

Beckles, 2010; Cain et al., 2016). Moreover, Augustine and McNaughton (2006) concluded that not only can ungulates have a range of impacts on plant communities, but those impacts become more pronounced in low productivity ecosystems. Xeric grasslands, then, warrant considerable attention where invasive and domestic ungulates are present.

1.6 CONCLUSIONS AND GOALS

Shrub encroachment threatens the persistence of dryland ecosystem services globally. Amid global climate change, expansive grassland degradation, as well as possible biodiversity declines, are expected in drylands experiencing shrub encroachment. Our current understanding of the role that native herbivores play in the triggers and feedbacks of shrub encroachment is incomplete. Further, the expansion of African oryx across shrub-encroached landscapes injects novel dimensions into the shrub encroachment equation. Here, we highlight the need to reassess current models of the role mammalian herbivores play in driving and reinforcing grassland-to-shrubland state transitions in the Chihuahuan Desert. This is especially true given future climate change projections because coupled herbivore-climate pressures can interact synergistically to trigger state transitions in low-productivity landscapes.

Broadly, we address the roles of a suite of mammalian herbivores at multiple spatial and temporal scales, and in the context of multiple biotic and abiotic factors, to answer a central question: Do herbivores trigger or reinforce ecosystem change in a dryland experiencing shrub encroachment? In Chapter 2, we demonstrate that native lagomorphs and rodents contribute to perennial grass declines and plant community dynamics over very long time periods (i.e., 25 years). During an extensive dry period, climate drove declines in perennial grass cover, allowing shrubs to expand across a previously unencroached grassland. In the wet period following, a critical period for grass recovery, native lagomorphs and rodents contributed the strongest role in reducing perennial grass cover. In Chapter 3, we examined such grass reductions from native rodents and lagomorphs in the context of perennial grass cover, recovery from disturbance, and seedling survival across a shrub encroachment gradient to unveil the direct mechanisms through which native rodents and lagomorphs contribute to reinforcement of shrubland states and grassland loss. Native rodents exerted strong control over perennial grass cover, recovery from disturbance, and seedling survival. Such outcomes were especially apparent in ecotones and shrublands, indicating native rodents and lagomorphs strongly reinforce desertified shrubland states through multiple pathways. In Chapter 4, I discuss these results in the context of drylands in a changing climate, and in drylands where shrub encroachment persists despite efforts to conserve or restore arid grasslands. In sum, this work provides compelling evidence that herbivory by native small mammals, interacting with climate and habitat structure, can reinforce the establishment of persistent shrubland states and should be integral to conceptual models of state transitions in drylands.

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CHAPTER 2: THE ROLES OF MULTIPLE MAMMALIAN HERBIVORES AND CLIMATE IN GRASSLAND-SHRUBLAND TRANSITIONS IN THE CHIHUAHUAN DESERT[1]

2.1 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. In the Chihuahuan Desert, past livestock overgrazing interacted with prolonged drought to convert vast expanses of black grama (*Bouteloua eriopoda*) grasslands to honey mesquite (*Prosopis glandulosa*) shrublands. The potential for wild herbivores to trigger or reinforce shrubland states may be underappreciated, however, and comparative analyses of 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 exclosure treatments and surveyed plant foliar cover over 25 years. Native lagomorphs interacted with climate to limit perennial grass cover during wet periods. Native rodents strongly decreased plant diversity, increased evenness, and altered community composition. Surprisingly, cattle and African oryx exclusion had only marginal effects on perennial grass cover at their current densities. Mesquite cover proliferated, responding primarily to climate, and was

[1] Andreoni, K.J., Bestelmeyer, B.T., Lightfoot, D.C., Schooley, R.L. The roles of multiple mammalian herbivores and climate in grassland-shrubland transitions in the Chihuahuan Desert. *Ecology,* in revision.

unaffected by herbivore treatments. 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 if increased perennial grass cover from exclusion of native lagomorphs and rodents slows the transition to a dense shrubland.

2.2 INTRODUCTION

Humans have modified 75% of the Earth's terrestrial surface (IPBES, 2018) with consequences for food security (FAO, 2022), habitat loss and species extinction (Mittermeier et al., 2011), and land degradation including desertification (MEA, 2005; Bestelmeyer et al., 2015; Huang et al., 2016). Drylands 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 (Huang et al., 2017; Berdugo et al., 2020). Droughts interacting with livestock overgrazing have already catalyzed landscape change across much of the Earth's drylands (Gaitán et al., 2018; Souther et al., 2020; Maestre et al., 2022). Moreover, wild herbivores can have profound effects on arid ecosystems including altering nutrient cycling and plant community composition (Forbes et al., 2019; Tuomi et al., 2019; Kristensen et al., 2022).

Globally, shrub encroachment into grasslands with expansion of bare ground (i.e., xerification) is a dominant form of landscape change in drylands (Schreiner-McGraw et al., 2020; Berdugo et al., 2022; Ding & Eldridge, 2023). Although livestock grazing-climate interactions were the main triggers of grass loss and shrub encroachment, 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 et al., 2019a). Selective herbivory by a suite of large and small mammals may also modulate grassland-shrubland transitions (Davidson et al., 2010), but the effects of domestic livestock versus wild herbivores on desert ecosystems remain uncertain because studies typically focus on these taxa in isolation (Maestre et al., 2022; Davies et al., 2023). Furthermore, long-term studies are necessary to understand the role of herbivore-climate interactions on vegetation change that occurs 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). 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 and poorly understood. 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 (Bestelmeyer et al., 2007; Abercrombie et al., 2019). However, parallel research has documented rodents and lagomorphs as imposing little to no effect on grass recruitment and recovery (Havstad et al., 1999; Báez et al., 2006; 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 (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 (Thibault et al., 2010; Schooley et al., 2018; Wagnon, 2023).

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; Spear & Chown, 2009; Mihailou & Massaro, 2021), and their effects are more severe in arid regions (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 ≥50% of their diet in their exotic range (Smith et al., 1998; Marquez & Boecklen, 2010; Cain et al., 2016). However, the effects of African oryx on imperiled black grama grasslands have yet to be directly assessed.

Here, we experimentally excluded domestic cattle, native mammalian herbivores, and exotic oryx from a Chihuahuan Desert grassland and evaluated herbivore-climate interactions on vegetation as this grassland transitioned toward a shrubland over 25 years. We asked whether herbivore effects were modified by long-term aridity trends (Christensen et al., 2023), current and legacy precipitation (Sala et al., 2012; Monger et al., 2015), and interspecific grass-shrub competition (Pierce et al., 2019a, 2019b).

We hypothesized that large bovids (cattle and oryx) would interact with drought to trigger perennial grass loss and subsequent honey mesquite expansion (D'Odorico et al., 2011), with oryx replacing the historical role of cattle in driving shrub encroachment. In contrast, we hypothesized that native rodents and lagomorphs would primarily reinforce shrubland transitions by reducing herbaceous cover (Brown & Heske, 1990; Bestelmeyer et al., 2007; Kerley &

Whitford, 2009), especially during wet periods when consumer populations may be high enough to exert top-down control (Schooley et al., 2018; Wagnon, 2023). Moreover, we expected desert rodents to drive trends in diversity and composition of plant communities through selective herbivory (Brown & Heske, 1990; Maron et al., 2021). We hypothesized that perennial grasses would respond negatively to drought periods and positively to pulses in wet season precipitation (Christensen et al., 2023). We also anticipated legacy effects in which previous-year wet season precipitation would benefit perennial grasses (Sala et al., 2012). That is, there would be greater grass cover than expected from current wet season precipitation alone following a year with high wet season precipitation. Conversely, we hypothesized that honey mesquite shrubs would be limited when at low densities by interspecific competition with perennial grasses (Pierce et al., 2019b) but would be more resistant to variable drought periods (Gherardi & Sala, 2015). Thus, we expected droughts would be advantageous for honey mesquite, allowing for competitive release from perennial grasses.

2.3 METHODS

2.3.1 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 a.s.l.). 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 (*S. 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 and pocket mice (*Perognathus flavus*, *Chaetodipus eremicus*), folivorous woodrats (*Neotoma leucodon*, *N. micropus*) and cotton rats (*Sigmodon hispidus*), and omnivorous mice (e.g., *Onychomys* spp.). 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). 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 currently receiving light-to-moderate grazing (Havstad & Bestelmeyer, 2019). Cattle were removed from the pasture containing our study site in 2008, but oryx have increased across the Jornada Basin since then (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).

2.3.2 Experimental design

The herbivore exclosure experiment was established in 1995 in a black grama grassland (Lightfoot & Bestelmeyer, 2022). The grassland site (1 x 0.5 km) consisted of four replicate spatial blocks that each included four 36 x 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 (Fig. 2.1a). We used a randomized complete block design in which each block included plots receiving three herbivore exclosure treatments and an unfenced control. Treatments excluded only bovids (cattle and oryx) via barbed wire ('B' treatment), bovids and lagomorphs via barbed wire overlaid by 2.5 x 2.5-cm poultry wire fencing ('B + L' treatment), or all mammal herbivores, including rodents, via barbed wire overlaid by 1 x 1-cm hardware cloth ('B + L + R' 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 (Fig. 2.1b).

2.3.3 Vegetation cover and precipitation

We measured percent foliar cover 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 Sept-Oct (Lightfoot & Bestelmeyer, 2022). From 2005 to 2020, sampling frequency was relaxed to every five 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 36 1 x 1-m permanent vegetation cover quadrats, spaced 5.8 m from neighboring quadrats. We summed percent foliar cover at each plot and divided by 36 to attain mean percent foliar cover for each plant functional type and species. We focused functional type analyses on responses of perennial grasses and honey mesquite. 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-yr lag), and a 5-yr 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 precipitation (October [previous year]-September [current year]) and wet season precipitation (June-September). We calculated the 5-yr 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 $D_i = P_i - PET_i$ (Eq. 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-yr 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 indicate water surpluses.

2.3.4 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 $\varepsilon_t \sim N(0, \sigma_t^2),\ t = 1, \ldots, 26$ (Eq. 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 $h(s, \phi) = \phi s, s \geq 0, \phi \geq 0$ (Eq. 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 five years, creating unequal time steps. We opted for 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 for honey mesquite cover.

Once model assumptions were met, we implemented a two-stage model selection approach that is efficient and reliable (Morin et al., 2020). Stage one consisted of fitting fixed effects of herbivore treatment (control [intercept], B, B + L, B + L + R), annual precipitation, current wet season precipitation, current wet season + previous-year wet season precipitation (legacy effects), 5-yr SPEI, their stepwise additive effects, herbivore treatment x precipitation or aridity interactive effects, and a null model using maximum likelihood estimation (Appendix A: Table A1). We then selected stage one models (ΔAIC < 4) and fit these models in stage two 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 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 ($\Delta AIC < 2$) for foliar cover of 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 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 non-metric 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 (Eq. 2), and a first-order continuous-time autocorrelation structure (Eq. 3). We then fit fixed effects for year, treatment, and year x treatment using restricted maximum likelihood and applied a marginal F-test.

2.4 RESULTS

Vegetation cover shifted dramatically over the 25-yr experiment (Fig. 2.2). Perennial grasses decreased from 2000 to 2005, with precipitous declines starting in 2003 (Fig. 2.2a) concurrent with deepening of the long-term drought (Fig. 2.2c). A shift to wetter conditions (Fig. 2.2c) 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 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 (Fig. 2.2b), which included a three-fold 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 A: Fig. A1a) and displayed trends similar to wet season precipitation (1990-2020: mean = 152 mm, range = 28-371; Appendix A: Fig. A1b). Prior to and during the collapse of perennial grass cover in 2003-2005, wet season precipitation was often scarce with ten years of below average rainfall between 1990 and 2005.

2.4.1 Perennial grasses

Perennial grasses and honey mesquite shrubs responded differently to herbivore exclosure treatments, precipitation, long-term aridity, and interspecific competition. For perennial grasses, a single model including treatment x wet season precipitation + previous-year wet season precipitation + SPEI (5-yr) was selected in stage one (Appendix A: Table A2). In stage two, the addition of interspecific competition did not improve model fit (Table 2.1). Thus, perennial grasses displayed interactive effects of herbivore treatments and current-year wet season precipitation; specifically, exclusion effects were most apparent during wet years (Fig. 2.3a, Appendix A: Table A4). Overall, perennial grasses responded positively to wet season precipitation (β = 0.035, SE = 0.007). The addition of lagomorph exclusion to bovid exclusion (Treatment B + L) strongly increased grass cover during wet periods (β = 0.027, SE = 0.009) compared to bovid only exclusion and controls (Fig. 2.3a). The additional exclusion of rodents (Treatment B + L + R) did not increase the strength of the treatment x wet season precipitation interaction (β = 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 (Fig. 2.2a). Perennial grasses also responded positively to SPEI (β = 5.36, SE = 0.56; Fig. 2.3b) and to a legacy effect of previous-year wet season precipitation (β = 0.018, SE =

0.004; Fig. 2.3c), whereby perennial grass cover saw subsidiary improvement following years with high monsoonal rains.

2.4.2 Honey mesquite

In stage one selection for honey mesquite, two models with ΔAIC < 4 proceeded to stage two (Appendix A: Table A3). Because both models contained wet season precipitation as a fixed effect, no grass-on-shrub competition effects were fit in stage two (Table 2.1). Thus, the final model for honey mesquite contained herbivore treatment + wet season precipitation + previous-year wet season precipitation + SPEI (5-yr) (Table 2.1). 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 A: Table A3). Thus, treatment was identified as an uninformative parameter. This conclusion was supported by the 95% CIs for parameter estimates for the herbivore treatments that all included 0 (Appendix A: Table A4).

Honey mesquite cover responded positively and strongly to SPEI (β = 1.12, SE = 0.17; Appendix A: Fig. A2). Expansion of mesquite during extended wet periods was ubiquitous across herbivore treatments and controls. Honey mesquite cover also responded negatively to wet season precipitation (β = -0.009, SE = 0.003), however, suggesting potential competitive limitation from perennial grasses that increased during wet years.

2.4.3 Plant diversity and community dynamics

The perMANOVA analysis of plant community composition indicated an herbivore treatment x year effect (F = 1.91, df = 3, p = 0.001; Appendix B: Table B1). The NMDS ordination (Stress = 0.182) illustrated that the treatment effect was due to a separation of plant communities when rodents were excluded (B + L + R treatment vs. others; Fig. 2.4). Indicator species analysis further elucidated strong compositional associations among herbivore treatments that varied over time (Appendix B: Table B2). Key perennial grass species, including *Aristida pansa, Sporobolous flexuosus, S. contractus,* and *S. cryptandrus*, were associated with rodent exclusion during the dry, early phase of the study, as were numerous perennial forb species (Appendix B: Table B2a). Conversely, *Bouteloua 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 *Yucca elata* (Appendix B: Table B2b).

We recorded 136 plant species during the study. Species richness decreased over time (β = -1.21, SE = 0.056; Appendix B: Table B3a, Fig. B1a) but was not affected by herbivore exclusion treatments (F = 3.38, p = 0.068; Appendix B: Fig. B1d). Conversely, Shannon diversity was higher in herbivore treatments excluding rodents (β = 0.46, SE = 0.13; Appendix B: Table B3b, Fig. B1e), but varied considerably by year (F = 3.24, p = 0.023; Appendix B: Fig. B1b), whereby plots excluding rodents were most diverse in the dry, early phase of the study (β = -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 (β = 0.12, SE = 0.038; Appendix B: Table B3c, Fig. B1c), but evenness also declined over time (β = -0.006, SE = 0.003) providing additional evidence of a shift toward honey mesquite and black grama dominance late in the study.

2.5 DISCUSSION

Because shrub encroachment is a concern for global drylands (Eldridge et al., 2011; Ding and Eldridge, 2023), it is critical to understand if herbivores trigger or reinforce transitions to shrublands 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 in the Chihuahuan Desert.

Native lagomorphs contributed heavily to the herbivore-climate interaction, best measured with wet season precipitation, which was a driver of perennial grass cover. After recovery from a drought-induced collapse, perennial grass cover was two times higher on plots excluding lagomorphs compared to plots allowing lagomorph access, until a decline during the last five years. 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 B: Fig. B2c). Thus, our results indicate desert rodents 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 (Brown & Heske, 1990; Lightfoot et al., 2012; Maron et al., 2021). However, such grass reductions from herbivory did not increase the rate of shrub expansion (Kerley & Whitford, 2009). 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 limiting rodent abundances (Báez et al., 2006).

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. Population 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 exploit honey 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.

Rodents also fundamentally altered the composition, diversity, and evenness of the grassland plant community, particularly in the early period of the experiment. Thus, rodent effects on plant communities appear strongest in unencroached grasslands during drought (Maron et al., 2021). 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; Wieczorkowski & Lehmann, 2022), although 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 shifted to a lower diversity, grassland-shrubland ecotone. In that encroached state, black grama was a key indicator of rodent exclusion (Appendix B: Table B2b).

Surprisingly, cattle and African oryx exclusion provided only a marginal increase in perennial grass cover compared to controls. Cattle were grazed at moderate levels that may have limited their effects, even during a dry period. After cattle were removed from the site in 2008, oryx herbivory did not limit perennial grass recovery when both the SPEI and wet season precipitation were increasing. However, camera trap monitoring at JRN LTER indicates abundance indices for oryx are increasing over time (Andreoni et al., 2021). We expect 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. Management may become increasingly necessary to limit oryx impacts on arid grasslands in the southwestern US.

Honey mesquite expansion was ubiquitous across the site during a wet period, with no evidence of limitation by mammals. In other shrub-encroached systems, such as Gorongosa, 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). Chihuahuan Desert lagomorphs can reduce honey mesquite cover when it is a subordinate species in *Larrea tridentata* shrublands (Gibbens et al., 1993). Cattle and oryx also incorporate shrubs into their diet, but neither limited shrub cover in our system. Shrubs account for ~30% of oryx diets in the nearby San Andres National Wildlife Refuge, but most shrubs are non-dominant native species and not honey mesquite (Cain et al., 2016). 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.

Shrub cover was related negatively to wet season precipitation, which potentially acted as a proxy for competitive limitation by perennial grasses because grass cover was positively associated with wet season precipitation. Shrub cover remained at ~2.5% for the first ten years when the site was predominantly an unencroached grassland. Perennial grasses may have limited honey mesquite expansion early on, when competition for shallow soil moisture was high, supporting our hypothesis of grass-on-shrub competition as a stabilizing feedback maintaining grassland states (Pierce et al., 2019b). Then, a drought-induced perennial grass collapse released honey mesquite from competition, allowing shrubs to expand and access deeper soil moisture. Finally, although herbivores did not affect mesquite expansion as the site transitioned from a grassland to a mixed life-form savanna, higher perennial grass cover from exclusion of native mammals could inhibit future state change to a shrubland with very few grasses. Continued monitoring will determine if this scenario occurs, or if mesquite shrub expansion gradually reduces perennial grass cover irrespective of variations in herbivore pressure (Pierce et al., 2019b).

