Received: 2 September 2022 | Revised: 24 June 2023 | Accepted: 20 August 2023

DOI: 10.1111/avsc.12749

Applied Vegetation Science IAVS

RESEARCH ARTICLE

Exotic herbivores and fire energy drive standing herbaceous biomass but do not alter compositional patterns in a semiarid savanna ecosystem

Virginia D. Preiss[1] | Carissa L. Wonkka[2] | Devan A. McGranahan[3] | Alexandra G. Lodge[1] | Matthew B. Dickinson[4] | Kathleen L. Kavanagh[5] | Heath D. Starns[6] | Douglas R. Tolleson[6] | Morgan L. Treadwell[7] | Dirac Twidwell[8] | William E. Rogers[1]

[1]Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, USA

[2]USDA ARS, Northern Plains Agricultural Research Lab, Sidney, Montana, USA

[3]USDA ARS, Fort Keogh Livestock and Range Research Lab, Miles City, Montana, USA

[4]US Forest Service, Northern Research Station, Delaware, Ohio, USA

[5]College of Forestry, Oregon State University, Corvallis, Oregon, USA

[6]Rangeland, Wildlife and Fisheries Management Department, Texas A&M AgriLife Research, Sonora, Texas, USA

[7]Rangeland, Wildlife and Fisheries Management Department, Texas A&M AgriLife Extension Service, San Angelo, Texas, USA

[8]Department of Agronomy and Horticulture, University of Nebraska, Lincoln, Nebraska, USA

Correspondence
William E. Rogers, Department of Ecology and Conservation Biology, Texas A&M University, College Station, Texas, 77843-2258 USA.
Email: william.rogers@ag.tamu.edu

Funding information
United States Department of Agriculture-Bureau of Land Management Joint Fire Sciences, Grant/Award Number: 17-1-04-7; Department of Ecosystem Science and Management's Savanna Long Term Research and Education Initiative

Abstract

Questions: Fire regime alterations are pushing open ecosystems worldwide past tipping points where alternative steady states characterized by woody dominance prevail. This reduces the frequency and intensity of surface fires, further limiting their effectiveness for controlling cover of woody plants. In addition, grazing pressure (exotic or native grazers) can reinforce woody encroachment by potentially reducing fine-fuel loads. We investigated the effects of different fire energies on the herbaceous plant community, together with mammalian wildlife herbivory (exotic and native combined) exclusion, to inform best management practices.

Location: Texas semi-arid savanna, southern Great Plains, USA.

Methods: We conducted an experiment in which we manipulated fire intensity and herbivore access to herbaceous biomass in a split-plot design. We altered fire energy via fuel addition rather than applying fire under different environmental conditions to control for differences in standing biomass and composition attributable to differential plant physiological status and fire season.

Results: High-energy fire did not reduce herbaceous biomass or alter plant community composition, although it did increase among-plot variability in composition and forb biomass relative to low-energy fire and non-burned controls. Grazing pressure from native and non-native mammalian herbivores reduced above-ground herbaceous biomass regardless of fire treatments, but did not alter community composition.

Conclusions: Managers seeking to apply high-intensity prescribed fire to reduce woody encroachment will not negatively impact herbaceous plant productivity or alter community composition. However, they should be cognizant that repeated fires necessary for greatly reducing woody plants in heavily invaded areas might be difficult to accomplish due to fine-fuel reduction from wild herbivores. High fencing to

Co-ordinating Editor: Giselda Durigan

restrict access by wildlife herbivores or culling might be necessary to build fuels sufficient to conduct high-intensity burns for woody-plant reduction.

KEYWORDS
extreme fire, grassland community composition, herbaceous biomass, Indian axis deer, pyric herbivory, Texas semi-arid rangelands, white-tailed deer, woody encroachment

1 | INTRODUCTION

Fire and large mammalian herbivores control vegetation dynamics in many open ecosystems worldwide (Bond, 2022). Fire and grazers both consume vegetation within grassy and herbaceous layers, while fire and browsers both target woody plants; thus, interactions between fire and herbivores and among grazers and browsers shape the structure and composition of grasslands and savannas (Bond & Keeley, 2005). These dynamics are likely most apparent in the open ecosystems of Africa, where a high diversity of native mammalian herbivores maintain often strict dietary niches throughout a long evolutionary history of anthropogenic fire regimes (Hempson et al., 2019; McGranahan et al., 2022). But humans have altered disturbance processes in open ecosystems worldwide through fire suppression and simplification of herbivory regimes via the expansion of livestock production (Bowman et al., 2011; Ripple et al., 2015). Management for pre-colonial fire and grazing regimes and reintroduction of native ungulate species alongside domestic livestock are recognized as potential strategies to restore ecological structure and function in open ecosystems (McGranahan, 2008; Fuhlendorf et al., 2017).

Land use changes since the territorial expansion of European Americans have substantially altered open ecosystems in North America, which include prairie grasslands, mixed grass–shrub steppe, and deciduous savannas. The extirpation of most native ungulates and expansion of agriculture is common across all these ecosystems (Fite, 1977; Hartnett et al., 1997). While fire regimes have been substantially altered throughout the Great Plains, the drivers and ecosystem effects have been region-specific, ranging from fire exclusion and invasion by less-flammable exotic grass species in the northern mixed-grass prairie to fire suppression and encroachment of woody plants in areas of the southern Great Plains (McGranahan & Wonkka, 2021). This range in responses to fire regime alteration characterizes open ecosystems worldwide, but fire suppression has driven encroachment of woody plants in many parts of the world (Archer et al., 2017).

The increasing abundance of woody plants in open ecosystems worldwide is of growing concern for grazing and fire management alike (Engle et al., 2008; Scholtz et al., 2022). In Texas, USA, managers mostly target two types of native trees in grasslands, savannas, and open deciduous woodlands—*Juniperus* and *Prosopis* spp. (Twidwell, Rogers, et al., 2013; Andruk et al., 2014; Wonkka et al., 2016). Several of their effects on the structure and composition of herbaceous communities appear to be divergent—while increases in *Juniperus* density are associated with lower abundance and diversity of grasses and forbs (e.g., Limb et al., 2010), research suggests grass abundance and diversity increases under *Prosopis* stands because it creates favorable grass microsites (e.g., Ruthven III, 2001). However, *Prosopis* often acts as a nurse plant to other shrubs that develop in its understorey (Archer, 1989; Barnes & Archer, 1999); as these mixed-species thickets spread, they shade out and compete for resources with herbaceous vegetation, reducing grass and forb abundance and diversity at high canopy densities. In either case, extreme prescribed fire—intentional burns implemented under dry and windy weather conditions that can mitigate limitations on fire behavior due to reduced herbaceous fuel loads—are effective in reducing above-ground cover of both *Juniperus* and *Prosopis* and associated understorey species for up to three years after fire (Twidwell et al., 2016; Starns et al., 2022). The effects of high-intensity fires on herbaceous vegetation productivity and composition remain unclear, leading to concern among managers in the region that the high fire intensities needed to overcome the resilience of savannas encroached by woody plants and grasslands could damage grasses or sterilize the soil, resulting in long-term losses of biomass in areas where extreme prescribed fire is applied.

