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ARTICLE

Native megafauna (*Bison bison*) act as a surprising inhibitor of cedar tree expansion in a Great Plains grassland

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Abstract

In the Central Great Plains of North America, fire suppression is causing transitions from grasslands to shrublands and woodlands. This woody encroachment alters plant community composition, decreases grassland biodiversity, undermines key ecosystem services, and is difficult to reverse. How native grazers affect woody encroachment is largely unknown, especially compared to domesticated grazers. Bison were once the most widespread megafauna in North America and are typically categorized as grazers, with negative effects on grasses that indirectly benefit woody plants. However, bison can negatively impact woody plants through occasional browsing and mechanical disturbance. This study reports on a 30-year experiment at Konza Prairie Biological Station, a mesic grassland in the Central Great Plains of North America, under fire suppression and experimental presence/absence of bison. Based on remote sensing, deciduous tree canopy cover was lower with bison (6% grazed vs. 16% ungrazed). Shrub land cover showed no difference (42% grazed vs. 41% ungrazed), while herbaceous land cover was higher with bison (51% grazed vs. 40% ungrazed). Evergreen tree canopy cover (*Juniperus virginiana* L.), which decreases biodiversity and increases wildfire risk, was approximately 0% with bison compared to 4% without bison. In the survival trial of *J. virginiana* seedlings, we found a 40% overwinter mortality with bison, compared to 5% mortality without bison. Compared to ungrazed areas, native plant species richness was 97% and 38% higher in bison-grazed uplands and lowlands, respectively. Species evenness and Shannon's index were higher in the bison treatment in uplands, but not in lowlands. Bison affected community composition, resulting in higher cover of short grass species and lower tree cover. While grazers are generally assumed to favor woody plants, we found that bison had the opposite effect at low fire frequencies. We argue that the large size of bison and their behaviors account for this pattern, including trampling, horning, and occasional browsing. From a conservation perspective, bison might hamper tree expansion and increase plant diversity in tallgrass prairies and similar grasslands.

KEYWORDS
alternative stable states, diversity, fire, long-term experiments, resilience, rewilding, tallgrass prairie, woody plant expansion

INTRODUCTION

Woody encroachment—the expansion of woody plants into non-wooded areas—is one of the most acute threats to grasslands and savannas today, causing decreases in grassland biodiversity (Engle et al., 2008; Silber et al., 2024; Wieczorkowski & Lehmann, 2022), streamflow (Dodds et al., 2023; Huxman et al., 2005; Keen et al., 2022), and declines in forage for grazers (Anadón et al., 2014; Morford et al., 2022). Large grazers are typically thought to enhance woody plant encroachment (Bond, 2008; Roques et al., 2001; Scholes & Archer, 1997) by increasing woody seed dispersal (Bakker et al., 2016) and reducing grass dominance, with cascading effects like weaker competitive effects from grasses and less intense fires (Holdo et al., 2009; Van Auken, 2009). Evidence of grazers favoring woody encroachment is common globally (e.g., Archer et al., 2017; Koch et al., 2022; Scholes & Archer, 1997; Van Auken, 2009). In North American grasslands, most work on this topic has focused on the effects of domesticated cattle on woody encroachment (Archer, 1994, Briggs et al., 2002; Madany & West, 1983) rather than on native megafauna, such as the North American bison (*Bison bison*). This represents a knowledge gap in our understanding of these grasslands, which have coevolved with bison and other native megafauna for thousands of years (Flores, 2016; Strömberg, 2011).

Climate, fire, and grazing are pivotal in shaping the structure and function of grasslands and savannas (Fuhlendorf et al., 2009; Scholes & Archer, 1997; Strömberg, 2011). Frequent fire removes litter and kills fire-sensitive stems, favoring grasses over woody plants, altering plant community composition, and reducing woody plant encroachment (Van Auken, 2009). Grazers often have the opposite effect, reducing the abundance of palatable grasses, decreasing the competitive pressure from grasses, and lowering fuel loads, which allows more woody plants to become established (Bond, 2008; Holdo et al., 2009). Some grazers also increase heterogeneity by intensively grazing certain areas, creating a mosaic of patches with differing fuel loads and fire intensity (Adler et al., 2001; Bond, 2008; Roques et al., 2001; Scholes & Archer, 1997). Fire and grazers can effectively "compete" with each other—frequently burned areas leave less forage for grazers, whereas heavily grazed areas burn less intensely, if at all (Archibald & Hempson, 2016). However, fires also attract grazers (Fuhlendorf et al., 2009; Raynor et al., 2016). Understanding the effects of fire and grazers is crucial, particularly in the face of global environmental changes such as woody encroachment.