Overall, our results demonstrate the importance of long-term monitoring of both native and managed mammalian herbivores in studies of grassland-shrubland transitions. Ecosystem change was governed by the overriding influence of climate during dry periods, whereas lagomorphs and rodents exhibited top-down effects on herbaceous vegetation 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.

Conflict of Interest Statement

The authors declare no conflict of interest.

Acknowledgments

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Table and Figures

Table 2.1 Results of stage two 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 x Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)	**27**	**0.00**	**0.57**	**-677.07**
Treatment x Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr) + Competition	28	1.11	0.33	-676.63
Honey mesquite				
Treatment + Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)	**11**	**0.00**	**0.75**	**-501.89**
Treatment + Ppt(wet season) + SPEI(5-yr)	10	3.57	0.13	-504.68

Note: Models in stage one with ΔAIC < 4 proceeded to stage 2 (Appendix 1: Table 2, Table 3) and were fit with additive interspecific competition effects where applicable. Models in bold were refit using restricted maximum likelihood to yield parameter estimates (Appendix 1: Table 4). SPEI is a drought index (Standardized Precipitation-Evapotranspiration Index) and Ppt is precipitation. K = no. parameters, ΔAIC = difference between model AIC and AIC for top model, AIC Wt. = weight of evidence that model is top model, and LL = log-likelihood.

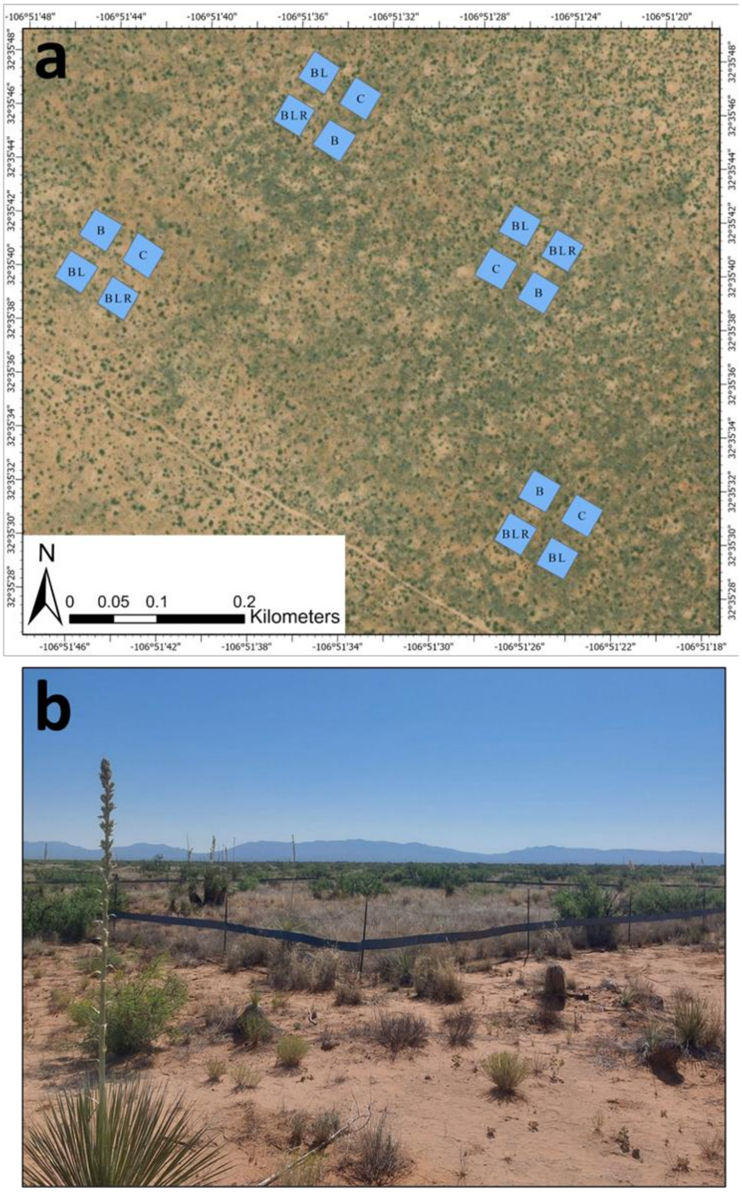

Fig. 2.1 (a) Aerial view of the herbivore exclosure experiment at the Jornada Basin Long Term Ecological Research site, New Mexico, USA. Blue squares represent plots receiving one of three treatments (B = bovids excluded, B + L = bovids and lagomorphs excluded, B + L + R = bovids, lagomorphs, and rodents excluded) or serving as a control (C). (b) An example of a 36 x 36-m plot that excluded all mammal groups (B + L + R treatment). The photograph is from July 2023 and shows surrounding area in foreground with open access to all mammalian herbivores.

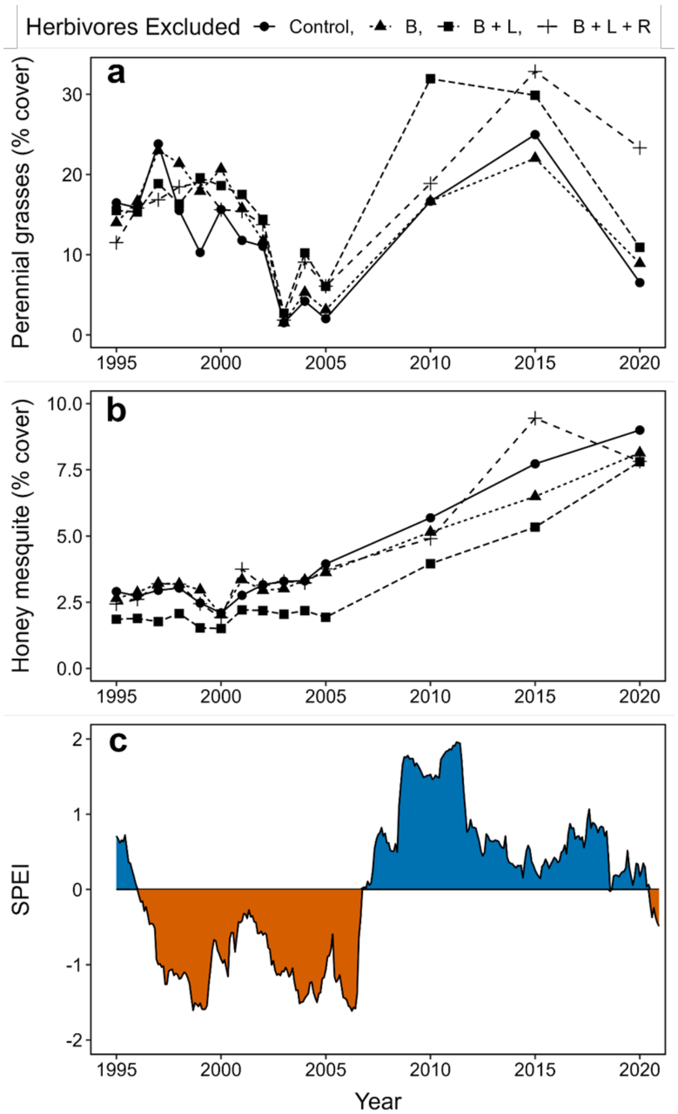

Fig. 2.2 Mean percent foliar cover for (a) perennial grasses and (b) honey mesquite from 1995-2020 from the herbivore exclosure study at Jornada Basin Long Term Ecological Research site, New Mexico. Error bars were removed for legibility (see Appendix 1: Fig. 3). Treatments included exclusion of bovids (B), bovids and lagomorphs (B + L), and bovids, lagomorphs, plus rodents (B + L + R). (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.

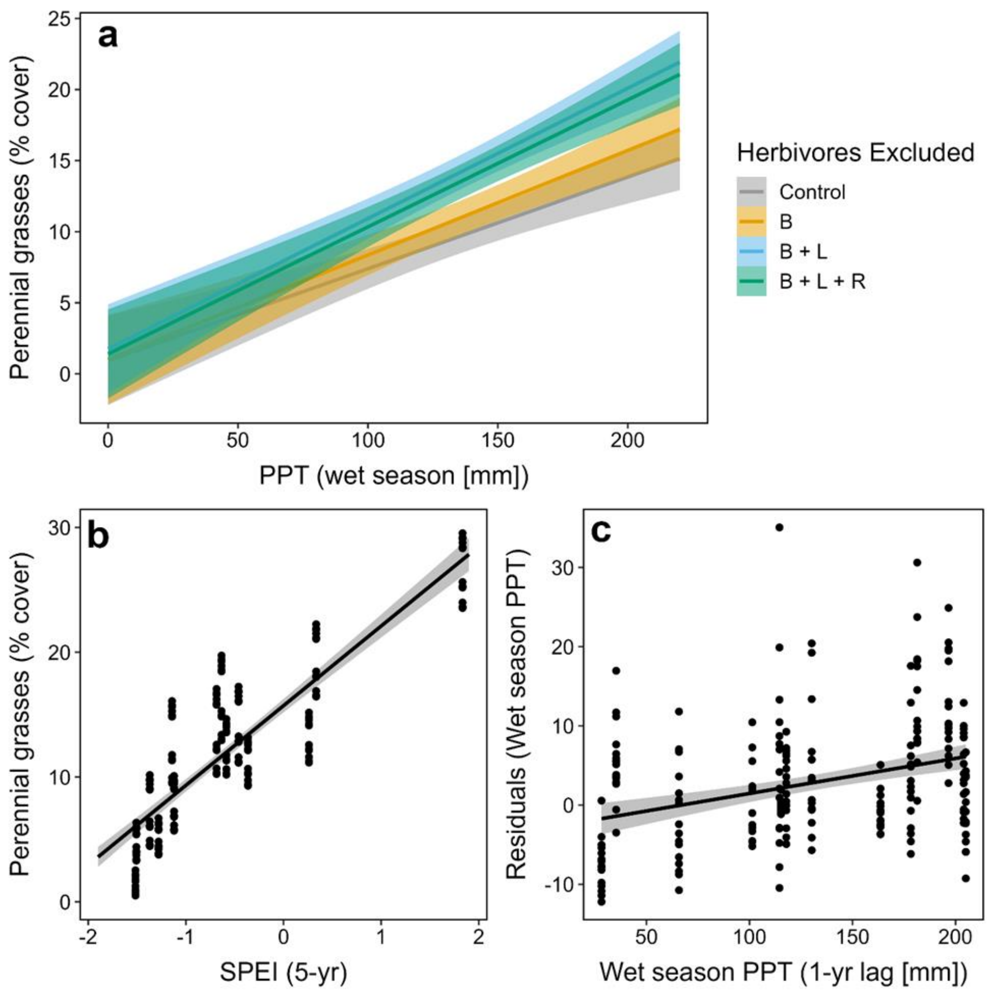

Fig. 2.3 Predictive plots from the top linear mixed model for perennial grasses (see Table 2.1) at the herbivore exclosure experiment at the Jornada Basin Long Term Ecological Research site, New Mexico. Perennial grass cover responded to (a) herbivore-climate interactions in which current wet season precipitation most strongly affected grass cover in plots excluding lagomorphs (B + L and B + L + R treatments), (b) 5-yr SPEI (Standardized Precipitation-Evapotranspiration Index) aridity, 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.

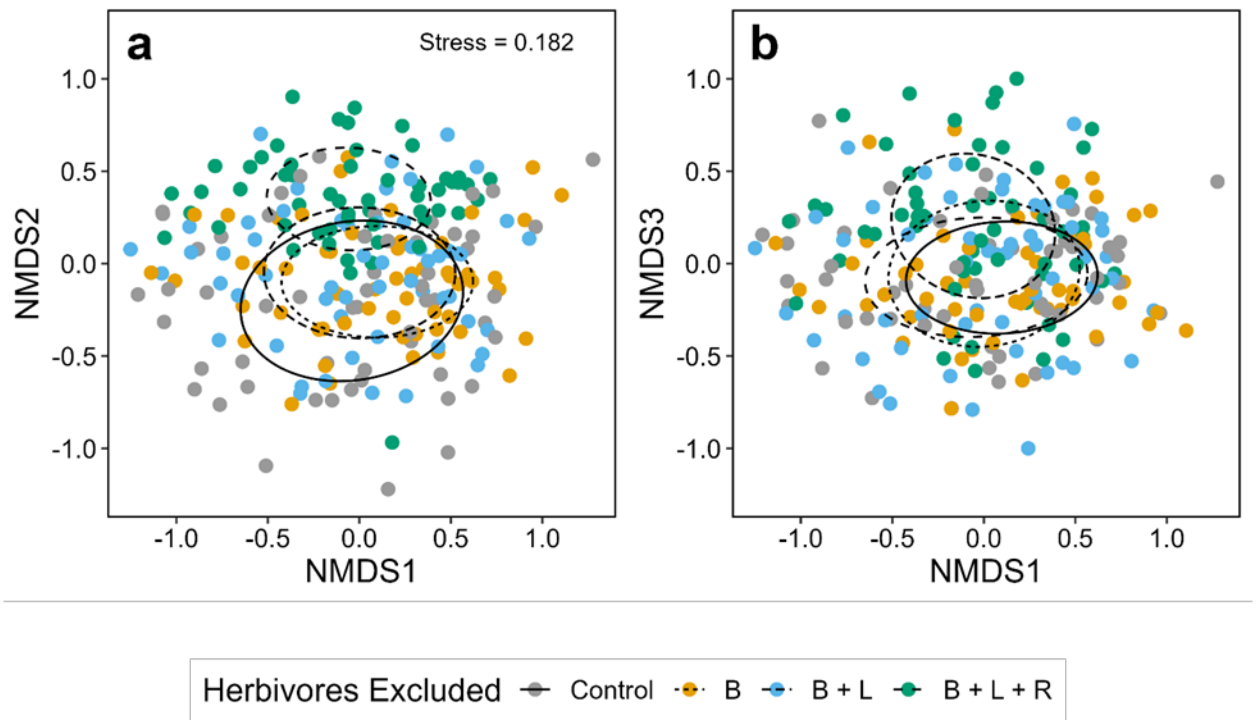

Fig. 2.4 Non-metric multidimensional scaling (NMDS) of plant species foliar cover following hierarchical herbivore exclusion (B = Bovids, L = Lagomorphs, R = Rodents) from 1995-2020 at the Jornada Basin Long Term Ecological Research site, New Mexico. Ellipses represent the 95% CI around the centroid of plant community composition for herbivore treatments and controls. Rodent exclusion resulted in a distinct plant community (see perMANOVA analysis, Appendix B: Table B1).

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CHAPTER 3: SHRUB ENCROACHMENT PROMOTES POSITIVE FEEDBACKS FROM HERBIVORY THAT REINFORCE ECOSYSTEM CHANGE

3.1 INTRODUCTION

Herbivores strongly influence ecosystem change and restoration globally (Lundgren et al., 2020; Xu et al., 2023; Kamaru et al., 2024). However, discerning how herbivores affect ecosystems remains difficult because herbivore dynamics and herbivore-plant interactions are mediated by numerous factors (Hawkes & Sullivan, 2001; Maron et al., 2014). Moreover, herbivores can induce landscape change through multiple mechanisms including selective consumption of plant biomass (Brown & Heske, 1990; Maron et al., 2021), physical disturbances (Davidson et al., 2012; Nickell et al., 2018), and facilitation or inhibition of exotic plant species (Garrett et al., 2023; Mungi et al., 2023). Effects of herbivory on plant communities can also cascade to alter biodiversity (Foster et al., 2014; Filazzola et al., 2020) and nutrient and hydrologic cycling (Eldridge et al., 2017).

Drylands are especially at risk of ecosystem change from herbivory because coupled herbivore-climate interactions can drive abrupt shifts in vegetation in these low-productivity systems (Chapter 2; Bestelmeyer et al., 2011; Gaitán et al., 2018; Berdugo et al., 2022). Encroachment of honey mesquite (*Prosopis glandulosa*) shrubs into black grama (*Bouteloua eriopoda*) grasslands in the Chihuahuan Desert represents an unequivocal example of ecological state transitions occurring in drylands (D’Odorico et al., 2011). The current model for such grassland-shrubland transitions emphasizes historical triggers including drought and livestock overgrazing, additional drivers including precipitation variability, increased atmospheric CO_2, and spatial contagion, and feedbacks from reduced fire and soil and nutrient redistribution

(Bestelmeyer et al., 2018). In addition, domestic cattle (Havstad et al., 2006), native lagomorphs (Bestelmeyer et al., 2007) and rodents (Kerley & Whitford, 2009), and exotic African oryx (*Oryx gazella*, Andreoni et al., 2021) have all been implicated as drivers. However, it remains unclear whether these mammalian herbivores mainly (1) trigger grassland-to-shrubland transitions by reducing grass cover and facilitating shrub establishment in grassland states, or (2) reinforce these transitions through reducing grass cover and recruitment in shrublands (Bestelmeyer et al., 2007; Abercrombie et al., 2019).

Shrub encroachment could alter herbivory pressure in two main ways. First, abundances of herbivores could change across shrub encroachment gradients (Hernández et al., 2005). For example, African oryx are more abundant in unencroached grassland habitats, especially in dry periods (Andreoni et al., 2021), when grasslands are most vulnerable to transformations (Gherardi & Sala, 2015). The biomass of Chihuahuan Desert rodents varies among ecological states depending on lagged monsoonal rains, but rodents have higher biomass on shrub-encroached sites when they irrupt (Schooley et al., 2018). Likewise, abundances of lagomorphs are greater on shrublands than grasslands during wet periods when their numbers are high (Wagnon, 2023). Second, shrub encroachment could alter the landscape of fear for herbivores by providing microhabitats with lower perceived predation risk and increased foraging opportunities (Loggins et al., 2019). Many nocturnal species of desert rodents behave as if shrub microhabitats are safer than open microhabitats (Thompson, 1987; Bowers, 1988; Kotler et al., 1991; Kelt, 2011). Similarly, desert lagomorphs perceive habitats with high shrub cover to have lower predation risk (Wagnon et al., 2020), and consume more food under shrubs than in open areas (Longland, 1991), which may be a mechanism for reinforcing shrubland states (Bestelmeyer et al., 2007; Abercrombie et al., 2019). Fine-scale foraging may further be mediated by precipitation events that create windows with lower ambient temperatures and increased water availability (Levy et al., 2016) and are linked to the phenology of grass seedling germination (Peters, 2000). Thus, mechanisms at multiple scales could mediate herbivore-plant interactions and feedbacks in drylands.