Plant–herbivore interactions in Texas are unique within the Great Plains due to relatively high ungulate diversity following several introductions of exotic game species. While many native ungulate populations in North America have been restored since their initial extirpation (Krausman & Bleich, 2013), iconic Great Plains species like bison (*Bos bison*) and elk (*Cervus canadensis*) have limited functional presence on open ecosystems throughout much of their original range. But in Texas, several deer (Cervidae) species have been introduced to diversify sport hunting opportunities and have escaped captivity to form free-ranging populations. These are exploiting ecological niches assumed to be unoccupied by native fauna (Demarais et al., 1990). While one of the most common introduced ungulates in Texas, the Indian axis deer *Axis axis*, does appear to eat much more grass than native white-tailed deer *Odocoileus virginianus*, other components of interspecies competition likely preclude the long-term coexistence of axis deer and white-tailed deer within the same range (Faas & Weckerly, 2010). Meanwhile, a primary preference for grass puts the axis deer into direct forage competition with grazing livestock and contributes to severe rangeland degradation when overabundant axis deer displace white-tailed deer (Elliot & Barrett, 1985; Karlin & Rankin, 2016). Extreme prescribed fire in Texas has

been shown to have the specific advantage of increasing grass production following encroachment by woody plants (Twidwell, Fuhlendorf, et al., 2013). However, given that burned areas attract grazers (Archibald et al., 2005), research must address post-fire vegetation dynamics when prescribed fires are applied to areas with non-native deer that prefer to graze grasses rather than browse on woody vegetation.

Given increasing use of high-energy fire for woody-brush control in the region and potential for increased wildlife herbivore consumption of grasses and forbs, our objective was to assess the individual and interactive effects of fire energy and mammalian wildlife herbivory (both native and exotic herbivores) on herbaceous plant biomass and community composition in a semi-arid savanna in Texas, USA. Since 2008, an increasing axis deer population at the study location has prompted researchers to speculate that vegetation dynamics in study plots from which grazing livestock were excluded might still be greatly affected by grazing disturbance (Tolleson et al., 2019; Starns et al., 2020). Thus, this study was designed to specifically control for deer access to burned and non-burned vegetation in an area otherwise excluded from livestock. In addition, we manipulated fire energy via fuel addition rather than environmental conditions to control for potentially confounding influences of fire season and plant physiological and phenological status on plant growth and community composition. Our hypotheses are: (1) fire effects on herbaceous biomass and composition are transient regardless of fire energy, because other studies assessing high-energy fire applied to reduce woody plants also showed that herbaceous biomass was comparable to that in non-burned grassland in as little as a single growing season (Twidwell et al., 2012; Arterburn et al., 2018; Bielski et al., 2021); (2) fire and grazing interact to influence standing herbaceous biomass because mammalian herbivores are attracted to recently burned areas, removing more biomass in those plots; and (3) herbivore exclusion increases biomass and alters community composition because of high wildlife grazing pressure and selectivity.

2 | MATERIALS AND METHODS

This study was conducted at the Texas A&M Sonora Agrilife Research Station, Texas, USA (−100.574°, 30.251°). The average annual temperature is approximately 18°C. The range of temperatures observed during the study was −11°C to 41°C. This site is a semi-arid savanna and receives between 533- and 711 mm of precipitation per year. Yearly precipitation pattern is generally bimodal with peaks in spring and fall. Precipitation was variable for the duration of the experiment (Figure S1). Thirty-year average precipitation in the study region is 556.3 mm, but this was exceeded in 2018 (586.5 mm), 2019 (558.8 mm), and 2020 (594.106 mm). In the year prior to treatment establishment (2017), there was a precipitation deficit (428.752 mm). Historic fire return intervals are between 1 and 12 years, with fires more common in late summer and late winter (Guyette et al., 2012).

The soils are in the Tarrant soil series, characterized as cobbly silty clay in the upper horizons. Exposed limestone bed and medium to large rocks are common in this area. The vegetation horizon is a continuous grass layer interspersed with large, long-lived trees and occasional shrubs and succulents. The dominant grass species are *Hilaria belangeri*, *Nassella leucotricha*, *Bouteloua curtipendula*, and *Aristida purpurea*. Dominant tree species are *Quercus* spp., *Juniperus* spp., and *Prosopis glandulosa*. The study site had last been burned in August 2000 in a high-intensity prescribed burn. The area was periodically moderately grazed by sheep and goats until summer 2016, one growing season prior to the establishment of this experiment. Mammalian wildlife grazers and browsers such as native *Odocoileus virginianus* (white-tailed deer) and *Lepus californicus* (black-tailed jackrabbit), and exotic *Axis axis* (axis deer) continued to freely access the area.

2.1 | Experimental design

We established 72 plots of 100 m^2, each centered on a mature (10+ year) *Prosopis glandulosa* within a pasture with a large number of fairly evenly distributed similarly sized *P. glandulosa* individuals. Plots were centered on *P. glandulosa* individuals as part of a study assessing fire energy impacts on resprouting and survival (Starns et al., 2022), but the focal tree is not relevant to the current study. Each plot was at least 5 m from all surrounding plots to allow for the creation of fire breaks around each plot. We randomly assigned one of three fire treatments (no fire, low-energy fire, and high-energy fire), to each whole plot, resulting in 24 replicates. We then divided each of the 72 whole plots into four quadrants and established a subplot in the middle of each quadrant (Figure S2). We randomly assigned one of two herbivory treatments to two subplots within each whole plot, with an herbivore exclusion cage (hereafter exclosure) randomly assigned to two subplots; the remaining two subplots served as controls (herbivore-accessible with no exclosure; hereafter herbivore-accessible). We constructed exclosures from 0.13 × 0.76 m 19-gauge steel hardware cloth encircled into a 0.5 m diameter cage. We secured them with wires to ensure there were no gaps and securely anchored them to be flush with the soil surface. Similar hardware cloth roofs were constructed and affixed on the top of the exclosures to ensure exclusion of vertebrate herbivores. The herbivore-accessible controls were equivalent-diameter subplots without an exclosure.

We conducted fires independently for each plot. Each plot had a 5 m wide mineral firebreak around the perimeter. Control plots received no further treatment. Low-energy fire treatment plots received a layer of dry hay (61 ± 1 kg) to achieve a continuous, low-intensity fire. High-energy fire treatment plots received a layer of dry hay (61 ± 1 kg) mixed with dry juniper (201 ± 1 kg) to achieve a continuous, high-energy fire. Plots were ignited using a ring-fire ignition pattern. Fires were conducted between July 30th and August 4th, 2018 (see Hiers et al., 2021 and Starns et al., 2022 for more experimental details and fire energy measurements).

2.2 | Sampling

During the growing season one year after treatment implementation (April 2019) we selected one exclosure and one herbivore-accessible subplot for above-ground biomass harvesting. We removed exclosures and hand-clipped all vegetation in the plot to soil level, separated it by functional group, placed it in paper bags, and dried it at 60°C for approximately 24 h prior to weighing. We clipped herbivore-accessible subplots in the same manner using a 0.5 m diameter circular wire-frame to mimic the caged area in adjacent subplots. This process was repeated in August 2020 on the two remaining unharvested subplots. Before clipping, for each subplot, we visually assessed the percent cover of each species present following the Daubenmire classification system (Mueller-DomBois & Ellenberg, 1974).

2.3 | Statistical analysis

Given our split-plot design with herbivory treatment nested as subplots within the fire treatment applied at the whole plot level, we modeled fire and herbivory effects on biomass using mixed-effects models. We assessed treatment effects on total biomass, forb biomass, and grass biomass separately for each year of the study. The models included biomass (total, forb, or grass) as the response variable, fire treatment, herbivory treatment, and their interaction as fixed effects and a unique identifier for 'plot' as a random effect. We used generalized linear models with a Gaussian distribution where model residuals were normally distributed (total biomass and grass biomass in 2020 followed a normal distribution), and a gamma distribution with a log link for all other models. We conducted post-hoc multiple comparisons with a Tukey adjustment. We used the R statistical computing environment (R Core Team, 2021) for all analyses. We used the *nlme* package to fit the mixed-effect models with a Gaussian distribution (Pinheiro et al., 2021) and the *glmmADMB* package to fit generalized linear mixed-effects models with gamma distributions (Fournier et al., 2012). We used the *emmeans* package to conduct multiple comparisons (Lenth, 2022).