Since the Last Glacial Maximum, fire and grazing have varied across the Great Plains of North America (Axelrod, 1985; Guyette et al., 2015; Stambaugh et al., 2006, 2013). Before European arrival, fire was common throughout much of the eastern Great Plains due to frequent ignitions by Native Americans to attract game and by natural causes such as lightning (Courtwright, 2011; Roos et al., 2018; Stambaugh et al., 2013). In our specific study region, the Flint Hills of the Central Great Plains, fire intervals typically averaged every 3–5 years, with occasional longer intervals (Allen & Palmer, 2011; Stambaugh et al., 2013). Today, fire intervals vary from burning every 1–2 years to complete fire suppression (>40 years without fire), with complete suppression accounting for about half of the grassland area in the Flint Hills (Ratajczak et al., 2016; Scholtz & Twidwell, 2022). This kind of fire suppression is common throughout many ecoregions in the Great Plains (Chen et al., 2023).

Historically, megafauna were an important component of most grasslands (Galetti et al., 2018; Ripple et al., 2015; Svenning et al., 2016a). In the Great Plains of North America, bison were abundant and widespread, especially in open grassland habitats, but also in wooded habitats (Martin et al., 2023; Shaw, 1995; Wendt et al., 2023). In the late 1800s, humans nearly hunted bison to extinction, with bison numbers dwindling to fewer than ~1000 by 1890 (Hornaday, 1889; Isenberg, 2020). Bison in North America now exceed 400,000, with approximately 20,000 in conservation herds (Freese et al., 2007; Martin et al., 2021; Sanderson et al., 2008). As these reintroductions continue, we need empirical studies that can project their potential impacts in the context of ecosystems that now exist in an altered global change context, the Anthropocene (Rubenstein & Rubenstein, 2016; Svenning et al., 2016a, 2016b). This includes large-scale pressures, such as greater atmospheric CO_2, invasion pressures from non-native species, and land use changes, such as habitat fragmentation, and in many places, less frequent prescribed fire.

The effects of grazing and fire on grasslands in the Great Plains have been well studied (e.g., Collins & Smith, 2006; Hartnett et al., 1996; McMillan et al., 2019). However, research on the interaction between grazers and woody plant encroachment remains limited, with most studies primarily concentrating on the effects of domesticated large grazers, such as cattle, within ecosystems subject to frequent burning (typical fire intervals from 1 to 4 years) (e.g., Briggs et al., 2005; Ratajczak et al., 2014). The notable exception is more mountainous areas, such as Yellowstone National Park (e.g., Beschta et al., 2020; Painter et al., 2023). In mesic grasslands such as the Central Great Plains, we have few studies on how native grazers impact grasslands in the absence or near absence of fire (see Briggs et al., 2005; Ratajczak et al., 2014; Twidwell, Fuhlendorf, et al., 2013; Twidwell, Rogers, et al., 2013, for reviews). Until recently, we would have assumed that bison promote woody encroachment because their diet was thought to be almost purely graminoids in the Central Great Plains (Griffith et al., 2017; Raynor et al., 2015, 2016). However, high-throughput sequencing has revealed that bison dung contains some non-graminoids, including woody plants (Bergmann et al., 2015; Craine, 2021; Craine et al., 2015), suggesting that although bison are often categorized as grazers, they might supplement their diet with small amounts of forbs and woody plants. Some paleo diet reconstructions support this argument (Griffith et al., 2017; Rivals et al., 2007). While graminoids are the overwhelming portion of bison diet (Griffith et al., 2017; Raynor et al., 2016), this browsing, along with woody mortality by trampling and scratching (Coppedge & Shaw, 1997), could potentially limit woody plant expansion if these effects outweigh grazing of grasses. For instance, work in African savannas has shown that many large grazers promote grazing lawns—areas of high grazer activity and forage quality (Hempson et al., 2015). These areas tend to have low tree recruitment due to high trample damage (Voysey et al., 2021), and bison can create similar grazing lawns (Towne et al., 2005). These examples underscore that the effects of grazers and megafauna are often complex (Galetti et al., 2018), highlighting the need for further research on their net effects on woody plant dynamics.