It has been difficult to detect herbivory effects, however, especially over short time scales (i.e., <10 years; Báez et al., 2006). For example, Svejcar et al. (2019) found rodent and lagomorph exclusion across grassland-shrubland gradients had no effect on black grama recovery from disturbance over eight years. Yet, long-term studies demonstrate herbivory effects from native mammals, whose populations are strongly linked to climate and ecosystem dynamics, may take decades to become apparent (Chapter 2; Brown & Heske, 1990). Thus, we resampled black grama recovery from disturbance, and overall perennial grass cover, on plots initially established by Svejcar et al. (2019) in 2001 to test whether effects on perennial grasses could be detected after 21 years of herbivore exclusion. Linking herbivory rates to consumer abundances has also been challenging. Bestelmeyer et al. (2007) measured grass seedling survival across grassland-shrubland gradients, and while seedling herbivory was highest in encroached states, this outcome was not explained by rodent and lagomorph abundances.

Our goal was to examine the long-term influences of multiple herbivore taxa on perennial grass cover and recovery across a shrub encroachment gradient, and to determine if grass seedling survival was related to habitat structure and herbivore abundances. 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 asked whether habitat-dependent seedling mortality (Bestelmeyer et al., 2007) persisted when a major consumer group was decimated by a disease outbreak.

Generally, we hypothesized that mammalian herbivores could either (1) trigger or (2) reinforce shrub encroachment into grassland ecosystems. (1) If certain herbivore taxa trigger shrub encroachment, then we expected their negative effects on perennial grass cover would be highest in grassland states. (2) If herbivores instead mainly reinforce shrub encroachment, then we expected they would reduce perennial grass cover the most in shrubland states where ongoing shrub expansion is being triggered by other factors including climate. Specifically, we predicted long-term exclusion of native rodents and lagomorphs would increase perennial grass cover (Chapter 2), especially in shrublands (Bestelmeyer et al., 2007; Abercrombie et al., 2019), where populations obtain their highest abundances following precipitation pulses (Schooley et al., 2018; Wagnon, 2023), and where habitat structure provides cover from predators (Wagnon et al., 2020). Such outcomes would indicate native rodents and lagomorphs are reinforcing shrub encroachment via positive feedbacks mediated by habitat structure. Because lagomorphs are currently scarce due to disease, we predicted rodents would be the primary consumers of grass seedlings (Hope & Parmenter, 2007; Kerley & Whitford, 2009). We also expected the influence of habitat structure would scale down to microhabitats (Thompson, 1987; Kotler et al., 1991), with nearby shrubs increasing seedling mortality from rodents. We further predicted seedling herbivory would be highest following rainfall when natural seedlings were germinating (Peters, 2000) and rodent foraging should increase. Finally, we anticipated effects of cattle and oryx would be focused on established perennial grasses in grasslands (Andreoni et al., 2021) but would be relatively weak due to their current low densities.

3.2 METHODS

3.2.1 Study Area and Sampling Design

The Jornada Basin Long Term Ecological Research (JRN LTER; 32°35′ N, 106°51’ W; 1334-m a.s.l.) site typifies encroachment by honey mesquite shrublands into black grama grasslands occurring across the northern Chihuahuan Desert (D’Odorico et al., 2011; Fig. 3.1a). 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 sandy-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 co-dominated by alkali sacaton (*Sporobolus airoides*) and tobosa grass (*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 feedbacks to vegetation state change (Bestelmeyer et al., 2007; Schooley et al., 2018; Svejcar et al., 2019; Wagnon et al., 2020). Three spatial blocks (i.e., CDRRC Pasture 3; JER Pastures 9 and 12A; Fig. 3.1b) were established with each containing three states (3 ha each; 100 x 300 m) representing three ecological states typical of shrub encroachment gradients: grassland, ecotone, shrubland (Fig.

3.1c-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 the percent plant foliar cover (Herrick et al., 2005) over five, 50-m transects with 25-cm intervals (n = 200 points per transect; Bestelmeyer & Schooley, 2024). In 2021, grassland states had a mean of 23.5% perennial grass cover, 5.8% perennial shrub cover, and 41.6% bare ground cover (Fig. 3.2). Ecotones had a mean of 14.9% grass cover, 12.5% shrub cover, and 48.7% bare ground. Shrublands had 6.1% grass cover, 14.0% shrub cover, and 56% bare ground cover. Therefore, due to ongoing shrub encroachment since the study was initiated in 2001, ecotone states had shrub cover similar to shrubland states by 2021. However, ecotone states still retained greater grass cover and less bare ground than shrubland states. We used this contrast to explore whether shrub or grass cover played the strongest role in herbivory dynamics across ecological states. Our focal species, black grama, accounted for a mean of 64.1% of overall perennial grass cover at states, whereas honey mesquite accounted for a mean of 93.3% of perennial shrub cover (Appendix C: Fig. C1).

3.2.2 Mammalian Herbivores

The mammalian herbivore community at the JRN LTER site consists of domestic cattle, exotic African oryx, native lagomorphs, and native rodents. Cattle stocking on spatial blocks Pasture 3 and Pasture 12A of the Ecotone Study is currently intermittent and light-to-moderate in intensity, whereas cattle grazing was removed entirely from Pasture 9 in 2008 (Havstad & Bestelmeyer, 2019). Conversely, oryx relative abundances have been increasing since 2014 (Andreoni et al., 2021). Native lagomorphs include the black-tailed jackrabbit (*Lepus californicus*) and desert cottontail (*Sylvilagus audubonii*). The rodent community (Schooley et al., 2018) consists 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.).

3.2.3 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 (Fig. 3.1). Clusters were located in patches dominated by black grama with ≥75% vegetation cover. Treatment plots included a 2 x 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 x 0.5-m (L x H) entries at 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 biomass was physically removed (i.e., resulting in 0% black grama cover and 100% bare ground cover) from a 40 x 40-cm subplot at the center of each treatment and control plot. Then, black grama recruitment and recovery from disturbance (i.e., physical removal) in relation to herbivore exclusion treatments was assessed from 2002-2008 (Svejcar et al., 2019). We asked whether the absence of herbivore effects in that study was due to its limited duration (i.e., 8 years). In September of 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 x 1-m vegetation quadrats, strung with a grid of masonry twine at 10-cm intervals (100 10 x 10-cm cells, 1 cell = 1% foliar cover), with each quadrat covering ¼ of the area of the plot. We then averaged cover estimates for the four quadrats to attain mean perennial grass cover for each 2 x 2-m treatment and control plot. 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 x 20-cm (2 x 2 cells, 1 cell = 25% foliar cover) subsection of vegetation quadrats with quadrat subsections covering ¼ 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.

3.2.4 Statistical Analysis: Exclosure Experiment

To test whether long-term herbivore effects on grass cover and recovery varied by taxa 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 and perennial grass cover within disturbed subplots, we fit separate models with fixed effects for herbivore treatment plot (control [intercept], large herbivore exclosure, full exclosure), ecosystem state (grassland [intercept], ecotone, 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 + ecosystem state fixed effects using restricted maximum likelihood to yield our parameter estimates.

3.2.5 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 first 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 16-27 °C (Sabo, 1979), and they are morphologically and phylogenetically similar to black grama. 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 28 x 28 x 6-cm (L x W x H; 5 x 5 cells) trays of 22-25 seedlings at our Ecotone exclosure cluster for 15-day trials and recorded their mortality from herbivory during repeat visits every 3-4 days. Most trays included 25 seedlings (88%), but in some trays <25 seedlings germinated. All seedlings were watered on day three of field trials to reduce seedling mortality from desiccation.

Each of the 45 clusters included a control tray and an exclusion tray with placement linked to the exclosure study design. Control trays were buried at ground level and placed 1 m north of unfenced control plots. Exclusion trays were buried at ground level, placed 1 m north of full exclosure plots, and covered with a cage constructed of 1 x 1-cm hardware cloth with 8.9 x 8.9-cm openings on each side, allowing access only to rodents. To gauge any effects of local microhabitat structure on grass seedling survival, we used 1 x 1-m (100 cells, 1 cell = 1% foliar cover) quadrats to estimate cover of shrubs directly to the east and west of seedling trays.

3.2.6 Mammalian Herbivore Abundances

We used state-level estimates of relative abundance for herbivores to quantify whether seedling herbivory rates were due to habitat-dependent herbivore abundances 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; Wagnon, 2023; Schooley et al., 2024). From mid-July to mid-October, two unbaited cameras (Bushnell Trophy Cam, model no. 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 states, combined across the two camera stations, and divided by the number of trap-nights (i.e., number of 24-hr 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 were undetected during our 2023 sampling period, so we focused on oryx as the primary bovid in seedling survival analyses (Appendix C: Fig. C2). Likewise, desert cottontails were absent in 2023, so we focused on black-tailed jackrabbits for lagomorphs in analyses.

For rodents, we used the summed mass (g) of captured individuals per ha from a standardized livetrapping protocol to attain a measure of rodent biomass for each state (Bestelmeyer & Schooley, 2022; Appendix C: Table C1). In October 2023, rodent livetrapping was conducted at each state using a 6 x 16 grid (n = 96 traps; Sherman model XLKR baited with oats; NMSU IACUC Protocol #2309000636), with 20-m spacing between traps (Schooley et al., 2018; Appendix C: Fig. C2). We included only species whose diet includes non-trivial amounts of green plant tissues (Appendix C: Table C2) 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.).

3.2.7 Statistical Analysis: Seedling Survival

To estimate the survival of perennial grass seedlings across the shrub encroachment gradient, and to identify which herbivore taxa may drive such patterns, we employed a mixed effects Cox proportional hazard model using package *survival* (Ver. 3.4-0; Therneau 2022) in R. We included a random intercept for cluster nested in spatial block, and fixed effects for ecosystem state (grassland [baseline], ecotone, shrubland) and herbivore treatment (uncaged control [baseline], rodent-only access). We used the hazard ratio (HR) to estimate changes in the risk of seedling mortality from herbivory across these covariates, where HR > 1 indicated percentage increases in risk of mortality from herbivory, and HR < 1 indicated decreased risk in mortality from herbivory, compared to baselines. Because we found no differences between control trays and rodent treatment trays (see Results), we fit an additional model using only control trays with a fixed effect for ecosystem state and a random intercept for spatial block.

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; Fig. 3.3a). We used a piecewise SEM approach to construct our models in package *piecewiseSEM* (Ver. 2.3.0; Lefcheck 2016) in R. We characterized the shrub encroachment gradient using state-level estimates of perennial shrub cover to quantify current relationships across grassland, ecotone, and shrubland states (Fig. 3.2a). 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 C: Fig. C4b; Anderson, 2023a; Anderson, 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 C: Fig. C2]; jackrabbit and oryx photoactivity [Appendix C: Fig. C3]). Our primary variable of interest was the proportion of seedlings within control trays that experienced mortality from herbivory by the end of trials (Appendix C: Fig. C6c).

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* (Ver. 1.1.32; Bates et al., 2015) in R.

For the SEMs, we modelled the influence of ecosystem state on herbivore groups to examine how broad-scale habitat structure affected consumer abundances (Fig. 3a). For rodents and oryx, we modelled their abundances with a fixed effect for state-level shrub cover. Because lagomorphs were scarce in 2023 and had not recovered from a disease-induced decline, we did not model a link between shrub cover and their abundances. Moreover, we modelled microhabitat shrub cover as a function of ecosystem state (shrub cover), but ultimately excluded this pathway from our SEMs because these variables were not strongly correlated within our data set ($R = 0.24$, $P = 0.11$). We included a direct pathway from precipitation during field trials to seedling mortality (Fig. 3.3a).

To explore whether certain rodent functional groups were driving trends in seedling mortality, we fit separate SEMs using three metrics as the rodent fixed effect: (1) folivore biomass, (2) folivore and medium granivore biomass, or (3) total rodent biomass including all relevant functional groups (*see* Appendix C: Table C2). The three SEMs using alternate metrics for rodent biomass were compared during the last stage of model selection.

We fit our initial SEMs (Fig. 3.3a) including the above relationships and used tests of directed separation to discern whether unspecified pathways should be included as either explicit pathways or correlated errors to improve the SEM's global goodness-of-fit. We assessed global goodness-of-fit using Fisher's C and considered models as having an 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.

3.3 RESULTS

3.3.1 Long-term Herbivore Exclosure Experiment

Overall, both perennial grass cover and recovery responded markedly to long-term manipulations in herbivore access. In 2022, mean foliar cover of perennial grasses on controls was 15.3% (SD = 15.8) compared to 28.8% (SD = 26.8) in full exclosures (Fig. 3.4a). In subplots recovering from disturbance (i.e., 0% perennial grass cover in 2001), mean perennial grass cover in 2022 had recovered to 2.4% (SD = 4.4, range = 0-40) on control plots compared to 4.8% (SD = 11.5, range = 0-87.5) in full exclosures (Fig. 3.4b).

The effects of herbivore exclusion treatments on perennial grass cover differed among ecosystem states ($F = 6.62$, $P < 0.001$; Appendix C: Table C3). 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 3.1, Fig. 3.4a). Thus, negative effects of rodents and lagomorphs on grasses were strongest where shrub cover was highest across the encroachment gradient (Fig. 3.2a).

For perennial grasses in subplots recovering from past disturbance (Fig. 3.4b), there was no ecosystem state x herbivore treatment interaction ($F = 1.44$, $P = 0.229$; Appendix C: Table C3). 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 3.1).

Positive grass recovery and recruitment into disturbed patches was highest in treatments excluding rodents and lagomorphs (β = 4.13, SE = 1.67).

3.3.2 Seedling Herbivory Experiment: Cox Models

Seedling survival trials occurred during a particularly dry year in 2023, in which wet season precipitation (mean = 76 mm, SD = 7.5; Appendix C: Fig. C4b) across our study spatial blocks was well below mean wet season precipitation since the establishment of the Ecotone exclosure study (2001-2023: mean = 137 mm, SD = 65.3), and coincided with extreme heat in late July (July: mean daily maximum = 39.9 °C, SD = 1.8) and early August (Appendix C: Fig. C5). By the conclusion of field trials, the number of seedlings consumed by herbivores was 401 in shrubland states, 407 in ecotone states, and 324 in grassland states.

The mixed effects Cox proportional hazard model showed that the risk of mortality from herbivory did not differ between exclosure treatments allowing rodent-only access (*HR* = 1.06, SE = 0.06) and uncaged controls, indicating rodents were contributing strongly to rates of seedling herbivory (Appendix C: Fig. C6c). However, the risk of mortality from herbivory for perennial grasses differed across ecosystem states (Appendix C: Table C4). In relation to grasslands, seedlings in ecotone (*HR* = 1.33, SE = 0.11) and shrubland (*HR* = 1.55, SE = 0.11) states were at higher risk of mortality from herbivory (Fig. 3.5). In combination, these results pointed towards rodent herbivory, particularly in shrubland and ecotone states, as a main driver of grass seedling mortality.

3.3.3 Seedling Survival Experiment: 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 C: Fig. C2c). 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 1,561 total trap-nights, across 18 camera stations (Appendix C: Fig. C3). Jackrabbits showed no sign of substantial population recovery from rabbit hemorrhagic disease virus compared to estimates from past camera trap (Wagnon, 2023) or spotlight (Appendix C: Fig. C8) surveys.

Across ecosystem states, the number of grass seedlings from control trays experiencing mortality from herbivory was consistent with results from the Cox proportional hazard analysis. By the end of trials, a mean of 12.5 (SD = 6.58) seedlings were consumed in shrublands, 12.3 (SD = 6.59) in ecotones, and 10.5 (SD = 8.24) in grasslands.

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 C: Fig. C7a) or total rodent biomass ($C = 10.44$, $df = 8$, $P = 0.236$; Appendix C: Fig. C7b). Thus, our final SEM (Fig. 3.3b) 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 3.2). However, grass seedling mortality was unrelated to the 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. Seedling mortality from herbivory was directly associated with habitat structure at two spatial scales. Seedling mortality was positively related to state-level shrub cover (β_{std} = 0.12), as well as shrub cover directly surrounding seedlings at the microhabitat scale (β_{std} = 0.18). Precipitation during trials was not a predictor of grass seedling mortality (Fig. 3.3b).

3.4 DISCUSSION

With drylands experiencing shrub encroachment globally (D'Odorico et al., 2011; Berdugo et al., 2022; Ding & Eldridge, 2023), it is critical to identify whether herbivores trigger or reinforce such ecosystem state transitions (Kerley & Whitford, 2009; Gaitán et al., 2018). We demonstrate that native small mammals can strongly reinforce shrub encroachment into arid grasslands through multiple pathways. Across grassland-shrubland gradients, long-term exclusion of native rodents and lagomorphs produced substantial increases in perennial grass cover in ecotone and shrubland states, where habitat structure provided consumers with cover. Rodents and lagomorphs also inhibited perennial grass recovery from disturbance across all ecosystem states, although grass patches displayed limited resilience to disturbance. Moreover, seedling herbivory was highest in shrub-encroached states, despite the decimation of lagomorphs due to a disease outbreak. Overall, in response to altered habitat structure, small mammals reduced perennial grass cover, recovery, and seedling survival, thus providing positive feedbacks that reinforce grassland-to-shrubland transitions.

Exclusion of rodents and lagomorphs in our study produced no noticeable effects on perennial grass cover or recovery after eight years (Svejcar et al., 2019). Yet, our follow-up surveys after 21 years of herbivore exclusion revealed perennial grass cover on shrubland and ecotone states was two to three times higher in treatment plots excluding rodents and lagomorphs versus control plots (Fig. 3.4a). Moreover, these exclusion treatments included some of the only remaining perennial grass patches visible at our shrubland sites (e.g., Fig. 3.1e). Our study provides further evidence that long-term studies are crucial to unveiling herbivory effects from native small mammals (Chapter 2; Brown & Heske, 1990; Maron et al., 2021; Davies et al., 2023) because the drivers and feedbacks of dryland transformations can be decoupled from their outcomes for decades (Bestelmeyer et al., 2011).