We assessed community composition data visually using non-metric multidimensional scaling (NMDS). We ordinated plots in species space for each year of the study separately to visually assess differences in community composition among fire treatments and between herbivory treatments. We statistically assessed plant community compositional differences among treatments using permutational multivariate analysis of variance (PERMANOVA) with fire treatment, herbivory treatment, and their interaction included as terms in the model and a unique identifier for plot as a random effect. We assessed treatment effects on beta diversity by assessing homogeneity of group variance for fire treatment and herbivory treatment using a multivariate analog of Levene's test following McGranahan et al. (2018). We used the *vegan* package for all multivariate analyses (Oksanen et al., 2020). We fit NMDS with function "MDS" using Bray–Curtis distances and four dimensions. We used the "adonis" function to perform PERMANOVA with 999 permutations and Bray–Curtis distances. We accounted for the split-plot design by assigning a unique identifier for "plot" to the "strata" option. We used the function "Betadisper" to test for multivariate homogeneity of group variance. We excluded three species found in fewer than 5% of subplots, each of which was only found in one plot each, from analyses to prevent their outsized effects on ordination outcomes, convergence, and stress levels.

3 | RESULTS

3.1 | Above-ground biomass response to treatments

Counter to our predictions, there was not a significant fire-by-herbivory treatment interaction in either year of the study for total biomass and fire did not affect total biomass in either year. Herbivory treatment was the only significant variable in models assessing total biomass production in both 2019 and 2020 (Table S2; Figure 1). Mean difference between biomass collected in exclosures and herbivore-accessible control plots for all fire treatments was similar in 2019 and 2020 (73 and 96 g/m^2 respectively; p-value < 0.001). For a given fire treatment, exclosures had 216 g/m^2 more biomass than herbivore-accessible subplots in 2020. Fire treatment did not have a significant effect on total herbaceous biomass (Table S2; Figure 1). Mean biomass in 2019 for fire treatment plots was 112.6 ± 12.2 g/m^2 for control, 99.5 ± 8.9 g/m^2 for low energy, and 136.2 ± 19.0 g/m^2 for high energy ($p = 0.378$ for differences between high energy and control and between low energy and control, $p = 0.843$). Mean biomass in 2020 for fire treatment plots was 298.8 ± 35.9 g/m^2 for control, 232.7 ± 26.8 g/m^2 for low-energy fire, and 185.0 ± 25.4 g/m^2 for high-energy fire ($p = 0.071$ for differences between high energy and control and between low energy and control, $p = 0.907$).

Models assessing forb and grass biomass independently showed effects from both herbivore exclosures and high-energy fires. In 2019, herbivory exclosures had 2.6 times more grass biomass than herbivore-accessible subplots (95% confidence interval [CI] = 1.16–5.79; p-value = 0.02) and the high-energy fire plots had 0.43 times less biomass than non-burned controls (95% CI = 0.19–0.97; p-value = 0.041; Tables S3, S4; Figure 2). Forb biomass was not affected by either herbivory treatment or fire treatment in 2019. In 2020, there was a significant herbivory treatment by fire treatment interaction for forb biomass (Table S3, S4; Figure 3). Multiple comparisons (Table S4) showed that high fire energy plots (both exclosures and herbivore-accessible subplots) and non-burned herbivore-accessible subplots had more forb biomass than non-burned exclosures and low energy fire plots (both exclosures and herbivore-accessible subplots).

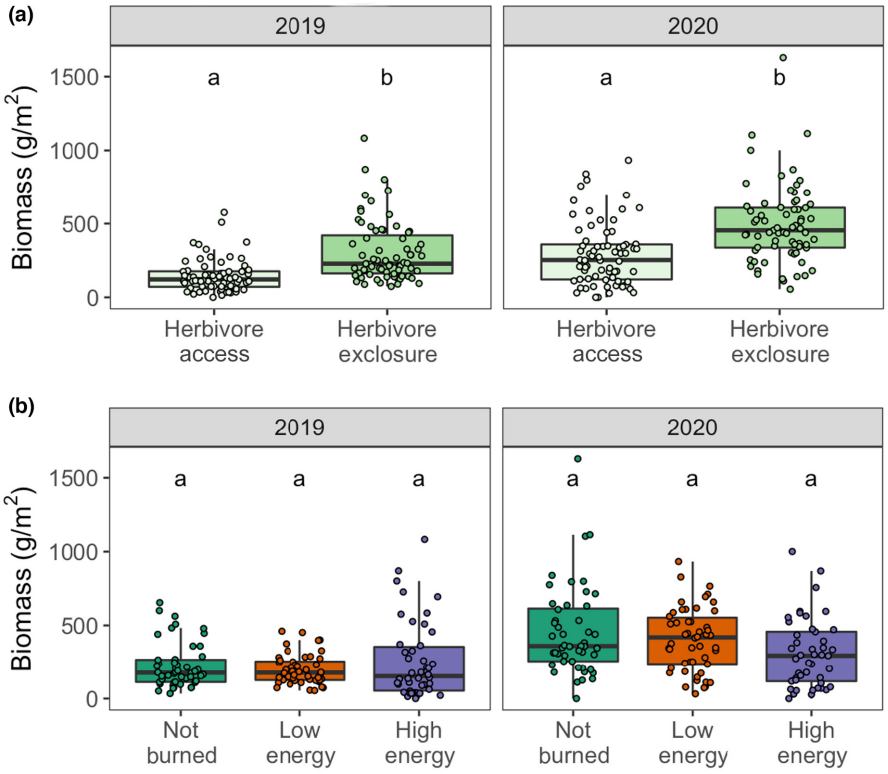

FIGURE 1 Boxplots (median, first, and third quantiles represented) for total biomass by herbivory treatment (a) and fire treatment (b) main effects. There was not a significant interaction between herbivory treatment and fire treatment on total biomass. Letters denote significant treatment differences.