Long-term effects of rodents and lagomorphs on grass recovery following disturbance were apparent across all ecosystem states, indicating these native herbivores could modulate the ability of perennial grasses to recover following natural or managed disturbances (e.g., drought, livestock grazing; Roth et al., 2009; Gherardi & Sala, 2015; Gaitán et al., 2018). Grasses recovering from disturbance may be more sensitive to herbivory than established grass patches (Daleo et al., 2014; Sharp Bowman et al., 2017; Xu et al., 2023). Even small inputs from consumers in grasslands may alter the trajectory of recovery in low-productivity environments (Hawkes & Sullivan, 2001; Davies et al., 2023). Moreover, perennial grass recovery into these disturbed patches was low overall, indicating plant biomass removal can have lasting impacts on black grama grasslands even where surrounding grass cover is high (Seabloom et al., 2020). In fact, only three of the 135 (2.2%) disturbed subplots had achieved >50% perennial grass cover after 21 years, and each of them was in an exclosure plot without rodent and lagomorph access. Collectively, these results demonstrate black grama grasslands can be remarkably sensitive to disturbances and their recovery can be inhibited by herbivory by native small mammals (Chapter 2). Such lasting effects from disturbance on perennial grasses may explain why it takes many years for herbivory effects from native small mammals to become evident. 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.

With the rarity of lagomorphs, rodents drove mortality of perennial grass seedlings. Thus, the pattern of higher seedling herbivory in ecotone and shrubland states previously documented by Bestelmeyer et al. (2007) persisted despite the collapse of a major consumer group from disease (Asin et al., 2021; Appendix C: Fig. C8). These results indicate desert rodents play a strong role in habitat-dependent herbivory (Eldridge et al., 2009; Kerley & Whitford, 2009), and feedbacks to state change, but lagomorphs can amplify these processes in years when they are more abundant. Furthermore, our seedling herbivory experiment in 2023 occurred during an especially hot, dry year and displayed much higher overall rates of seedling herbivory compared to our 2022 pilot trial during cooler, wetter conditions (Appendix C: Fig. C6a). This outcome indicates weather patterns also could affect grass seedling herbivory by influencing background abundance of alternative foods for consumers.

The top SEM model indicated seedling herbivory from rodents was best predicted by habitat structure at two scales, whereby 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 so in our data set) so that grassland-shrubland transitions create more foraging space with nearby shrubs. Thus, habitat structure may be a better predictor of herbivory pressure than abundances of herbivores (Bestelmeyer et al., 2007; Svejcar et al., 2019) as long as the consumer abundances are above some threshold. Individual shrubs act as resource islands (Davies et al., 2022) that capture wind-blown seeds (Thompson, 1987; Chen et al., 2012), provide shade from solar radiation for plants (Gornish et al., 2021) and diurnal consumers (Levy et al., 2016), and especially conceal rodents from predators (Bowers, 1988; Loggins et al., 2019). Thus, shrub encroachment establishes conditions that alter the landscape of fear for rodents, which then translates into an altered landscape of risk for grass seedlings.

We found no evidence that cattle and African oryx contributed strongly to vegetation dynamics. Although cattle grazing is currently light-to-moderate across some of our spatial blocks (Havstad & Bestelmeyer, 2019), oryx populations are increasing and abundances are higher on grassland states (Andreoni et al., 2021; Appendix C: Fig. C3b) where cover of herbaceous forage is high. No current estimate exists for oryx population size in the Jornada Basin, but their numbers could be relatively low compared to the carrying capacity of remaining black grama grasslands. Future increases in oryx population size due to predator release in lowlands (Prude & Cain, 2021) could lead to higher herbivory pressure across remaining grassland ecosystems, functioning as a novel trigger facilitating shrub invasion.

In conclusion, our results provide evidence that native small mammals can exert strong control over perennial grass dynamics, ultimately reinforcing arid grassland loss (Kerley & Whitford, 2009; Eldridge et al., 2009). The conceptual model for grassland-shrubland transitions is continually expanding beyond the historical triggers of drought and overgrazing as our understanding increases (Bestelmeyer et al., 2018). We contend that herbivory from small mammals is a key feedback mechanism 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.

Acknowledgments

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Tables and Figures

Table 3.1 Results of linear mixed models for perennial grass cover within herbivore exclosures and controls, and for disturbed subplots within center of exclosures and controls, across shrubland, ecotone, and grassland ecosystem states. Herbivore treatments included large herbivore exclosures (cattle and oryx excluded), full exclosures (cattle, oryx, lagomorphs, and rodents excluded), and controls (no herbivores excluded).

Exclosures

Predictors	***β***	**SE**	**95% CI**
(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 x Treatment:			
Ecotone x Large Herbivore Exclosure	2.01	2.85	-3.58 — 7.61
Shrubland x Large Herbivore Exclosure	4.29	2.85	-1.30 — 9.89
Ecotone x Full Exclosure	6.89	2.85	1.30 — 12.48
Shrubland x Full Exclosure	14.31	2.85	8.72 — 19.90

Recovery from Disturbance

Predictors	***β***	**SE**	**95% CI**
(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

Table 3.2 Results from the top structural equation model for perennial grass seedling mortality in response to state-level and microhabitat shrub cover, herbivore, and weather predictors. Rodent folivores included *Neotoma* spp. and *Xerospermophilus spilosoma*. Seedling mortality from herbivory consisted of the proportion of seedlings in control trays with full access by mammalian herbivores consumed by the end of field trials. Estimates of coefficients (β) and standardized coefficients (β_{std}) are presented for significant pathways (Fig. 3a) and correlated errors.

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

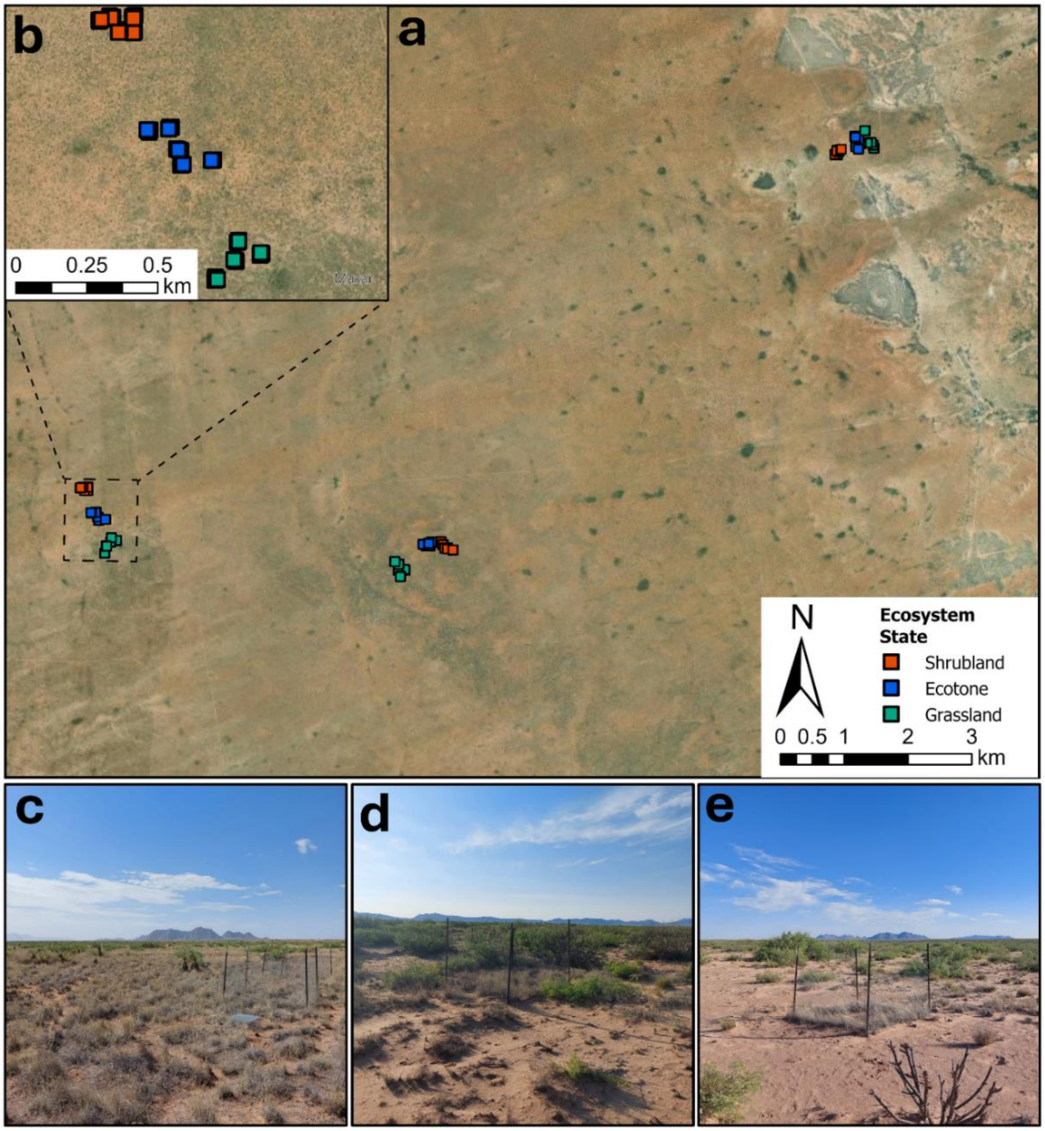

Fig. 3.1 (a) The Ecotone exclosure experiment includes clusters with large herbivore treatment plots (cattle and oryx excluded), full treatment plots (cattle, oryx, lagomorphs, rodents excluded), and control plots (no mammals excluded) established across a shrub encroachment gradient at the Jornada Basin Long Term Ecological Research Site, New Mexico, USA. (b) Inset shows clusters including treatment and control plots within one spatial block. 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.

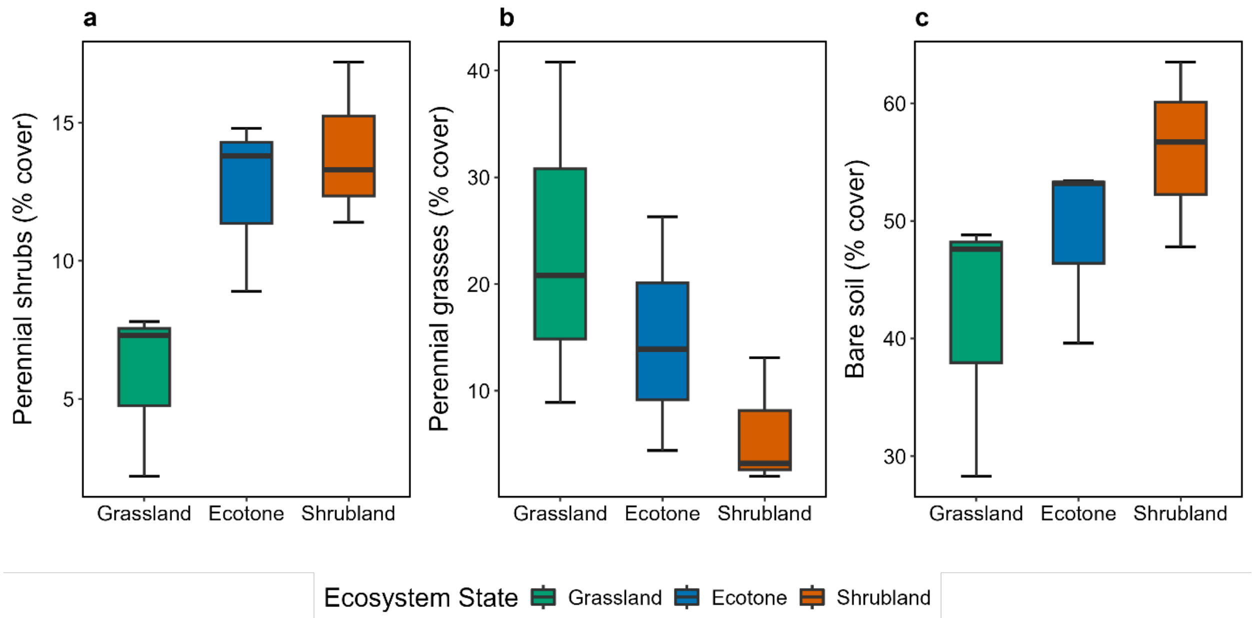

Fig. 3.2 Percent foliar cover of (a) perennial shrubs, (b) perennial grasses, and (c) bare soil across shrubland, ecotone, and grassland ecosystem states in 2021 on the Ecotone exclosure experiment, Jornada Basin Long term Ecological Research site, New Mexico, USA. Box plots represent the mean and interquartile range of percent foliar cover for each functional group.

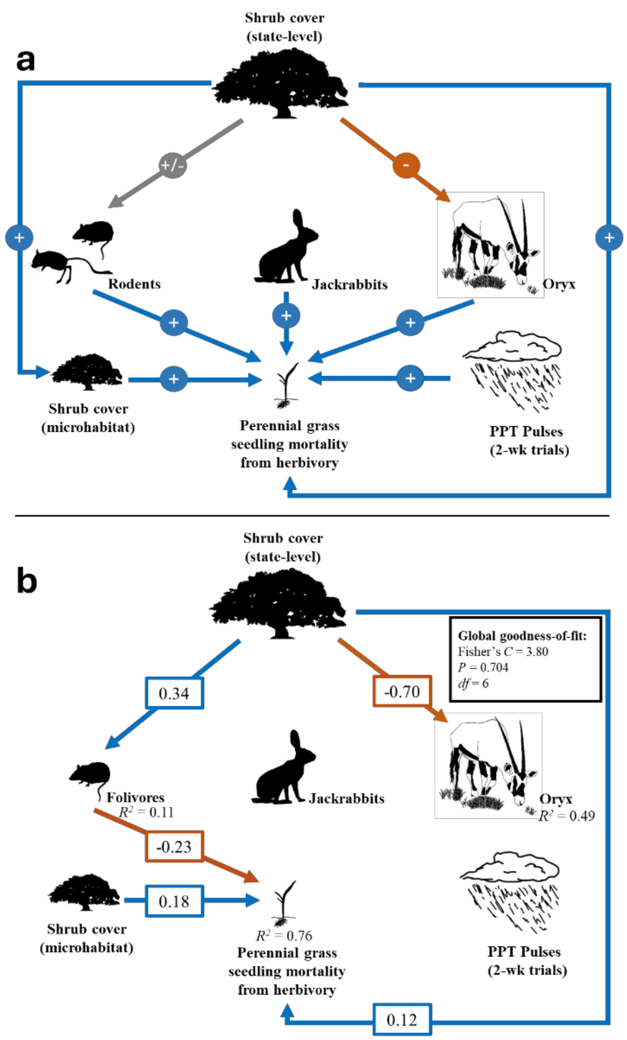

Fig. 3.3 (a) Conceptual diagram for a structural equation model for the influences of shrub cover (state-level, microhabitat), weather, and multiple mammalian herbivore taxa on perennial grass seedling mortality across a shrub encroachment gradient. The direction of pathways is from exogenous (predictor) 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 responses dependent on external factors. (b) Results from the top structural equation model include folivore (*Neotoma* spp., *Xerospermophilus spilosoma*) biomass as the metric for rodents. Significant pathways are shown and include standardized coefficient estimates (Table 2).

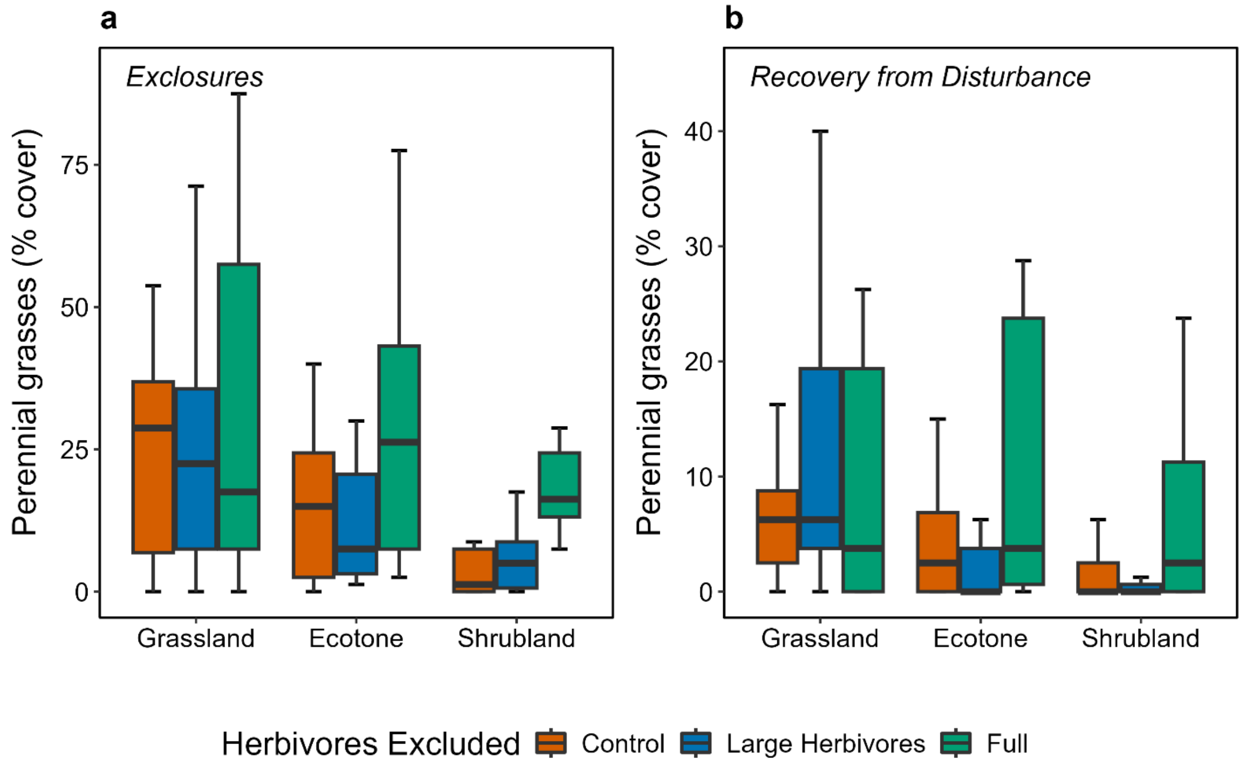

Fig. 3.4 Perennial grass cover across ecosystem states within (a) 2 x 2-m herbivore exclosure treatment and control plots, and (b) disturbed 40 x 40-cm subplots within treatment and control plots. Exclosures were established in 2001 and disturbance was simulated within subplots through removal of all plant biomass. Box plots represent mean percent foliar cover of perennial grasses bounded by their interquartile range.

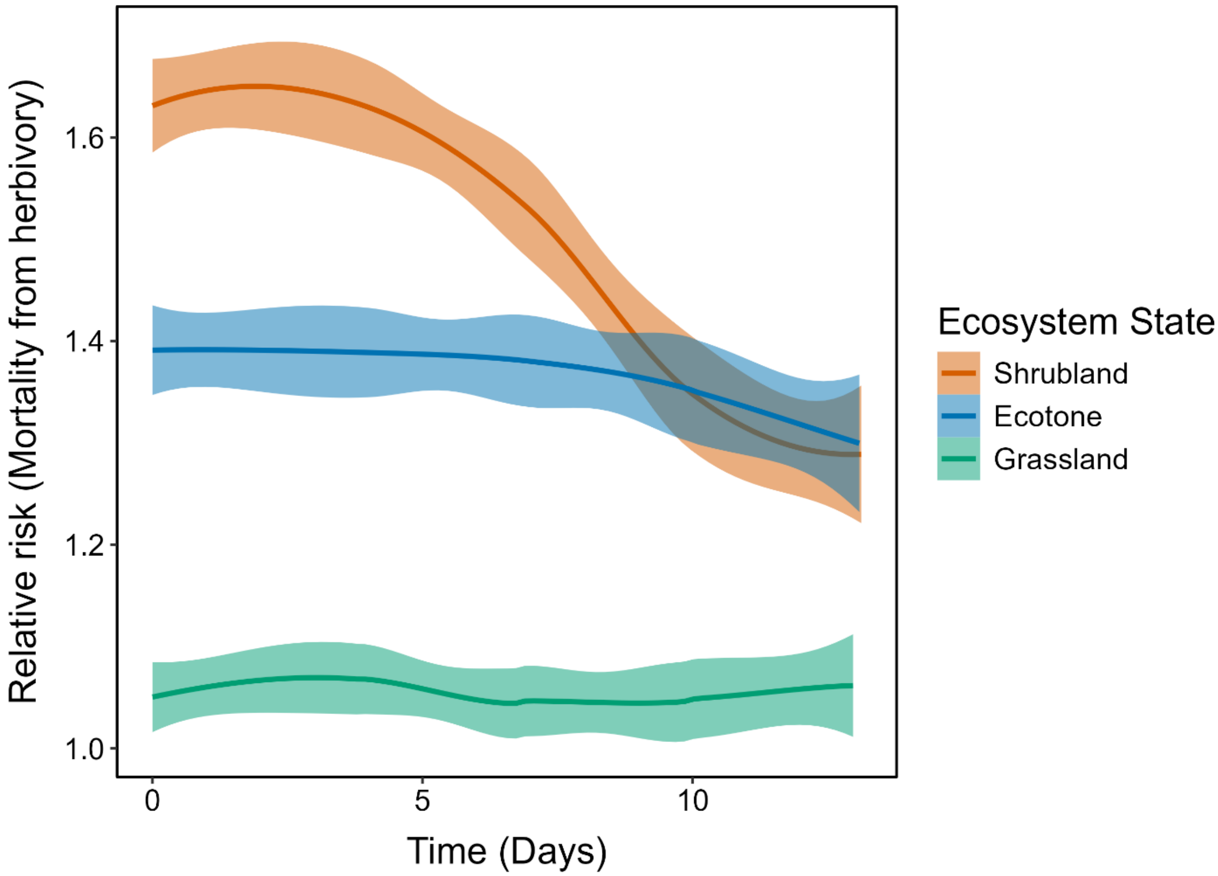

Fig. 3.5 Model predictions from the mixed effects Cox proportional hazard model for the risk of mortality from herbivory for perennial grass seedlings in control trays across ecosystem states (see Table S4). Lines indicate the predicted relative risk of perennial grass seedling mortality from herbivory and shaded regions indicate the 95% confidence interval around estimates.

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CHAPTER 4: SUMMARY AND CONCLUSIONS

Global drylands are experiencing unprecedented challenges due to ecosystem changes driven by an increasingly arid climate, livestock overgrazing, and soil and nutrient feedbacks. Drylands are home to more than two billion people, of which an estimated one billion are rural-dwelling, impoverished, and depend directly on the delivery of ecosystem services from drylands for subsistence. Thus, it is crucial to understand the biotic mechanisms that lead to the establishment of ecosystem states with low ecological and economic value to their local communities. This work provides compelling evidence that small mammals interact with climate (Chapter 2) and habitat structure (Chapter 3) to strongly reinforce the establishment of persistent, desertified shrubland ecosystems. Moreover, such herbivory effects from small mammals did not become apparent for decades, highlighting the value of long-term monitoring in capturing dryland ecosystem processes.

In an unencroached grassland at the Herbivore Exclosure Study, prolonged drought drove the collapse of perennial grass cover after 10 years, which allowed honey mesquite shrubs to expand across the landscape (Chapter 2). Then, in an ensuing wet period, perennial grasses recovered from drought, but their recovery was inhibited by native lagomorphs and rodents. Rodents additionally played a strong role in altering plant community composition, decreasing plant species diversity, and decreasing evenness, but these community changes disappeared following the onset of shrub encroachment. Yet, cover of our focal perennial grass species, black grama (*Bouteloua eriopoda*), was three times higher 15 years after the drought-induced perennial grass collapse in plots excluding rodents.

Thus, desert rodents can inhibit the dominance of plant species with small seeds through graminivory, in addition to altering plant community dynamics through granivory of large-seeded annual species. Conversely, there was no indication that mammals of the northern Chihuahuan Desert limit honey mesquite encroachment, despite evidence that large herbivores in African savannas can reverse broad-scale shrub encroachment through browsing. Overall, shrub encroachment into this grassland was triggered by prolonged drought and reinforced by native small mammals during an ensuing wet period.

However, the question remained as to whether this shift in habitat structure with shrub encroachment would increase herbivory pressure from native rodents and lagomorphs because these groups respond most strongly to resource pulses in shrubland habitats, or because favorable microhabitats would be created. Shrublands could provide native small mammals with shade from solar radiation and cover from predators, such that individuals may balance their forage requirements with thermoregulation and reduced perceived predation risk. Increased foraging in shrublands should then be a mechanism for reinforced grass loss.

To address this question, we complemented the Herbivore Exclosure Study with an exclosure experiment established across a shrub encroachment gradient on the Ecotone Study (Chapter 3), which allowed us to directly identify shifts in small mammal herbivory pressure across habitats (grassland, ecotone, shrubland). Native rodents and lagomorphs depleted remaining perennial grass patches over 21 years, particularly in ecotone and shrubland habitats where habitat structure was highest. This habitat-dependent herbivory further scaled down to increased mortality of perennial grass seedlings in shrub-dominated sites, with this pattern persisting despite the decimation of lagomorph populations. Conversely, the response of perennial grass patches to disturbance was generally poor, with these patches showing little resilience to disturbance over decades. However, native rodents and lagomorphs amplified this trend by further reducing the ability of perennial grasses to recolonize disturbed patches. Collectively, these results indicated that native small mammals reinforce shrub encroachment into arid grasslands through direct effects on perennial grass cover, seedling survival, and recovery from disturbance.

There is a growing recognition of the need to incorporate the role of herbivores into ecosystem restoration because herbivores can enhance restoration goals in some scenarios and diminish them in others. In cases where wild herbivores have inhibited ecological restoration efforts, it has been suggested that herbivore exclusion (i.e., fencing) and restoring trophic structures (i.e., predator reintroduction) can be effective methods for limiting the negative impacts that herbivores can impose on desirable plant communities. Such interventions have proven more effective than approaches that use passive vegetation regeneration but could be logistically difficult to implement for small-bodied herbivores. Fencing, for example, would need to include safeguards that deter rodents from either burrowing under or climbing over fences and would need to remain in place for decades. Restoring trophic structures through predator reintroduction could be especially difficult where stakeholder concerns or ongoing recovery of rare, threatened, or endangered prey species create potential conflicts.

Our work suggests that considering the influences that climate and habitat exert on specific herbivore taxa could elucidate alternative management options available to restoration practitioners. To illustrate, two options are commonly employed as restoration actions to restore shrub-encroached grasslands: broadleaf-specific defoliant herbicides used to treat shrubs and physical shrub removal. Because our results suggest that native rodents and lagomorphs reinforce shrub encroachment through interactions with habitat structures, physical removal of shrub structures may be necessary for positive grass recovery. In the case of defoliant herbicides, shrub structures remaining after herbicide application could still act as resource islands that collect seeds and reduce perceived predation risk for native rodents and lagomorphs, thus inhibiting grassland restoration through continued herbivory feedbacks. Future research efforts focused on shrubland reversal could compare the alternative options of shrub removal, herbicide application, fencing, and predator reintroduction to identify which option has the greatest potential for positive restoration outcomes while being logistically and financially feasible.

In conclusion, we found that native rodents and lagomorphs can interact with climate and habitat structure to strongly reinforce arid grassland loss due to shrub encroachment. This work highlights that small mammals can play an asymmetrically large role in the processes governing ecosystem change in drylands. As such, positive feedbacks from herbivory by native small mammals should be incorporated as a critical facet of conceptual models of dryland ecosystem change. Moreover, such conceptual models should consider the long-term nature of herbivore-ecosystem interactions because it can take many years for these processes to play out. Within the current framework for state transitions in dryland ecosystems, an increasingly arid climate, coupled with high precipitation variability, will benefit shrubs over grasses, thus altering grass-shrub competitive interactions and triggering shrub expansion. Even in an ensuing wet period following drought, grass recovery will be inhibited by high population responses from native rodents and lagomorphs, especially in shrubland states. Such feedbacks from native herbivores may then enhance wind erosion and soil degradation processes through reductions in herbaceous cover, burrowing, and trampling in shrub interspaces, ultimately leading to the loss of perennial grass communities and the establishment of recalcitrant shrubland states.

APPENDIX A: CHAPTER 2 MIXED MODEL SUPPLEMENTALS

Table A1 Set of candidate models showing fixed effects for mixed models used to examine the separate responses of perennial grasses and honey mesquite shrubs.

	Stage 1
1	~ Null
2	~ Treatment
3	~ Ppt(full year)
4	~ Ppt(wet season)
5	~ Ppt(wet season) + Ppt(wet 1-yr lag)
6	~ SPEI(5-yr)
7	~ Treatment + Ppt(full year)
8	~ Treatment + Ppt(wet season)
9	~ Treatment + Ppt(wet season) + Ppt(wet 1-yr lag)
10	~ Treatment + SPEI(5-yr)
11	~ Treatment + Ppt(full year) + SPEI(5-yr)
12	~ Treatment + Ppt(wet season) + SPEI(5-yr)
13	~ Treatment + Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)
14	~ Treatment x Ppt(full year)
15	~ Treatment x Ppt(wet season)
16	~ Treatment x Ppt(wet season) + Ppt(wet 1-yr lag)
17	~ Treatment x SPEI(5-yr)
18	~ Treatment x Ppt(full year) + SPEI(5-yr)
19	~ Treatment x SPEI(5-yr) + Ppt(full year)
20	~ Treatment x Ppt(wet season) + SPEI(5-yr)
21	~ Treatment x SPEI(5-yr) + Ppt(wet season)
22	~ Treatment x Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)
23	~ Treatment x SPEI(5-yr) + Ppt(wet season) + Ppt(wet 1-yr lag)
	Stage 2
24-46	~ Model 1…23 + Competition

Table A2 Stage one selection of models for the response of perennial grass cover to herbivore treatments, precipitation (wet season, wet 1-yr lag, full year), long-term aridity (5-yr SPEI), and interspecific competition (grass-shrub, shrub-grass).

Perennial grasses — Stage 1				
Model parameters	**K**	**ΔAIC**	**AIC Wt.**	**LL**
Treatment x Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)	**27**	**0.00**	**0.85**	**-677.07**
Treatment + Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)	24	4.39	0.09	-682.26
Treatment x SPEI(5-yr) + Ppt(wet season) + Ppt(wet 1-yr lag)	27	5.60	0.05	-679.87
Treatment x Ppt(wet season) + SPEI(5-yr)	26	11.30	0.00	-683.72
Treatment + Ppt(wet season) + SPEI(5-yr)	23	17.59	0.00	-689.86
Treatment x SPEI(5-yr) + Ppt(wet season)	26	18.23	0.00	-687.19
Ppt(wet season) + Ppt(wet 1-yr lag)	20	28.73	0.00	-698.43
Treatment x Ppt(wet season) + Ppt(wet 1-yr lag)	26	29.44	0.00	-692.79
Treatment + Ppt(wet season) + Ppt(wet 1-yr lag)	23	29.86	0.00	-696.00
Treatment + Ppt(wet season)	22	63.21	0.00	-713.67
Ppt(wet season)	19	65.34	0.00	-717.74
Treatment x Ppt(wet season)	25	66.60	0.00	-712.37
Treatment + Ppt(full year) + SPEI(5-yr)	22	90.41	0.00	-727.27
Treatment + SPEI(5-yr)	21	92.11	0.00	-729.12
Treatment x Ppt(full year) + SPEI(5-yr)	26	94.31	0.00	-725.23
Treatment x SPEI(5-yr) + Ppt(full year	26	97.87	0.00	-727.00
Treatment x SPEI(5-yr)	25	99.59	0.00	-728.86
SPEI(5-yr)	19	104.17	0.00	-737.15
Treatment	21	118.28	0.00	-742.21
Treatment + Ppt(full year)	22	120.27	0.00	-742.20
Null	18	121.00	0.00	-746.57
Treatment x Ppt(full year)	25	123.28	0.00	-740.71

Note: Models in stage one with ΔAIC < 4 (bold) proceeded to stage two (Table 1). SPEI is a drought index (Standardized Precipitation-Evapotranspiration Index) and Ppt is precipitation.

Table A3 Stage one selection of models for the response of honey mesquite shrub cover to herbivore treatments, precipitation (wet season, wet 1-yr lag, full year), long-term aridity (5-yr SPEI), and interspecific competition (grass-shrub, shrub-grass).

Honey mesquite — Stage 1				
Model parameters	**K**	**ΔAIC**	**AIC Wt.**	**LL**
Treatment + Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)	**11**	**0.00**	**0.75**	**-501.89**
Treatment + Ppt(wet season) + SPEI(5-yr)	**10**	**3.57**	**0.13**	**-504.68**
Treatment x SPEI(5-yr) + Ppt(wet season) + Ppt(wet 1-yr lag)	14	5.66	0.04	-501.72
Treatment x Ppt(wet season) + Ppt(wet 1-yr lag) + SPEI(5-yr)	14	5.93	0.04	-501.86
SPEI(5-yr)	6	7.26	0.02	-510.52
Treatment x SPEI(5-yr) + Ppt(wet season)	13	9.24	0.01	-504.51
Treatment x Ppt(wet season) + SPEI(5-yr)	13	9.51	0.01	-504.64
Treatment + SPEI(5-yr)	9	12.53	0.00	-510.15
Treatment + Ppt(full year) + SPEI(5-yr)	10	14.48	0.00	-510.13
Treatment x SPEI(5-yr)	12	18.21	0.00	-510.00
Treatment x SPEI(5-yr) + Ppt(full year	13	20.16	0.00	-509.97
Treatment x Ppt(full year) + SPEI(5-yr)	13	20.29	0.00	-510.04
Ppt(full year)	6	29.19	0.00	-521.48
Null	5	32.54	0.00	-524.16
Ppt(wet season) + Ppt(wet 1-yr lag)	7	33.11	0.00	-522.45
Ppt(wet season)	6	33.52	0.00	-523.65
Treatment + Ppt(full year)	9	34.46	0.00	-521.12
Treatment	8	37.81	0.00	-523.79
Treatment + Ppt(wet season) + Ppt(wet 1-yr lag)	10	38.38	0.00	-522.08
Treatment + Ppt(wet season)	9	38.79	0.00	-523.29
Treatment x Ppt(full year)	12	40.29	0.00	-521.04
Treatment x Ppt(wet season) + Ppt(wet 1-yr lag)	13	44.33	0.00	-522.05
Treatment x Ppt(wet season)	12	44.73	0.00	-523.26

Note: Models in stage one with ΔAIC < 4 (bold) proceeded to stage two (Table 1). SPEI is a drought index (Standardized Precipitation-Evapotranspiration Index) and Ppt is precipitation.

Table A4 Parameter estimates from the top models (see Table 2.1) for perennial grasses and honey mesquite at the herbivore exclosure experiment, Jornada Basin Long Term Ecological Research site, New Mexico, USA.

Model response variable and parameters	*β*	*SE*	95% CI
Perennial grasses			
(Intercept)	5.747	1.319	3.161 — 8.332
Treatment (B)	0.055	0.842	-1.596 — 1.706
Treatment (B+L)	0.815	0.842	-0.836 — 2.467
Treatment (B+L+R)	0.457	0.842	-1.194 — 2.109
Ppt (wet season)	0.035	0.007	0.021 — 0.048
Ppt (wet 1-yr lag)	0.018	0.004	0.009 — 0.026
SPEI (5-yr)	5.359	0.560	4.261 — 6.457
Treatment (B) x Ppt (wet season)	0.009	0.009	-0.008 — 0.026
Treatment (B+L) x Ppt (wet season)	0.027	0.009	0.010 — 0.044
Treatment (B+L+R) x Ppt (wet season)	0.025	0.009	0.008 — 0.042
Honey mesquite			
(Intercept)	5.026	1.437	2.210 — 7.841
Treatment (B)	-0.150	1.899	-3.872 — 3.572
Treatment (B+L)	-1.200	1.899	-4.922 — 2.523
Treatment (B+L+R)	0.004	1.899	-3.718 — 3.727
Ppt (wet season)	-0.009	0.003	-0.014 — -0.004
Ppt (wet 1-yr lag)	0.006	0.002	0.001 — 0.010
SPEI (5-yr)	1.119	0.169	0.788 — 1.450

Note: For treatments, B = bovid exclusion, L = lagomorph exclusion, R = rodent exclusion. SPEI is a drought index (Standardized Precipitation-Evapotranspiration Index), and Ppt is precipitation.