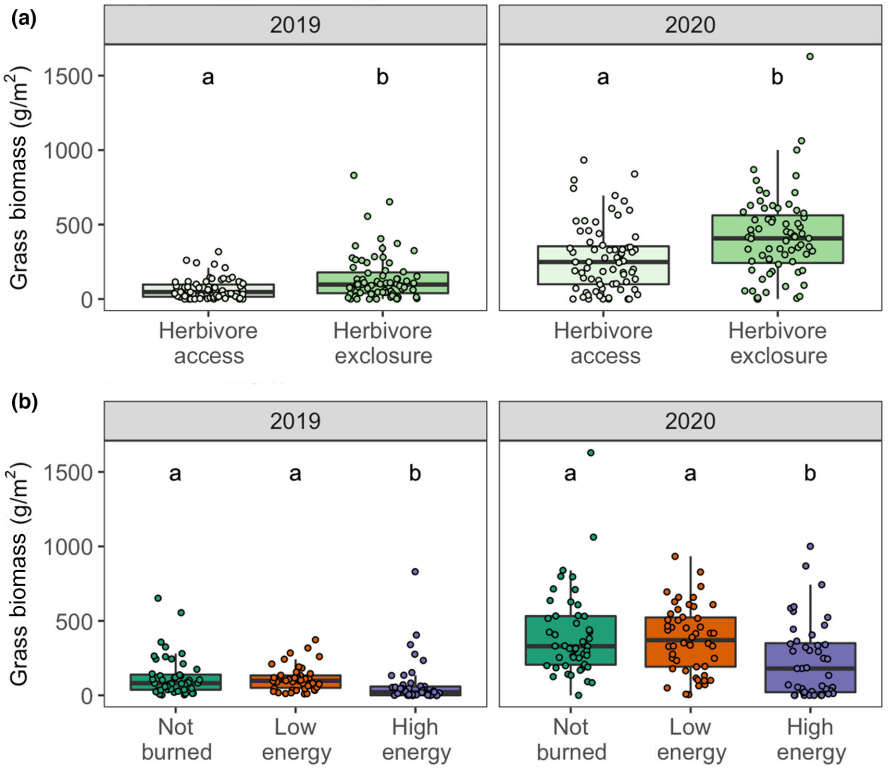

FIGURE 2 Boxplots (median, first, and third quantiles represented) for grass biomass by herbivory treatment (a) and fire treatment (b) main effects. There was not a significant interaction between herbivory treatment and fire treatment on grass biomass. Letters denote significant treatment differences.

3.2 | Plant community composition

Vegetation cover was comprised mainly of grass and forb species; though some succulents and woody debris were present, they were excluded from analysis because they were only present in a few subplots. The most frequent native species recorded were: *Nassella leucotricha* (Texas wintergrass), *Hilaria belangeri* (curly mesquite grass), *Glandularia bipinnatifida* (prairie verbena), and *Cirsium texanum* (Texas thistle). Several non-native grasses and forbs were present in low abundance (<1% cover on average among plots). Relative abundance of the most abundant species is depicted in Table S1.

FIGURE 3 Boxplots (median, first, and third quantiles represented) for forb biomass showing the herbivory treatment by fire treatment interaction. Letters denote significant treatment differences.

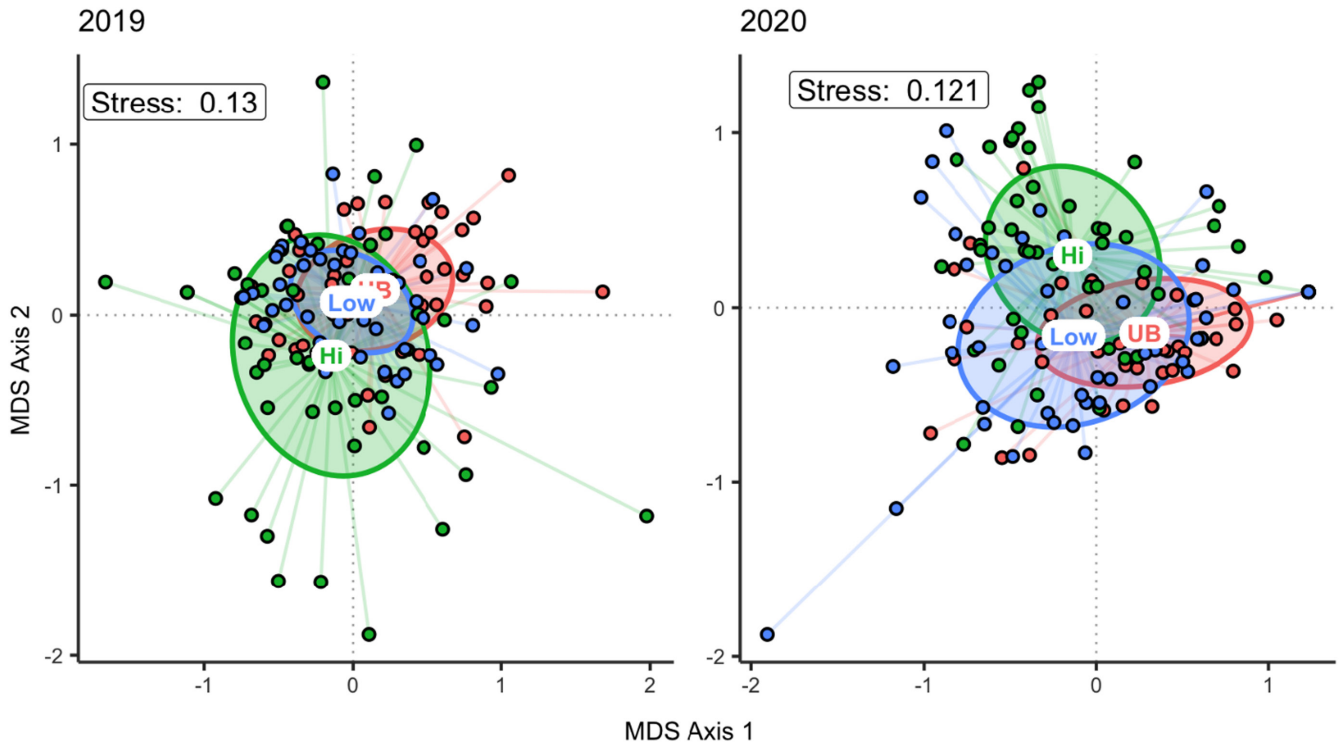

FIGURE 4 Non-metric multidimensional scaling using four axes (only axes 1 and 2 are shown). Points are plots in species space. Plots are color-coded by fire energy treatment (unburned = red, low energy = blue, high energy = green) and each plot is connected to the centroid for its treatment group by a line segment to visually present differences in group variance (overall longer line segments for a group represent more within-group variance). Centroids are located at treatment labels (unburned = UB, low energy = Low, high energy = Hi). Ellipses show one standard deviation for each treatment.

Multivariate tests for homogeneity of treatment variance indicated that in 2019, there were differences in beta diversity among fire treatments, with high-energy plots having the greatest among-plot variability and low-energy plots the least (difference in variability 0.22–0.10, p-value < 0.001; Table S5). However, that difference in variance was short-lived and did not persist in 2020. There was no difference in variance between herbivory treatments in either 2019 or 2020 (Table S5).

There were no differences in community composition in 2019 or 2020 among fire energy treatments or between herbivory treatments and there was no significant interaction between fire energy and herbivore access (Table S2). Ordinations of subplots in species space are depicted in Figure 4. The centroids of each level of fire energy treatment are labeled and each plot is connected to its centroid with line segments to show the range of plot spread over ordination spaces for each level (control, low-, and high-energy fire). There was no difference in community composition among treatments; PERMANOVA indicated that the difference is not significant. In 2019 there is a very slight, but not significant separation of high-energy fire plot centroids from other treatments along the MDS axis 2 (Figure 4) along with several forb species, but there is substantial overlap (Figures S3 and S4). In 2020 all treatments exhibited

substantial overlap with only very slight, insignificant separation of centroids. Low-energy and control plots were slightly more associated with *Nassella leucotricha* and *Eragrostis intermedia* on MDS axis 2, while high-energy plots were slightly more associated with *Verbena hastata* and *Bouteloua trifida* (Figure S4). There were no differences in community composition between herbivory treatments (Figures S5 and S6).

4 | DISCUSSION

Extreme fire is emerging as an important restoration approach in open ecosystems where fire suppression has caused encroachment by woody plants (Scholtz et al., 2022); however, recent increases in the abundance of non-native axis deer throughout the region, which graze more grasses than native white-tailed deer, are having a substantial impact on herbaceous fine-fuel loads (Elliot & Barrett, 1985). This could reduce the capacity for managers to conduct restoration of woody plants and maintenance fires; our study assessed interactive effects of high-energy fire and an exotic deer species on herbaceous plant community biomass and composition. We found that high-intensity fire did not reduce herbaceous biomass or alter plant community composition, but grazing pressure from native and non-native mammalian herbivores reduced above-ground herbaceous biomass.