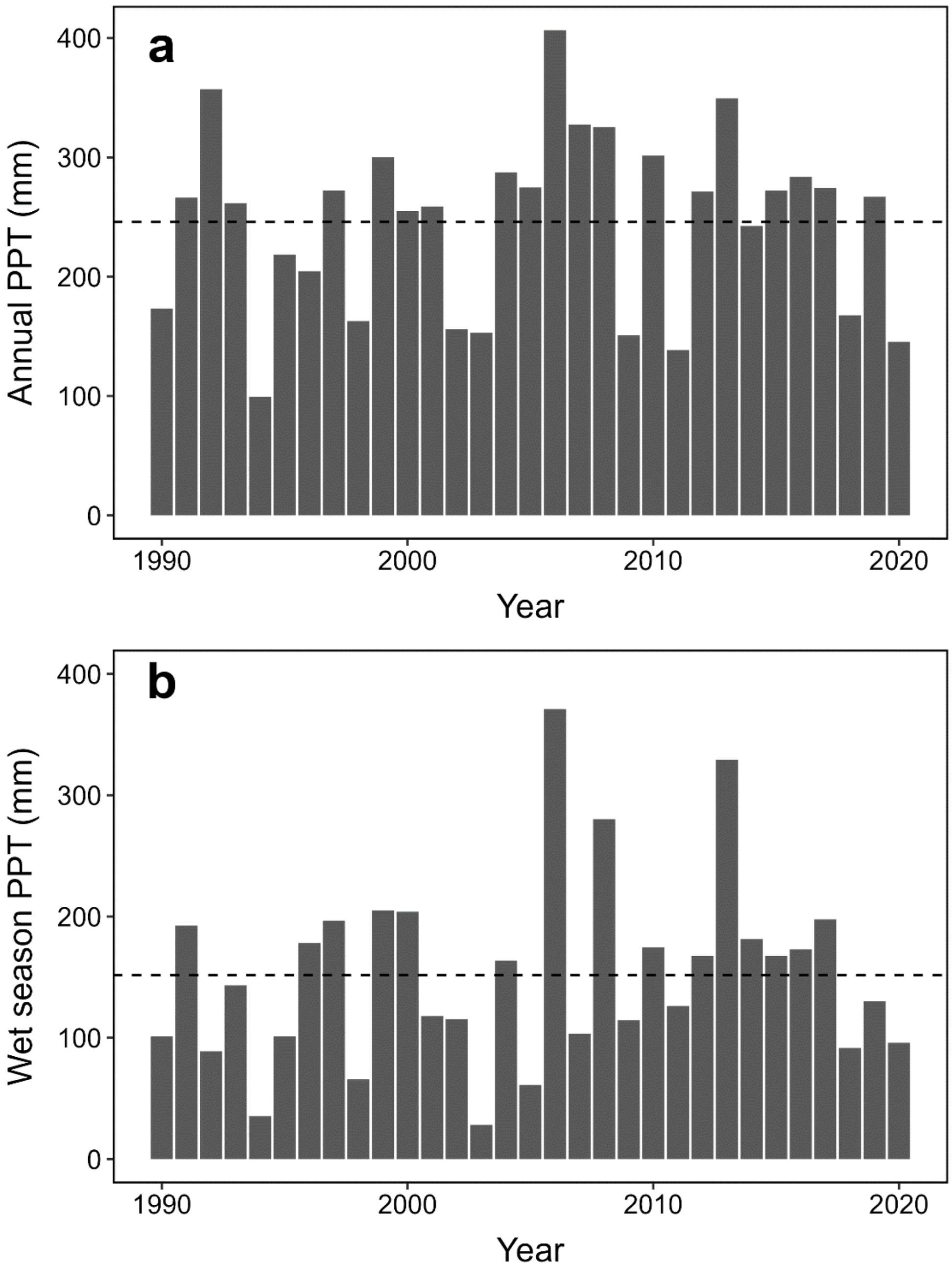

Fig. A1 (a) Annual precipitation (October [previous year] – September [current year]) and (b) wet season precipitation (June-September), from 1990-2020 at the herbivore exclosure study, Jornada Basin LTER site, New Mexico, USA. Dashed horizontal lines indicate mean rainfall.

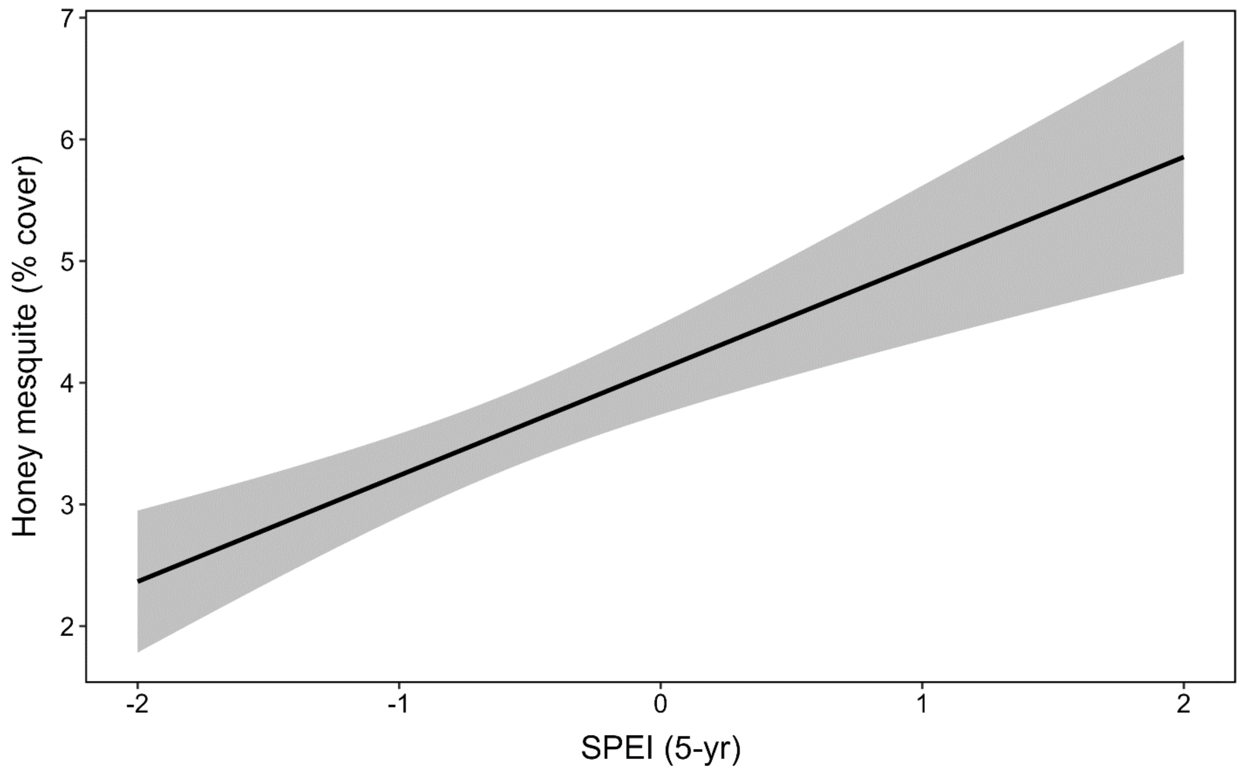

Fig. A2 Predictive plot from the top linear mixed model for honey mesquite. From 1995-2020, honey mesquite foliar cover increased strongly over time with increasing 5-yr SPEI (Standardized Precipitation-Evapotranspiration Index).

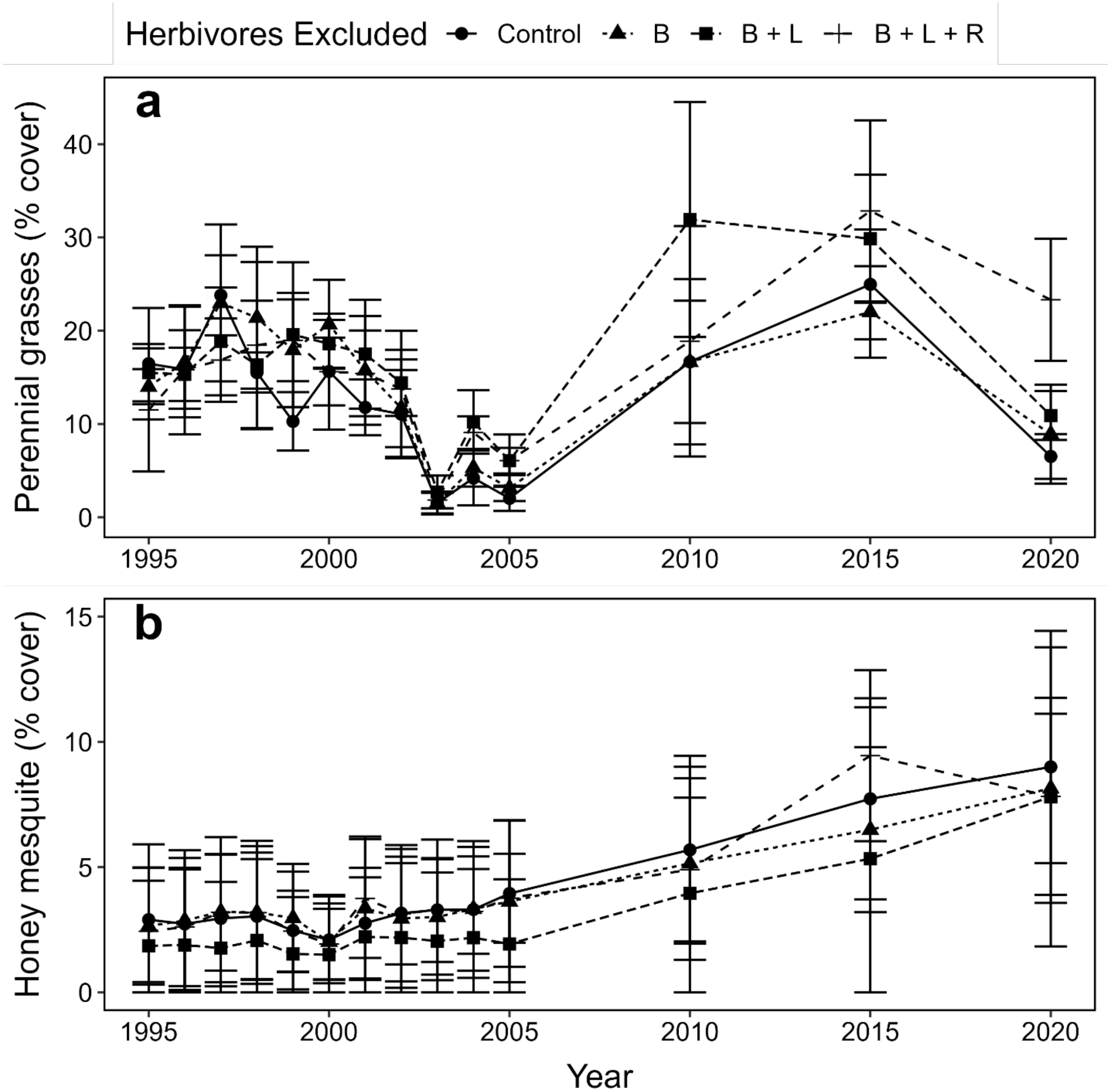

Fig. A3 Mean foliar cover for (a) perennial grasses and (b) honey mesquite from 1995-2020 at the herbivore exclosure study at the Jornada Basin Long Term Ecological Research site, New Mexico, USA. This figure is supplemental to Fig. 2.2 and includes error bars (± SD) that were omitted in the main text for legibility.

APPENDIX B: CHAPTER 2 PLANT COMMUNITY SUPPLEMENTALS

Table B1 Results from permutational multivariate analysis of variance used to assess plant community composition dynamics among hierarchical herbivore treatments over 25 years at the herbivore exclosure experiment, Jornada Basin LTER, New Mexico, USA.

Predictor	***df***	***SS***	***R^2***	***F***	***P***
Year	1	2.24	0.06	15.84	0.001
Treatment	3	2.02	0.06	4.76	0.219
Year x Treatment	3	0.81	0.02	1.91	0.001
Residual	216	30.58	0.86		
Total	223	35.66	1.00		

Table B2 Plant species associations with herbivore treatments from the (a) early (1995-2005) and (b) late (2010-2020) periods of the herbivore exclusion study, Jornada Basin LTER, New Mexico, USA.

Early Period (1995-2005)

Treatment	Code	Species	Habit	Form	Specificity	Fidelity	*P*
Control	EPTR	*Ephedra trifurca*	Perennial	SHRUB	1.00	0.20	0.001
	SPIN	*Sphaeralcea incana*	Perennial	FORB	0.80	0.16	0.012
	POPA	*Portulaca parvula*	Annual	FORB	0.45	0.68	0.032
	TILA	*Tidestromia lanuginosa*	Annual	FORB	0.40	0.77	0.045
	TRBE	*Tragus berteronian*	Annual	GRASS	0.79	0.18	0.007
B							
B+L	EVNU	*Evolvulus nuttallianus*	Perennial	FORB	1.00	0.14	0.002
	MUPO	*Muhlenbergia porteri*	Perennial	GRASS	0.42	0.43	0.007
	OPPH	*Opuntia phaeacantha*	Perennial	ST-SU	0.63	0.14	0.031
	SPSU	*Sphaeralcea subhastata*	Perennial	FORB	0.37	0.73	0.008
B+L+R	ARPA	*Aristida pansa*	Perennial	GRASS	0.73	0.36	0.001
	COSC	*Coryphantha scheeri*	Perennial	ST-SU	1.00	0.07	0.049
	DANA	*Dalea nana*	Perennial	FORB	0.48	0.61	0.012
	LEER	*Leucelene ericoides*	Perennial	FORB	1.00	0.16	0.001
	MAPI	*Machaeranthera pinnatifida*	Perennial	FORB	0.73	0.66	0.001
	PLPA	*Plantago patagonica*	Annual	FORB	0.77	0.11	0.044
	PSTA	*Psilostrophe tagetina*	Perennial	FORB	0.75	0.75	0.001
	SACY	*Sarcostemma cyanchoides*	Perennial	FORB	0.91	0.09	0.019
	SELE	*Setaria leucopila*	Perennial	GRASS	0.51	0.23	0.044
	SPCO	*Sporobolus contractus*	Perennial	GRASS	0.71	0.41	0.002
	SPCR	*Sporobolus cryptandrus*	Perennial	GRASS	0.76	0.30	0.004
	SPFL	*Sporobolus flexuosus*	Perennial	GRASS	0.70	0.84	0.001
	YUEL	*Yucca elata*	Perennial	LF-SU	0.58	0.98	0.001

Late Period (2010-2020)

Treatment	Code	Species	Habit	Form	Specificity	Fidelity	*P*
Control	CABA	*Cassia bauhinioides*	Perennial	FORB	0.55	0.83	0.034
B							
B+L							
B+L+R	BOER	*Bouteloua eriopoda*	Perennial	GRASS	0.33	1.00	0.045
	DANA	*Dalea nana*	Perennial	FORB	0.78	0.58	0.034
	YUEL	*Yucca elata*	Perennial	LF-SU	0.49	1.00	0.004

Note: For treatments, B = bovid exclusion, L = lagomorph exclusion, R = rodent exclusion. For plant forms, LF-SU = leaf succulent and ST-SU = stem succulent.

Table B3 Results from linear mixed models for assessing a set of plant community metrics at the herbivore exclusion experiment, Jornada Basin LTER, New Mexico, USA.

Model response variable and parameters	*β*	*SE*	95% CI
Species richness			
(Intercept)	39.851	1.177	37.545 — 42.158
Time	-1.210	0.056	-1.320 — -1.101
Treatment (B)	-2.081	1.467	-4.956 — 0.793
Treatment (B+L)	0.510	1.467	-2.364 — 3.385
Treatment (B+L+R)	0.348	1.467	-2.526 — 3.223
Time x Treatment (B)	0.032	0.079	-0.123 — 0.187
Time x Treatment (B+L)	-0.079	0.079	-0.234 — 0.076
Time x Treatment (B+L+R)	0.044	0.079	-0.112 — 0.199
Shannon diversity			
(Intercept)	1.702	0.117	1.473 — 1.931
Time	-0.024	0.006	-0.035 — -0.012
Treatment (B)	-0.212	0.130	-0.466 — 0.043
Treatment (B+L)	-0.117	0.130	-0.371 — 0.138
Treatment (B+L+R)	0.456	0.130	0.201 — 0.710
Time x Treatment (B)	0.009	0.008	-0.008 — 0.025
Time x Treatment (B+L)	0.007	0.008	-0.010 — 0.024
Time x Treatment (B+L+R)	-0.015	0.008	-0.031 — 0.002
Pielou's evenness			
(Intercept)	0.541	0.029	0.484 — 0.597
Time	0.001	0.002	-0.002 — 0.005
Treatment (B)	-0.038	0.038	-0.112 — 0.035
Treatment (B+L)	-0.053	0.038	-0.126 — 0.021
Treatment (B+L+R)	0.119	0.038	0.045 — 0.192
Time x Treatment (B)	0.003	0.003	-0.003 — 0.008
Time x Treatment (B+L)	0.002	0.003	-0.003 — 0.007
Time x Treatment (B+L+R)	-0.006	0.003	-0.012 — -0.001

Note: For treatments, B = bovid exclusion, L = lagomorph exclusion, R = rodent exclusion. SPEI is a drought index (Standardized Precipitation-Evapotranspiration Index), and Ppt is precipitation.