4.1 | Fire effects on herbaceous biomass

High-energy fires did not reduce total herbaceous biomass either directly or by attracting herbivores to recently burned areas. Extreme prescribed fire has been effective in reducing the density and cover of woody plants in the study region (Twidwell, Fuhlendorf, et al., 2013; Twidwell et al., 2016) and in other semi-arid savannas worldwide (Smit et al., 2010; Scholtz et al., 2022). This type of reduction in cover of woody plants in encroached areas typically leads to increases in herbaceous biomass as grasses and forbs are released from competition from woody plants for light and resources (Wonkka et al., 2016; Bielski et al., 2021). While the reduction in woody plants is considered a positive result of extreme prescribed fire among rangeland managers, there is concern that the high fire energy needed to kill woody resprouting plants can cause mortality of herbaceous plants or indirect effects that reduce herbaceous biomass. This did not occur in our study; herbaceous biomass in high-energy fire plots was not different from that in low-energy or control plots even in the growing season directly following fire. The most abundant species across treatments in our study is *Nassella leucotricha*, which is a cool-season grass preferred by most grazers in the region. *Nassella leucotricha* was equally abundant after high-energy fires as in control and low-energy plots. This is consistent with an assessment of grass bud dynamics for this species (Hiers et al., 2021). In a companion study assessing mortality of grass buds in the same plots, *Nassella leucotricha* experienced minimal bud mortality in high-energy fire plots and recovered within eight months of treatment (Hiers et al., 2021). This suggests that high-energy fires do not have negative repercussions for dominant graminoid species in this system and therefore could be an appropriate restoration approach for reducing resprouting woody plants without diminishing available forage for livestock or fuel for future fires. Other studies assessing high-energy fire applied to reduce woody plants also showed that herbaceous biomass was comparable to that in non-burned grassland in as little as a single growing season following high-energy fire (Twidwell et al., 2012; Arterburn et al., 2018; Bielski et al., 2021).

There was a reduction in grass biomass and an attendant increase in forb biomass in plots after high-energy fire that presents a short-term trade-off for rangeland managers interested in reducing dominance of woody plants to increase grass biomass in the long term. An increase in forb cover is not unusual following summer fires or high-intensity fires. Summer wildfire during an extreme heatwave in the Great Plains, USA, decreased grass cover by 75% and increased forb cover by 50% (Ratajczak et al., 2019). Similarly, forbs increased and displaced grass biomass following summer fires in Illinois, USA (Copeland et al., 2002). Some research has shown that summer fires can suppress C_4 grasses because of direct damage to reproductive structures and meristematic tissue during growth (Howe, 1994; Knapp et al., 2009). However other research suggests that this loss of dominance is the result of bud transition to dormancy, an adaptive response to combined fire and water stress which suggests loss of grass dominance is temporary (Ott & Hartnett, 2012). Our high-energy summer fires might have had a slightly stronger negative effect on C_4 grasses than low-energy summer fires, inflicting more direct damage on them, or might have caused bud transitions to dormancy. In addition, grass buds can be damaged by high-energy fires, especially in rhizomatous species with shallow buds, such as *Hilaria belangeri*, which is a dominant species at the study site (Hiers et al., 2021, but see Russell et al., 2015 where summer fire did not cause grass bud mortality). Whether the result of adaptive strategy or injury from fire, forbs benefit from this reduction in competition from grasses and resultant increases in light and germination sites (Blair, 1997; Howe, 2000; Ansley & Castellano, 2007; Ansley et al., 2010).

While an increase in forbs can be positive for pollinators and wildlife species, it could be undesirable to livestock producers focused on maximizing grass productivity. However, this increase in forb dominance is likely transient. A strong evolutionary history with fire for grasses in this region suggests short-term shifts in dominance resulting from adaptive responses, not long-term compositional change from fire-related damage to grasses (Ripley et al., 2015). For instance, even after severe forest fires in fire-adapted ecosystems, compositional shifts in herbaceous species were found to be short-lived, with increases in forbs of 1–3 years, which generally were replaced by graminoids over the 10 years following fire (Abella & Fornwalt, 2015). In our study region, there were no compositional shifts in the community relative to non-burned savanna 12 years following high-intensity fire despite an immediate increase in forb richness (Taylor et al., 2012). The perennial grass species in this system

tend to be resilient to fire, returning to pre-fire ranges in biomass relatively quickly even after wildfires (Donovan et al., 2020); therefore, managers need to weigh a short-term shift in proportion of biomass comprised of grasses versus forbs to long-term losses in total biomass as encroachment of woody plants proceeds. This trade-off might not be a ubiquitous result of high-energy fire. For instance, summer fires in the northern Great Plains increased dominance of native grass species and did not decrease biomass even in the short term (Vermeire & Russell, 2018).

4.2 | Fire effects on herbaceous plant community composition

Plant community composition was not influenced by fire. Low-energy, high-energy, and unburned plots had a high degree of overlap in community composition with only a very slight differentiation in the location of the centroids for high-energy plots in 2019 and for all treatments in 2020, which was related to a few forb species; these shifts were not statistically significant. Differences in fire intensity have been shown to modulate direct fire effects on plants (Moreno & Oechel, 1994) and indirect impacts to soil chemistry, soil microbes, and local microclimate, as well as direct damage to plants (Ewing & Engle, 1988; Verma & Jayakumar, 2012; Reinhart et al., 2016). This means that fire intensity typically influences plant–soil feedbacks and competitive interactions which are idiosyncratic across species (Hobbs & Yates, 2003; Brandt et al., 2009). We saw no indication of this fire effect in our study.

The slight and non-significant difference in forb composition likely drove the increase in forb biomass in the high-energy fire plots as the forb species associated with the slightly shifted centroids for high-energy fires included forbs that produce substantial biomass such as *Solanum* spp. and *Thymophylla pentachaeta*, while smaller forbs such as *Hordeum pusillum* and *Allium drummondii* were associated with centroids for low-energy and control plots. Consistent with the increase in forb biomass and decreased grass biomass in high-energy fire plots, in 2020 high-energy fires were slightly (not significantly) more associated with forbs (e.g. *Verbena hastata*, *Solanum* spp.), while low-energy fire and non-burned controls were slightly (not significantly) more associated with grasses (e.g. *Nassella leucotricha* and *Eragrostis intermedia*). These slight differences in community composition are also likely short-lived as an assessment of extreme prescribed fire in this region showed no differences in herbaceous community composition 12 years after fire (Taylor et al., 2012).

All fire treatments exhibited transient differences in beta diversity with high-energy fires resulting in the greatest variability among plots, low-energy fires showing intermediate levels, and unburned controls having the lowest. Fire reduces plant cover, can cause direct mortality of some plants, and provides a pulse of resources, creating niches for new plants to fill (McGranahan & Wonkka, 2021). Availability of new niche space scales with fire intensity and subsequent severity (Moradizadeh et al., 2020); in our study, high-energy fires likely provided more available niche space for new plants to occupy, increasing immediate beta diversity. However, with time successional dynamics drive a return to pre-fire levels of diversity, as observed in our study with convergent beta diversity among treatments in the second year following fire. Similar short-term increases in plant diversity have occurred in other grasslands following fire (Morgan & Lunt, 1999; Guo, 2001; Safford & Harrison, 2004; Overbeck et al., 2005).