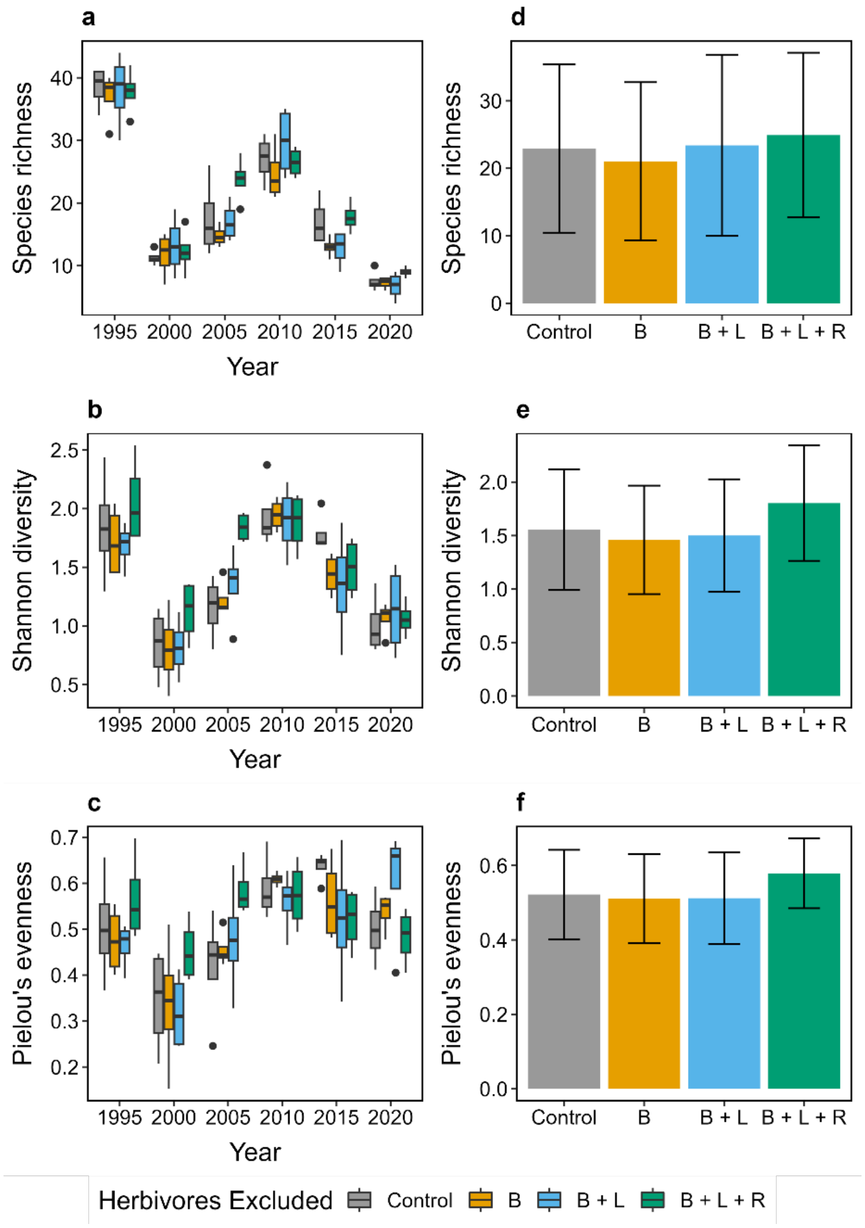

Fig. B1 Trends for three plant community metrics at the herbivore exclosure experiment, Jornada Basin LTER, New Mexico, USA from 1995 to 2020. Boxplots by year and herbivore treatment for plant (a) species richness, (b) Shannon diversity, and (c) Pielou's evenness represent potential year x herbivore treatment interactions. Bar plots by herbivore treatment for (d) species richness, (e) Shannon diversity, and (f) Pielou's evenness represent mean values (± SD) for each metric and were used to examine changes in plant community dynamics among herbivore treatments and controls.

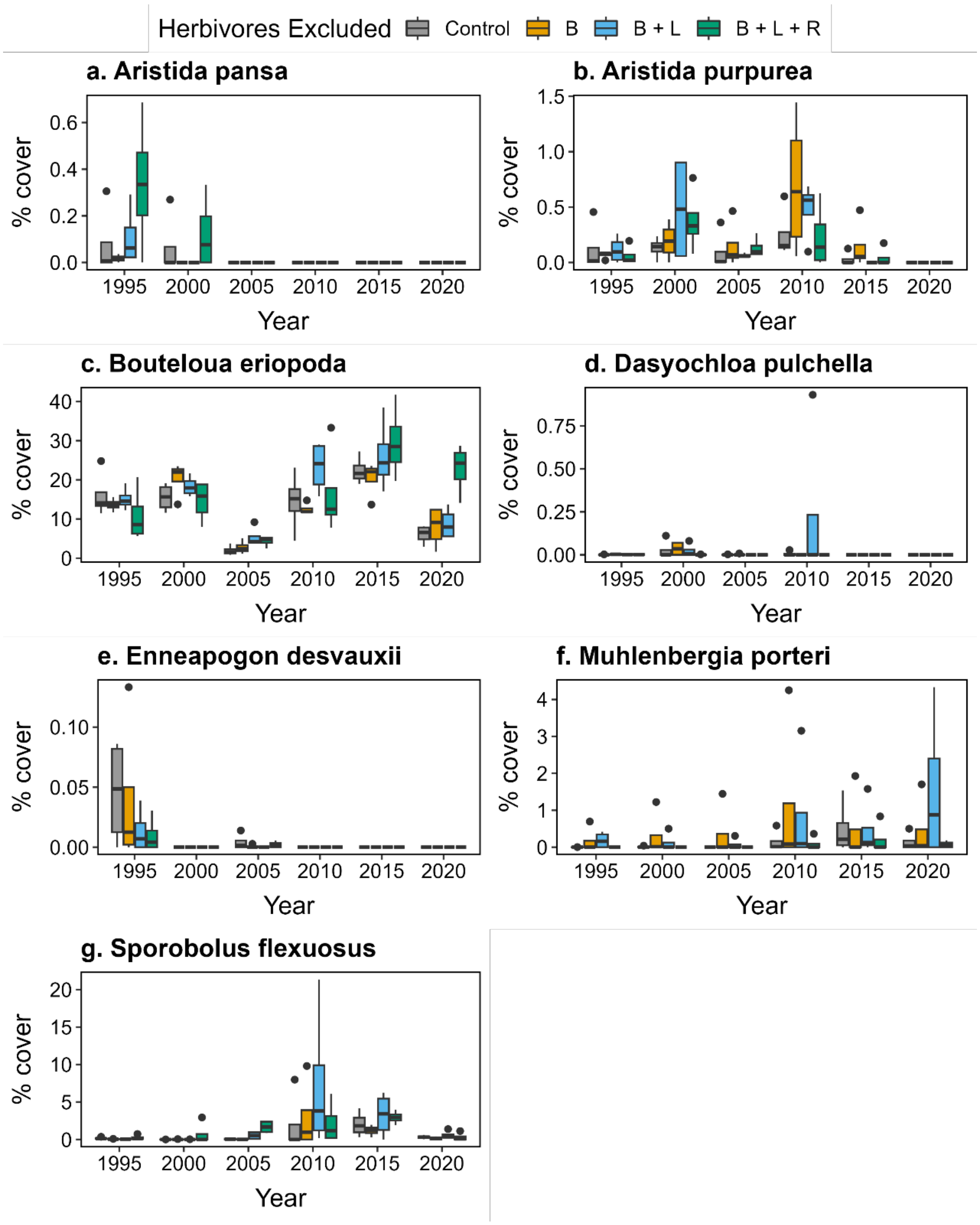

Fig. B2 Percent foliar cover of key perennial grass species monitored in the herbivore exclosure experiment at the Jornada Basin LTER site. The perennial grass functional group was primarily composed of black grama (*Bouteloua eriopoda*), with *Sporobolus flexuosus*, *Aristida purpurea*, and *Muhlenbergia porteri* as sub-dominant species.

APPENDIX C: CHAPTER 3 SUPPLEMENTARY MATERIALS

Table C1 State-level metrics for rodent abundance from 2023 used in analyses. Biomass is the total grams of rodent biomass per ha at a state within spatial block. Relative abundance included the number of unique individuals captured per ha at states.

Pasture	Ecosystem State	Biomass (g/ha)	Abundance (captures/ha)
3	Grassland	1102.0	22.0
3	Ecotone	907.3	21.3
3	Shrubland	898.7	19.3
9	Grassland	238.3	6.0
9	Ecotone	345.0	6.3
9	Shrubland	519.0	8.0
12	Grassland	523.0	9.0
12	Ecotone	575.7	11.0
12	Shrubland	453.0	9.0

Table C2 Rodent species at Jornada Basin Long Term Ecological Research site that were either included or excluded from herbivory analyses based on diet. Also presented are their dietary functional group, and whether these species were captured in 2023.

Included:

Species	Functional Group	Captured in 2023?
Dipodomys merriami	Medium granivore	Yes
Dipodomys ordii	Medium granivore	Yes
Dipodomys spectabilis	Large granivore	Yes
Neotoma leucopus	Folivore	Yes
Neotoma micropus	Folivore	Yes
Peromyscus maniculatus	Omnivore	Yes
Peromyscus leucopus	Omnivore	No
Peromyscus eremicus	Omnivore	Yes
Xerospermophilus spilosoma	Folivore	Yes

Excluded:

Species	Functional Group	Captured in 2023?
Perognathus flavus	Small granivore	Yes
Peromyscus boylii	Omnivore	No
Onychomys arenicola	Omnivore	Yes
Onychomys leucogaster	Omnivore	Yes
Chaetodipus eremicus	Small granivore	Yes
Chaetodipus intermedius	Small granivore	No
Chaetodipus penicillatus	Small granivore	No

Table C3 Results from marginal F-tests applied to mixed models for perennial grass cover in herbivore exclosure treatment and control plots, and disturbed subplots centered in exclosure treatments and controls, replicated across ecosystem states (grassland, ecotone, shrubland) at the Ecotone Study, Jornada Basin Long Term Ecological Research site, New Mexico, USA.

Exclosures

Predictor	***df***	***F***	***P***
(Intercept)	1, 84	6.44	0.013
Ecosystem State	2, 40	2.51	0.094
Treatment	2, 84	16.05	<0.001
Ecosystem State x Treatment	4, 84	6.62	<0.001

Recovery from Disturbance

Predictor	***df***	***F***	***P***
(Intercept)	1, 84	5.86	0.018
Ecosystem State	2, 40	1.92	0.159
Treatment	2, 84	3.06	0.052
Ecosystem State x Treatment	4, 84	1.44	0.229

Table C4 Results from mixed effects Cox proportional hazard models applied to perennial grass seedlings at risk of mortality from herbivory across grassland, ecotone, and shrubland states at the Jornada Basin Long Term Ecological Research site in 2023. Herbivore treatments excluding cattle, oryx, and lagomorphs (rodent access) did not affect seedling mortality risk compared to controls. For control trays open to all herbivores, the risk of seedling mortality from herbivory was higher in shrubland and ecotone ecosystem states compared to grasslands.

Predictor	***HR***	***SE***	**95% CI**	***P***
Ecosystem State:				
Ecotone	1.43	0.340	0.76 — 2.10	0.300
Shrubland	1.40	0.340	0.73 — 2.07	0.320
Treatment:				
Rodent Access	1.06	0.062	0.94 — 1.18	0.360

Predictor	***HR***	***SE***	**95% CI**	***P***
Ecosystem State:				
Ecotone	1.33	0.109	1.12 — 1.54	0.009
Shrubland	1.55	0.112	1.33 — 1.77	<0.001

Note: HR < 1 indicates decreased risk of mortality from herbivory compared to baseline (grassland, control). HR > 1 indicates increased risk of mortality from herbivory compared to baseline.

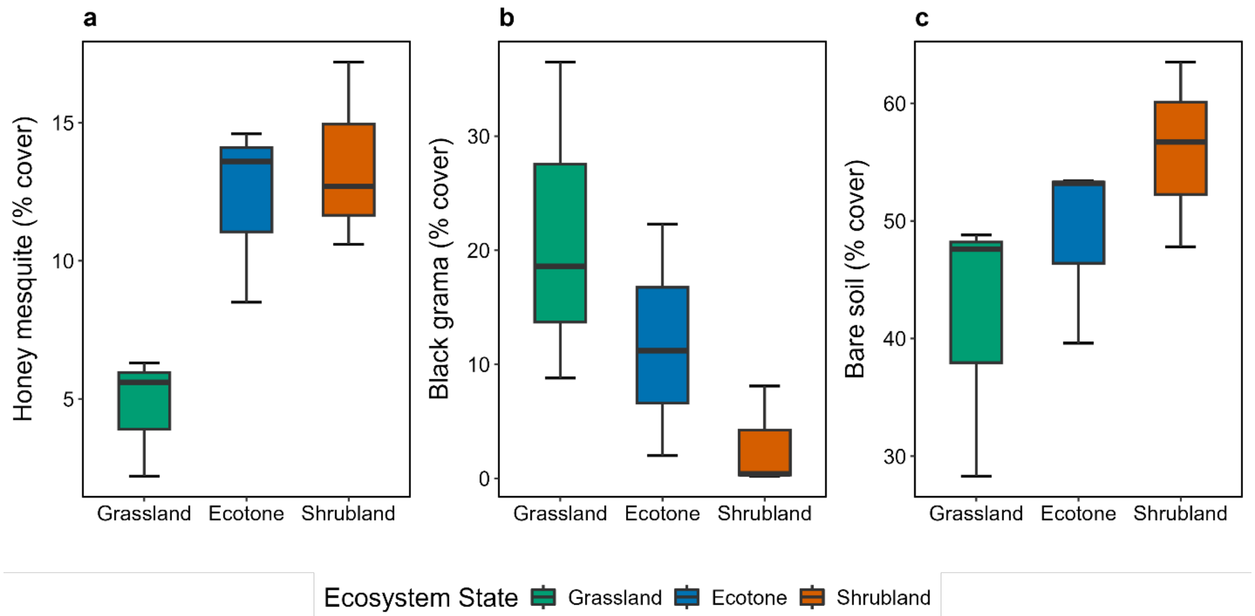

Fig. C1 Percent cover of (a) honey mesquite shrubs, (b) black grama grass, and (c) bare soil across shrubland, ecotone, and grassland ecosystem states in 2021. The bold horizontal line indicates the mean of percent foliar cover boxed by its interquartile range. Vertical lines indicate the first (lower) quartile and third (upper) quartile. Trends in cover for our focal species, honey mesquite and black grama, were consistent with overall levels of perennial shrub and grass cover at sites (Main Text: Fig. 3.2).

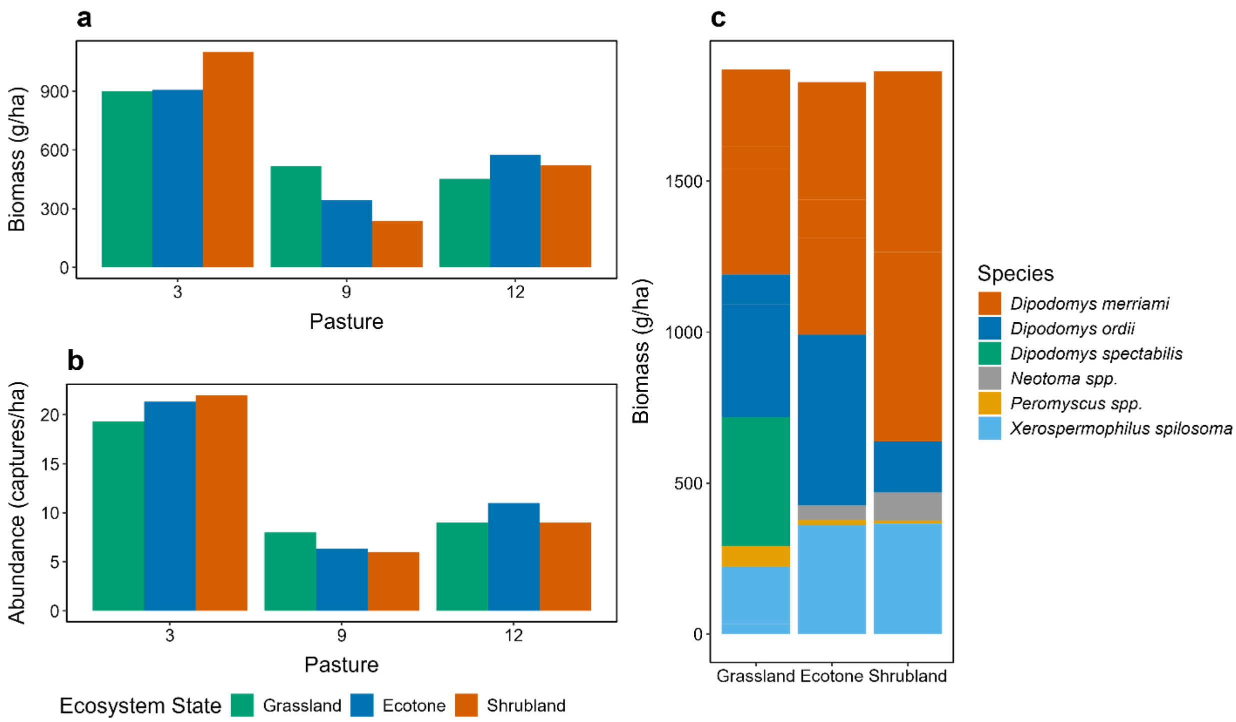

Fig. C2 Summaries for 2023 rodent (a) biomass and (b) relative abundance across ecosystem states and pastures (i.e., spatial blocks) at the Ecotone exclosure experiment, New Mexico, USA. (c) Total rodent biomass was similar among shrubland, ecotone, and grassland ecosystem states but species composition differed. Biomass of *Dipodomys merriami* and *Xerospermophilus spilosom*a both increased with shrub encroachment, whereas *D. ordii* and *D. spectabilis* had higher biomass in grasslands.

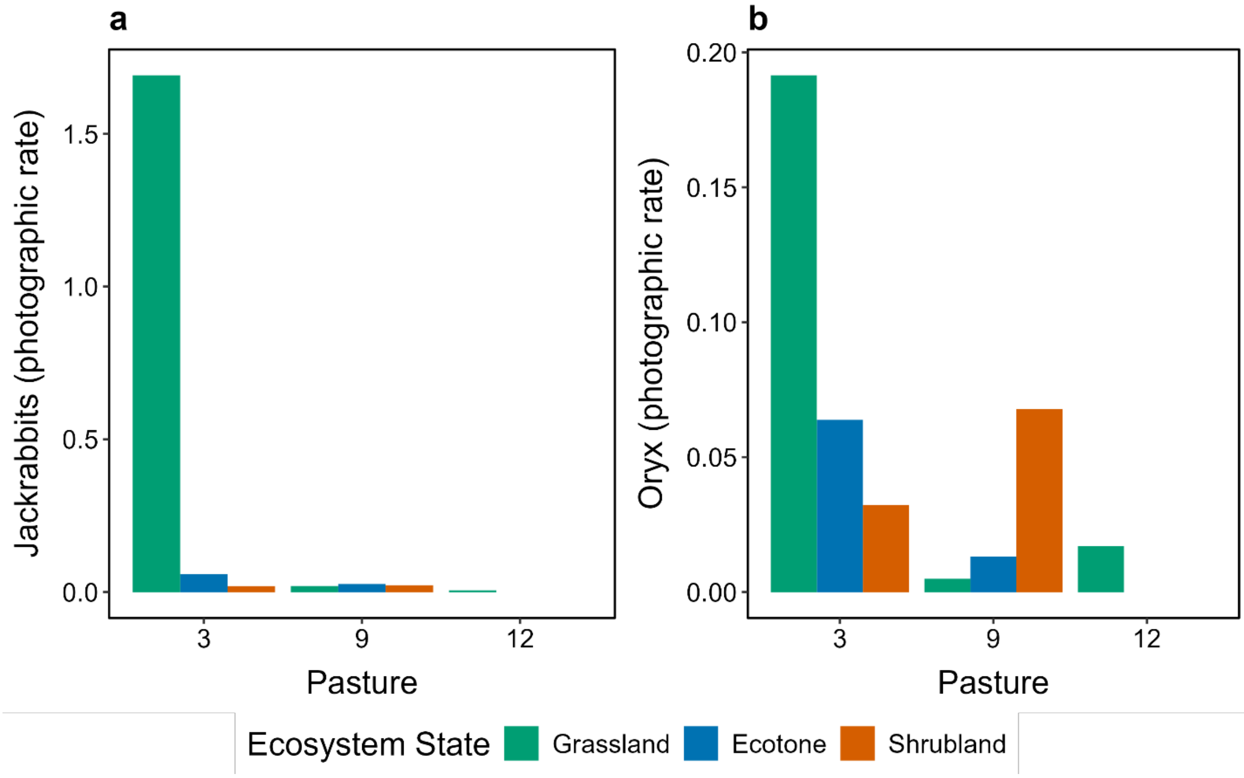

Fig. C3 Summaries for camera trap photographic rate (independent detections/sampling effort) in 2023 for (a) black-tailed jackrabbits, and (b) African oryx across ecosystem states and pastures (spatial blocks) at the herbivore exclosure experiment, Jornada Basin Long Term Ecological Research site, New Mexico, USA. Desert cottontail and domestic cattle were undetected during camera trap sampling and were excluded from analysis.