4.3 | Interactive effect between fire and grazing on biomass

Counter to our initial prediction, herbivore attraction to burned areas did not result in lower biomass on burned plots that were accessible to herbivores than on non-burned plots that were accessible to herbivores. Herbivore attraction to recently burned areas (the magnet effect of fire) is well established in the literature (Fuhlendorf & Engle, 2004; Archibald et al., 2005; Koerner & Collins, 2013; Burkepile et al., 2016). Recently burned areas attract grazing animals with high-quality regrowth, and can be essential for nutrient acquisition during drought or the dry season (Yoganand & Owen-Smith, 2014; Spiess et al., 2020). In fact, time since fire has been shown to be a primary factor for site selection by grazers and browsers—more influential even than slope or distance to water (Allred et al., 2011). It is likely that the magnet effect did not manifest in our study because of plot size and configuration. In order to have a well-replicated study with randomly assigned treatments we used small plots and burned plots were interspersed among controls. Our 10 × 10 m plots were likely too small an area in aggregate to keep herbivore focus entirely within the burned plots when interspersed with non-burned plots that herbivores had to move through to access burned areas. While herbivores might have been attracted to the area generally because of the burned plots, they likely grazed in both burned and non-burned plots since they were small and adjacent. Managers should consider that the magnet effect could cause a greater loss of biomass to herbivores attracted by fire if fires are applied to larger areas.

4.4 | Herbivore impacts on biomass and community composition.

Our findings show that mammalian wildlife, most likely recently introduced axis deer (the only wild large mammalian grazing herbivore in the region), in the study area is reducing herbaceous biomass that would otherwise be available to livestock or as fuel for fire to control woody plants. The introduction of exotic wildlife to the Texas Edwards Plateau in the 1930s has caused a hierarchical shift in dominant ungulate species throughout the region (Karlin & Rankin, 2016). Dietary differences between currently dominant exotic deer and previously dominant native deer impact forage and fuels while also affecting land management decisions involving domesticated livestock

(Elliot & Barrett, 1985). Indian axis deer have become increasingly common because of their ability to shift browsing and grazing patterns depending on forage availability (Elliot & Barrett, 1985). It is posited that axis deer and white-tailed deer will not be able to coexist indefinitely because axis deer are competitively dominant, forcing native deer into marginal habitat (Faas & Weckerly, 2010). This displacement of browsers of woody plants with a primarily grazing species could exacerbate the spread of woody plants by reducing browsing impacts on shrubs and seedlings and limiting the potential to conduct prescribed extreme fires needed to induce woody-plant mortality by limiting fine fuel.

5 | CONCLUSIONS

Using extreme prescribed fire for reduction of woody plants in shrub-encroached semi-arid savannas with exotic mammalian grazers presents some trade-offs for managers in the short term regarding herbaceous biomass. High-energy fire treatments did not deleteriously affect total vegetation biomass either directly by reducing herbaceous biomass, or indirectly by increasing herbivore attraction to burned areas. However, high-energy fires lowered grass biomass and increased forb biomass two years after high-energy fires. Our treatments represent the worst case for impacts to grass biomass. They are extreme in terms of soil heating given that we added dried juniper piles as fuel, which resulted in long residence times. Heat generation near the ground in a pile where woody material is burning leads to long residence times and maximal heat transfer to the soil. In standing and live vegetation with low fuel moisture, which is how the majority of management fires in the region are conducted, most of the heat will go up as convection and soil heating will be less extreme. There is likely to be less of a shift from grass to forb biomass in typical woody-plant management burns, which are conducted without fuel addition. In addition, given findings from long-term assessments of extreme prescribed fire on grass biomass, this is likely a transient effect; however, even short-term reductions of grass biomass in areas where grazing livestock are competing with wildlife grazers could impact grazing management. Therefore, there is a trade-off between long-term increases in forage from reductions of woody plants and short-term shifts in functional group biomass when using high-energy restoration fires. Mammalian herbivore grazing even in the absence of fire can substantially reduce herbaceous biomass. This has implications for management of open ecosystems both from a perspective of wildlife competition with cattle and availability of fuel for prescribed fires to reduce abundance of woody plants. A shift in dominance from native browsers to non-native grazing species could represent a substantial loss in capacity to conduct any prescribed fires necessary for reduction of woody plants in encroached rangelands. Managers should consider the potential for wildlife grazers to reduce fine fuel below levels sufficient for a woody-plant reduction fire. High fencing or exotic herbivore control might be necessary to limit wildlife grazers.

AUTHOR CONTRIBUTIONS

William E. Rogers, Alexandra G. Lodge, Carissa L. Wonkka, Matthew B. Dickinson, Dirac Twidwell, Morgan L. Treadwell, and Kathleen L. Kavanagh conceived the ideas and obtained funding; William E. Rogers, Alexandra G. Lodge, Carissa L. Wonkka, Matthew B. Dickinson, Dirac Twidwell, Morgan L. Treadwell, Kathleen L. Kavanagh, Heath D. Starns and Douglas R. Tolleson designed methodology and implemented fire treatments; Virginia D. Preiss, Alexandra G. Lodge, and William E. Rogers implemented herbivory treatments and collected the data; Virginia D. Preiss and Carissa L. Wonkka analyzed the data; Virginia D. Preiss, William E. Rogers, Carissa L. Wonkka, and Devan A. McGranahan led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

The authors thank Q. A. Heirs, L. Z. Culpepper, J. Lara, A. Labrecque, H. J. Hannusch, J. Gaster, C. Ferguson, W. Tanton, C. Fortenberry, B. O'Connor, J. Walker, N. Garza, R. Moen, T. W. Boutton, and A. P. Smith for technical assistance. This research was funded by the United States Department of Agriculture-Bureau of Land Management Joint Fire Sciences Program Project #17-1-04-7.

FUNDING INFORMATION

Texas A&M University, United States Department of Agriculture-Bureau of Land Management Joint Fire Sciences Program Project #17-1-04-7, and the Department of Ecosystem Science and Management's Savanna Long Term Research and Education Initiative (SLTREI).

CONFLICT OF INTEREST STATEMENT

Authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are publicly available via the Ag Data Commons (Preiss et al., 2023).

CODE AVAILABILITY

The R code used in all analyses in this study is available from the corresponding author upon reasonable request.

ORCID

Carissa L. Wonkka https://orcid.org/0000-0003-3901-5261
William E. Rogers https://orcid.org/0000-0002-3407-1101

REFERENCES

Abella, S.R. & Fornwalt, P.J. (2015) Ten years of vegetation assembly after a north American mega fire. *Global Change Biology*, 21, 789–802.
Allred, B.W., Fuhlendorf, S.D., Engle, D.M. & Elmore, R.D. (2011) Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, 1, 132–144.
Andruk, C.M., Schwope, C. & Fowler, N.L. (2014) The joint effects of fire and herbivory on hardwood regeneration in Central Texas woodlands. *Forest Ecology and Management*, 334, 193–200.

Ansley, R.J., Boutton, T.W., Mirik, M., Castellano, M.J. & Kramp, B.A. (2010) Restoration of C4 grasses with seasonal fires in a C3/C4 grassland invaded by Prosopis glandulosa, a fire-resistant shrub. *Applied Vegetation Science*, 13, 520–530.

Ansley, R.J. & Castellano, M.J. (2007) Texas Wintergrass and Buffalograss response to seasonal fires and clipping. *Rangeland Ecology & Management*, 60, 154–164.

Archer, S. (1989) Have southern Texas savannas been converted to woodlands in recent history? *The American Naturalist*, 134, 545–561.

Archer, S.R., Andersen, E.M., Predick, K.I., Schwinning, S., Steidl, R.J. & Woods, S.R. (2017) Woody plant encroachment: causes and consequences. In: Briske, D.D. (Ed.) *Rangeland Systems: Processes, Management and Challenges*. Cham, Switzerland: Springer, pp. 25–84.

Archibald, S., Bond, W.J., Stock, W.D. & Fairbanks, D.H.K. (2005) Shaping the landscape: fire-grazer interactions on an African savanna. *Ecological Applications*, 15, 96–109.

Arterburn, J.R., Twidwell, D., Schacht, W.H., Wonkka, C.L. & Wedin, D.A. (2018) Resilience of Sandhills grassland to wildfire during drought. *Rangeland Ecology & Management*, 71, 53–57.

Barnes, P.W. & Archer, S. (1999) Tree-shrub interactions in a subtropical savanna parkland: competition or facilitation? *Journal of Vegetation Science*, 10, 525–536.

Bielski, C.H., Scholtz, R., Donovan, V.M., Allen, C.R. & Twidwell, D. (2021) Overcoming an "irreversible" threshold: a 15-year fire experiment. *Journal of Environmental Management*, 291, 112550.

Blair, J.M. (1997) Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. *Ecology*, 78, 2359–2368.

Bond, W.J. (2022) Out of the shadows: ecology of open ecosystems. *Plant Ecology and Diversity*, 14, 205–222. Available from: https://doi.org/10.1080/17550874.2022.2034065

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20, 387–394.

Bowman, D.M.J.S., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M. et al. (2011) The human dimension of fire regimes on earth. *Journal of Biogeography*, 38, 2223–2236.

Brandt, A.J., Seabloom, E.W. & Hosseini, P.R. (2009) Phylogeny and provenance affect plant–soil feedbacks in invaded California grasslands. *Ecology*, 90, 1063–1072.

Burkepile, D.E., Thompson, D.I., Fynn, R.W.S., Koerner, S.E., Eby, S., Govender, N. et al. (2016) Fire frequency drives habitat selection by a diverse herbivore guild impacting top–down control of plant communities in an African savanna. *Oikos (Copenhagen, Denmark)*, 125, 1636–1646.

Copeland, T.E., Sluis, W. & Howe, H.F. (2002) Fire season and dominance in an Illinois tallgrass prairie restoration. *Restoration Ecology*, 10, 315–323.

Demarais, S., Osborn, D.A. & Jackley, J.J. (1990) Exotic big game: a controversial resource. *Rangelands*, 12, 121–125.

Donovan, V.M., Twidwell, D., Uden, D.R., Tadesse, T., Wardlow, B.D., Bielski, C.H. et al. (2020) Resilience to large, "catastrophic" wildfires in North America's grassland biome. *Earth's Future*, 8, e2020EF001487.

Elliot, H.W. & Barrett, R.H. (1985) Dietary overlap among axis, fallow, and black-tailed deer and cattle. *Journal of Range Management*, 38, 435–439.

Engle, D.M., Coppedge, B.R. & Fuhlendorf, S.D. (2008) From the dust bowl to the green glacier: human activity and environmental change in Great Plains grasslands: a dynamic vegetation type. In: Van Auken, O.W. (Ed.) *Western north American Juniperus communities*. New York, NY: Springer, pp. 253–271.

Ewing, A. & Engle, D. (1988) Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist*, 120, 212.

Faas, C.J. & Weckerly, F.W. (2010) Habitat interference by Axis deer on white-tailed deer. *The Journal of Wildlife Management*, 74, 698–706.

Fite, G.C. (1977) Great Plains farming: a century of change and adjustment. *Agricultural History*, 51, 244–256.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N. et al. (2012) AD model builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27, 233–249.

Fuhlendorf, S.D. & Engle, D.M. (2004) Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology*, 41, 604–614.

Fuhlendorf, S.D., Fynn, R.W., McGranahan, D.A. & Twidwell, D. (2017) Heterogeneity as the basis for rangeland management. In: *Rangeland systems*. Cham: Springer, pp. 169–196.

Guo, Q. (2001) Early post-fire succession in California chaparral: changes in diversity, density, cover and biomass. *Ecological Research*, 16, 471–485.

Guyette, R.P., Stambaugh, M.C., Dey, D.C. & Muzika, R.-M. (2012) Predicting fire frequency with chemistry and climate. *Ecosystems*, 15, 322–335.

Hartnett, D.C., Steuter, A.A. & Hickman, K.R. (1997) Comparative ecology of native and introduced ungulates. In: Knopf, F.L. & Samson, F.B. (Eds.) *Ecology and conservation of Great Plains vertebrates*. New York, NY: Springer, pp. 72–101.

Hempson, G.P., Archibald, S. & Staver, C. (2019) Fire and browsers in savannas: traits, interactions, and continent-level patterns. In: Scogings, P.F. & Sankaran, M. (Eds.) *Savanna Woody plants and large herbivores*. Hoboken, NJ, USA: John Wiley & Sons, pp. 439–468.

Hiers, Q.A., Treadwell, M.L., Dickinson, M.B., Kavanagh, K.L., Lodge, A.G., Starns, H.D. et al. (2021) Grass bud responses to fire in a semi-arid savanna system. *Ecology and Evolution*, 11, 6633.

Hobbs, R.J. & Yates, C.J. (2003) Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. *Australian Journal of Botany*, 51, 471–488.

Howe, H.F. (1994) Managing species diversity in tallgrass prairie: assumptions and implications. *Conservation Biology*, 8, 691–704.

Howe, H.F. (2000) Grass response to seasonal burns in experimental plantings. *Rangeland Ecology & Management/Journal of Range Management Archives*, 53, 437–441.

Karlin, M.L. & Rankin, J. (2016) Collecting baseline data on wildlife diversity and abundance in a fire-suppressed Edwards plateau woodland community, mountain home, TX. *Texas Journal of Science*, 68, 57–73.

Knapp, E.E., Estes, B.L. & Skinner, C.N. (2009) *Ecological effects of prescribed fire season: a literature review and synthesis for managers*. Pacific Southwest Research Station, Albany, CA: USDA Forest Service.

Koerner, S.E. & Collins, S.L. (2013) Small-scale patch structure in north American and south African grasslands responds differently to fire and grazing. *Landscape Ecology*, 28, 1293–1306.

Krausman, P.R. & Bleich, V.C. (2013) Conservation and management of ungulates in North America. *International Journal of Environmental Studies*, 70, 372–382.

Lenth, R. (2022) Emmeans: estimated marginal means, aka least-squares means. R Package Version 1.7.2.

Limb, R.F., Engle, D.M., Alford, A.L. & Hellgren, E.C. (2010) Tallgrass prairie plant community dynamics along a canopy cover gradient of eastern redcedar (Juniperus virginiana L.). *Rangeland Ecology & Management*, 63, 638–644.

McGranahan, D.A. (2008) Managing private, commercial rangelands for agricultural production and wildlife diversity in Namibia and Zambia. *Biodiversity and Conservation*, 17, 1965–1977.

McGranahan, D.A., Govender, N., Scholtz, R. & Kirkman, K. (2022) Sanctioned burning in sub-Saharan Africa. In: Weir, J.R. & Scasta, J.D. (Eds.) *Global application of prescribed fire*. Victoria, Auatralia: CSIRO PUBLISHING, 50.