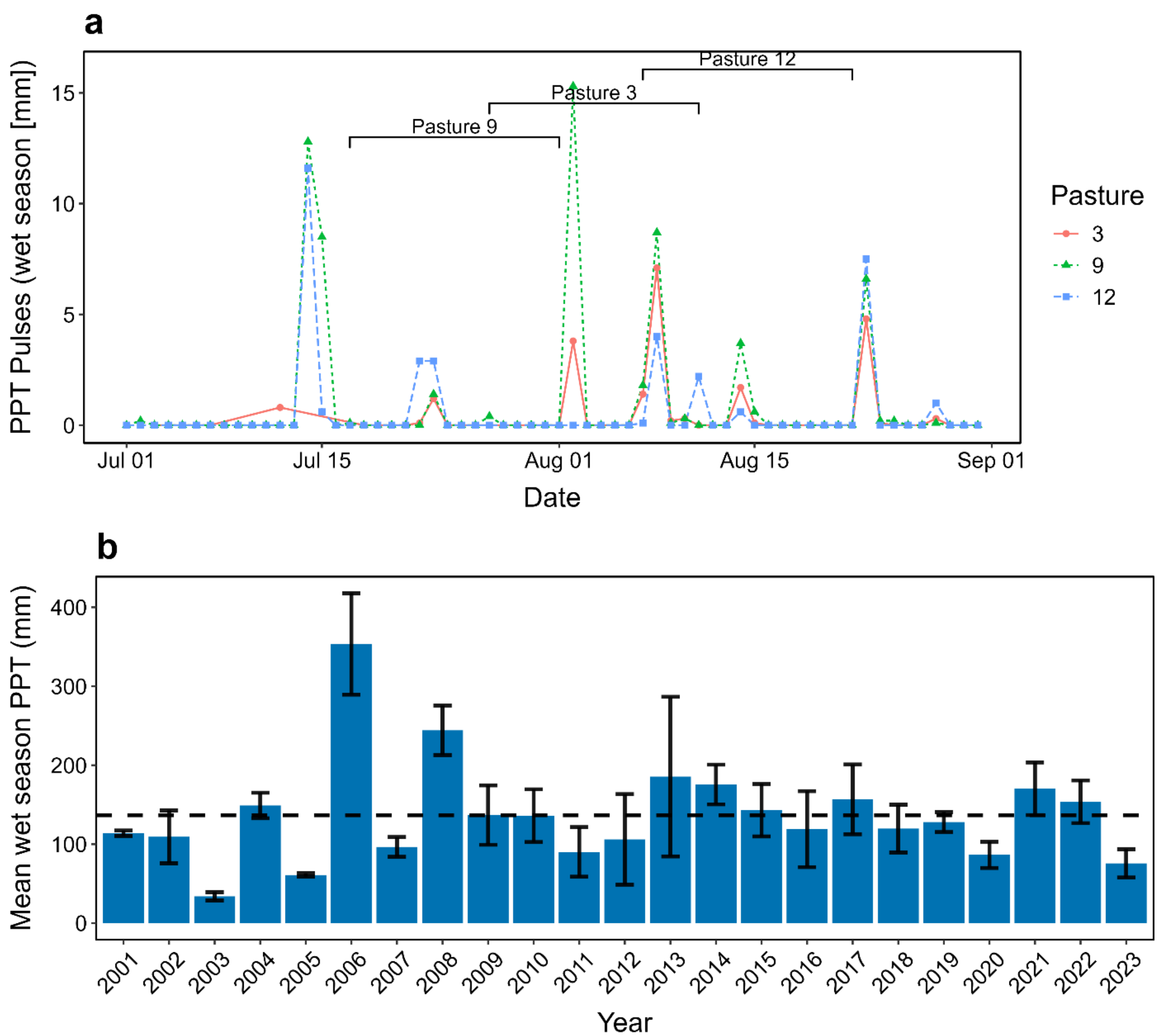

Fig. C4 Summary of (a) precipitation pulses occurring during seedling survival field trials from July-August 2023, at spatial blocks Pastures 3, 9, and 12 of the Ecotone exclosure experiment at the Jornada Basin Long Term Ecological Research site, New Mexico, USA. Brackets indicate the duration of field trials for each pasture. (b) Mean wet season precipitation (June-September) since the initiation of the Ecotone exclosure experiment in 2001. Error bars represent ± SD. The dashed horizontal line indicates the grand mean of wet season precipitation (137 mm) from 2001-2023.

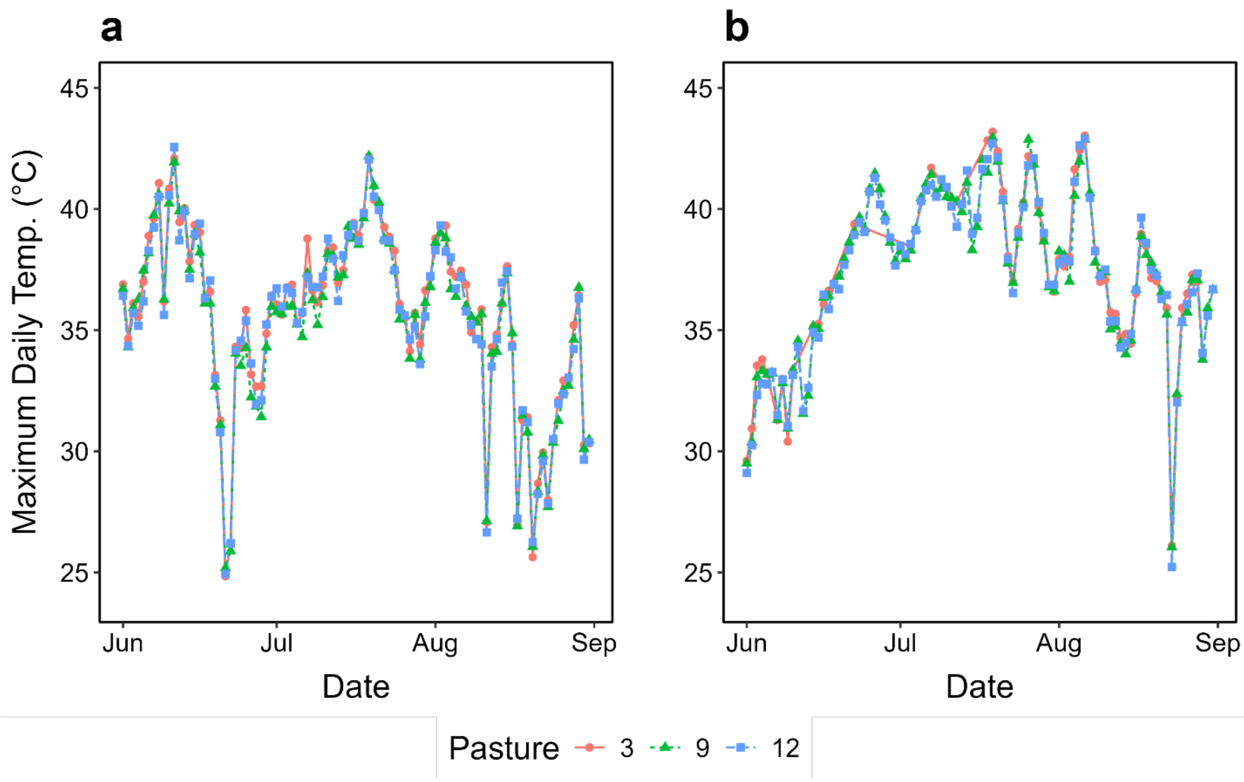

Fig. C5 Maximum daily temperature in (a) 2022 and (b) 2023 at the Ecotone exclosure experiment, Jornada Basin Long Term Ecological Research site, New Mexico, USA.

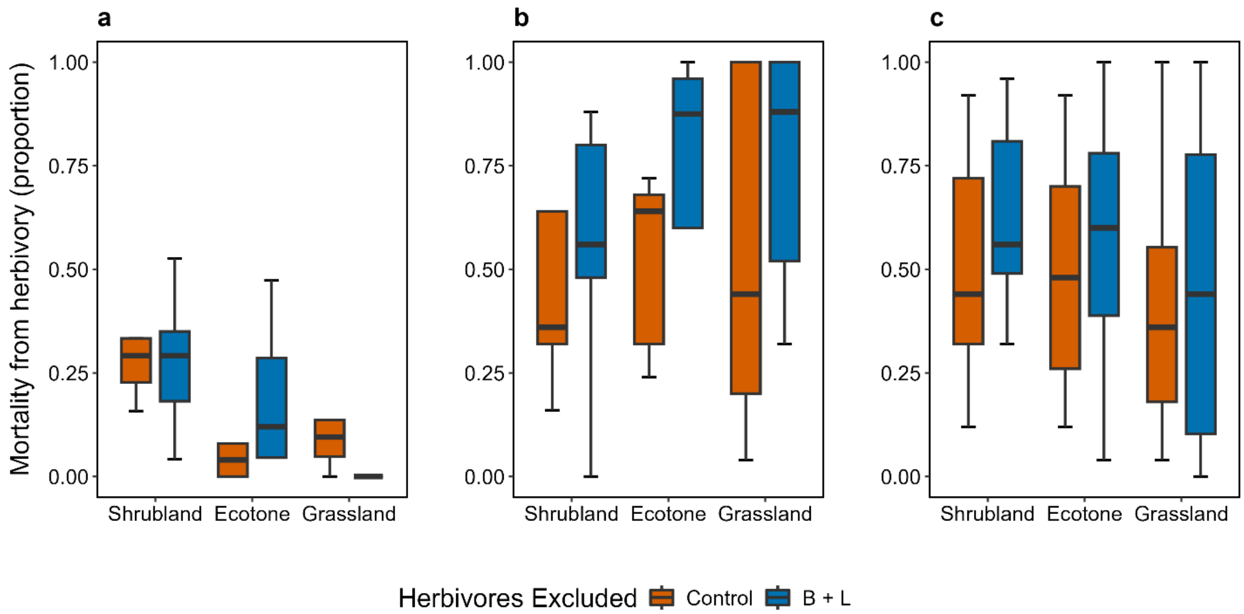

Fig. C6 Mortality of perennial grass seedlings in trays across rodent treatments (B + L) and controls and ecosystem states during (a) 2022 pilot trials on Pasture 12, (b) 2023 trials on Pasture 12, and (c) 2023 trials on Pastures 3, 9, and 12 of the Ecotone exclosure experiment, Jornada Basin Long Term Ecological Research site, New Mexico, USA. Controls had open access to all herbivores (i.e., bovids, lagomorphs, rodents), and B + L treatments excluded bovids and lagmorphs, allowing rodent-only access.

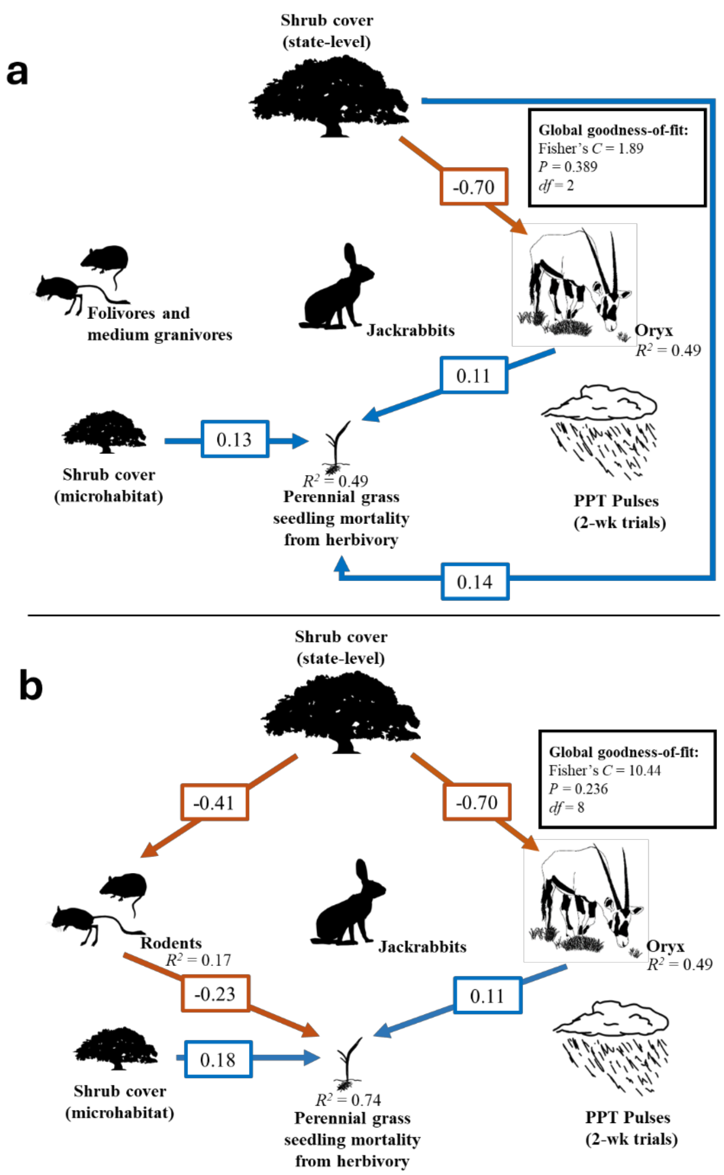

Fig. C7 Results from two candidate structural equation models (SEMs) for the influence of habitat structure at multiple scales (ecosystem state, microhabitat), herbivore populations, and precipitation on perennial grass seedling mortality from herbivory. The direction of pathways is from exogenous (predictor) to endogenous (response) variables. Blue pathways indicate a positive response to predictors, and orange pathways indicate negative responses. For rodent consumers, the SEMs included (a) folivores plus medium granivores, or (b) all rodents that consume non-trivial amounts of green plants.

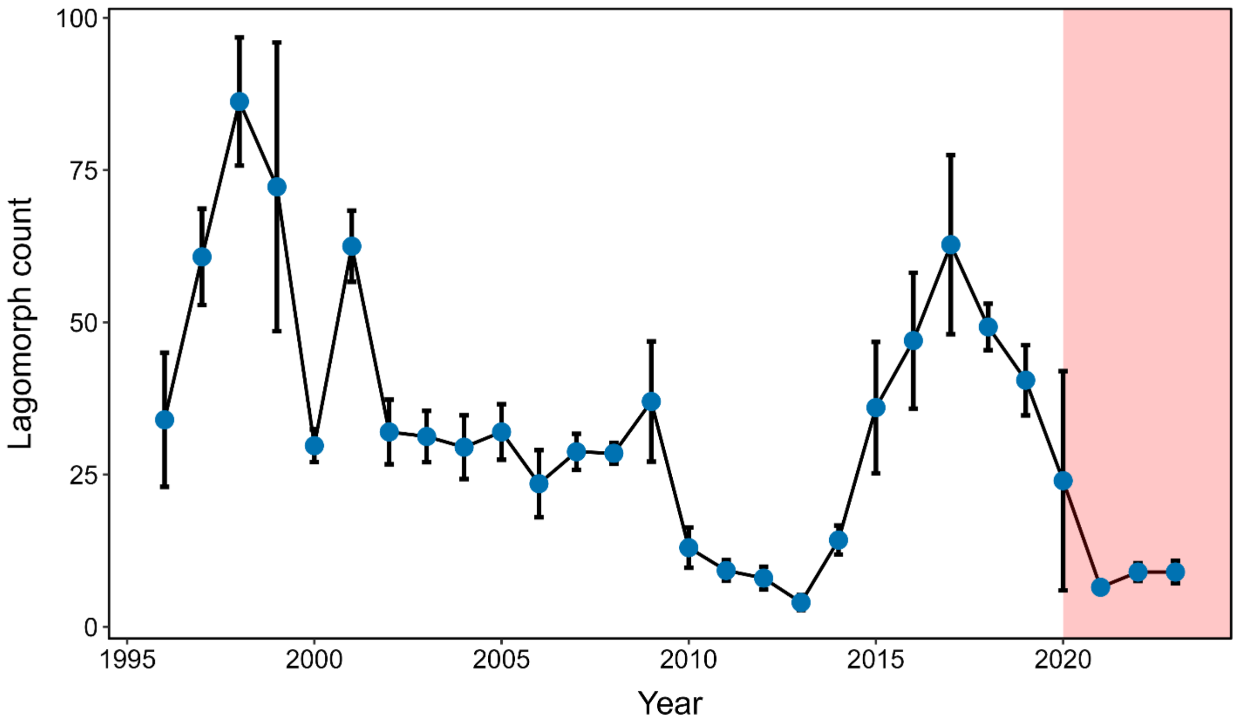

Fig. C8 Spotlight counts for lagomorphs (i.e., black-tailed jackrabbit, *Lepus californicus*; desert cottontail, *Sylvilagus audubonii*) from a grassland route (route length = 9.7 km) on Pasture 9 at the Jornada Basin Long Term Ecological Research site, New Mexico, USA from 1996-2023. Points indicate the mean count across four surveys each year (1996: n = 3; 2020: n = 2) with error bars representing the standard error of the mean. The shaded region (2020-2023) indicates the approximate time period in which the rabbit hemorrhagic disease virus drove population declines for lagomorphs.