McGranahan, D.A., Hovick, T.J., Elmore, R.D., Engle, D.M. & Fuhlendorf, S.D. (2018) Moderate patchiness optimizes heterogeneity, stability,

and beta diversity in Mesic grassland. *Ecology and Evolution*, 8, 5008–5015.
McGranahan, D.A. & Wonkka, C.L. (2021) *Ecology of fire-dependent ecosystems: wildland fire science, policy, and management*. Boca Raton, FL: CRC Press.
Moradizadeh, H., Heydari, M., Omidipour, R., Mezbani, A. & Prévosto, B. (2020) Ecological effects of fire severity and time since fire on the diversity partitioning, composition and niche apportionment models of post-fire understory vegetation in semi-arid oak forests of Western Iran. *Ecological Engineering*, 143, 105694.
Moreno, J.M. & Oechel, W.C. (Eds.). (1994) *The role of fire in Mediterranean-type ecosystems*. New York, NY: Springer-Verlag.
Morgan, J.W. & Lunt, I.D. (1999) Effects of time-since-fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. *Biological Conservation*, 88, 379–386.
Mueller-DomBois, D. & Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. New York, New York,USA: John Wiley and Sons.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2020) Vegan: community ecology package.
Ott, J.P. & Hartnett, D.C. (2012) Higher-order bud production increases tillering capacity in the perennial caespitose grass Scribner's panicum (*Dichanthelium oligosanthes*). *Botany*, 90, 884–890.
Overbeck, G.E., Müller, S.C., Pillar, V.D. & Pfadenhauer, J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science*, 16, 655–664.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2021) nlme: Linear and nonlinear mixed effects models.
Preiss, V.D., Wonkka, C.L., McGranahan, D.A., Lodge, A.G., Dickinson, M.B., Kavanagh, K.L., et al. (2023) Data from: Exotic herbivores and fire energy drive standing herbaceous biomass but do not alter compositional patterns in a semiarid savanna ecosystem. *Ag Data Commons*. Available from: https://doi.org/10.15482/USDA.ADC/1529770
R Core Team. (2021) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
Ratajczak, Z., Churchill, A.C., Ladwig, L.M., Taylor, J.H. & Collins, S.L. (2019) The combined effects of an extreme heatwave and wildfire on tallgrass prairie vegetation. *Journal of Vegetation Science*, 30, 687–697.
Reinhart, K.O., Dangi, S.R. & Vermeire, L.T. (2016) The effect of fire intensity, nutrients, soil microbes, and spatial distance on grassland productivity. *Plant and Soil*, 409, 203–216.
Ripley, B., Visser, V., Christin, P.-A., Archibald, S., Martin, T. & Osborne, C. (2015) Fire ecology of C3 and C4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology*, 96, 2679–2691.
Ripple, W.J., Newsome, T.M., Wolf, C., Dirzo, R., Everatt, K.T., Galetti, M. et al. (2015) Collapse of the world's largest herbivores. *Science Advances*, 1, e1400103.
Russell, M.L., Vermeire, L.T., Ganguli, A.C. & Hendrickson, J.R. (2015) Season of fire manipulates bud bank dynamics in northern mixed-grass prairie. *Plant Ecology*, 216, 835–846.
Ruthven, D.C., III. (2001) Herbaceous vegetation diversity and abundance beneath honey mesquite (*Prosopis glandulosa*) in the South Texas plains. *The Texas Journal of Science*, 53, 171.
Safford, H.D. & Harrison, S. (2004) Fire effects on plant diversity in serpentine vs. sandstone chaparral. *Ecology*, 85, 539–548.
Scholtz, R., Donovan, V.M., Strydom, T., Wonkka, C., Kreuter, U.P., Rogers, W.E. et al. (2022) High-intensity fire experiments to manage shrub encroachment: lessons learned in South Africa and the United States. *African Journal of Range and Forage Science*, 39, 148–159.
Smit, I.P., Asner, G.P., Govender, N., Kennedy-Bowdoin, T., Knapp, D.E. & Jacobson, J. (2010) Effects of fire on woody vegetation structure in African savanna. *Ecological Applications*, 20, 1865–1875.
Spiess, J., McGranahan, D.A., Geaumont, B. & Hovick, T.J. (2020) Patch-burning buffers forage resources and livestock performance to mitigate drought in the northern Great Plains. *Rangeland Ecology & Management*, 73(4), 473–481.
Starns, H.D., Taylor, C.A., Garza, N.E. & Tolleson, D.R. (2020) Effects of fire exclusion on previously fire-managed semiarid savanna ecosystem. *Rangeland Ecology & Management*, 73, 93–96.
Starns, H.D., Wonkka, C.L., Dickinson, M.B., Lodge, A.G., Treadwell, M.L., Kavanagh, K.L. et al. (2022) Prosopis glandulosa persistence is facilitated by differential protection of buds during low-and high-energy fires. *Journal of Environmental Management*, 303, 114141.
Taylor, C.A., Twidwell, D., Garza, N.E., Rosser, C., Hoffman, J.K. & Brooks, T.D. (2012) Long-term effects of fire, livestock herbivory removal, and weather variability in Texas semiarid savanna. *Rangeland Ecology & Management*, 65, 21–30.
Tolleson, D.R., Rhodes, E.C., Malambo, L., Angerer, J.P., Redden, R.R., Treadwell, M.L. et al. (2019) Old school and high tech: a comparison of methods to quantify Ashe Juniper biomass as fuel or forage. *Rangelands*, 41, 159–168.
Twidwell, D., Fuhlendorf, S.D., Taylor, C.A., Jr. & Rogers, W.E. (2013) Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands. *Journal of Applied Ecology*, 50, 603–613.
Twidwell, D., Rogers, W.E., Fuhlendorf, S.D., Wonkka, C.L., Engle, D.M., Weir, J.R. et al. (2013) The rising Great Plains fire campaign: citizens' response to woody plant encroachment. *Frontiers in Ecology and the Environment*, 11, e64–e71.
Twidwell, D., Rogers, W.E., McMahon, E.A., Thomas, B.R., Kreuter, U.P. & Blankenship, T.L. (2012) Prescribed extreme fire effects on richness and invasion in coastal prairie. *Invasive Plant Science and Management*, 5, 330–340.
Twidwell, D., Rogers, W.E., Wonkka, C.L., Taylor, C.A., Jr. & Kreuter, U.P. (2016) Extreme prescribed fire during drought reduces survival and density of woody resprouters. *Journal of Applied Ecology*, 53, 1585–1596.
Verma, S. & Jayakumar, S. (2012) Impact of forest fire on physical, chemical and biological properties of soil: a review. *Proceedings of the International Academy of Ecology and Environmental Sciences*, 2, 168.
Vermeire, L. & Russell, M. (2018) Seasonal timing of fire alters biomass and species composition of northern mixed prairie. *Rangeland Ecology & Management*, 71, 714–720.
Wonkka, C.L., Twidwell, D., West, J.B. & Rogers, W.E. (2016) Shrubland resilience varies across soil types: implications for operationalizing resilience in ecological restoration. *Ecological Applications*, 26, 128–145.
Yoganand, K. & Owen-Smith, N. (2014) Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, 37, 969–982.

SUPPORTING INFORMATION

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

Appendix S1. Additional methods and results figures and tables.

How to cite this article: Preiss, V.D., Wonkka, C.L., McGranahan, D.A., Lodge, A.G., Dickinson, M.B., Kavanagh, K.L. et al. (2023) Exotic herbivores and fire energy drive standing herbaceous biomass but do not alter compositional patterns in a semiarid savanna ecosystem. *Applied Vegetation Science*, 26, e12749. Available from: https://doi.org/10.1111/avsc.12749