Woody encroachment is not the only conservation threat facing grasslands; shifts in herbaceous plant community composition are also critical. Even if native grazers reduce woody encroachment, it is unclear how they will alter the remaining grassland matrix. Grazing by large ungulates can enhance or diminish biodiversity depending on grazer identity, behavior, management decisions (e.g., stocking rate, fire frequency), and other contexts (Koerner et al., 2017). Biodiversity losses often occur when grazing favors the dominance of grazing-tolerant species, such as stoloniferous grasses, certain forbs, or invasive species, which can displace native grassland plants (Hobbs, 2001; Koerner et al., 2017; Williamson et al., 2020). Conversely, grazers can promote plant diversity by preferentially suppressing dominant grasses, releasing subordinate species from competition (e.g., Koerner et al., 2017; Ratajczak et al., 2022). Given these contrasting pathways, it is essential to understand how bison and other megafauna affect both woody encroachment and the herbaceous plant community.

This study investigates the impact of American plains bison on a tallgrass prairie in the Central Great Plains, focusing on areas with extended fire return intervals (FRIs). Understanding the net effects of megafauna takes large experimental treatments, which capture the spatial variability of large-animal behavior (e.g., Raynor et al., 2016, 2017). It also requires long-term manipulations that capture the long lifespan of perennial plant species. Here, we take advantage of four replicated catchment basins where fire has been suppressed for over thirty years. We used ecosystem-scale treatments (>20 ha each), which necessarily limit statistical replication, but increase the realism of our results (Schindler, 1998). Two catchment basins had bison reintroduced between 1987 and 1992, with bison present in both from 1992 onward. The other two catchments had a nearly identical fire history but had no large grazers present since 1981. In all catchments, naturally occurring micro-grazers (e.g., grasshoppers) and meso-grazers were present (e.g., small rodents). We hypothesized that bison herbivory would still alter community composition and increase plant community diversity, despite long FRIs. Based on observations from local landowners and the presence of tree species DNA in bison dung, we hypothesized that bison would alter the woody plant community by browsing, breaking, and trampling trees. However, we did not expect bison to reduce the cover of shrubs because many shrubs in the region are capable of vigorously resprouting if fire or herbivores top-kill stems.

METHODS

Site description

This study took place at Konza Prairie Biological Station (KPBS), a 3487-ha native tallgrass prairie located in northeastern Kansas, USA (39°05′ N, 96°35′ W). KPBS is a National Science Foundation long-term ecological research (LTER) in the Flint Hills ecoregion of the Central Great Plains, the largest expanse of unplowed tallgrass prairie in North America (Samson & Knopf, 1994). The mean annual precipitation is 835 mm year^{-1}, and growing season mean temperature (May–September) is 32.6°C, with a mean monthly maximum in July (36.2°C). Typical grassland vegetation at KPBS is a dominant grass layer, with high cover of perennial C_4 grasses, such as *Andropogon gerardii* (Vitman), *Sorghastrum nutans* (L.) Nash, *Schizachyrium scoparium* (Michx.) Nash, and *Panicum virgatum* L. In the absence of grazers, these four grass species become dominant, accounting for >90% of aboveground net primary productivity (Smith & Knapp, 2003). In contrast, forbs and other subdominant species make up the bulk of species richness (Collins & Calabrese, 2012; Towne, 2002). Common perennial forbs include *Symphyotrichum* spp. (asters), *Eupatorium altissimum* L. (tall-joe pye weed), *Salvia azurea* Michx.

(blue sage), and *Solidago* spp. (goldenrods). In frequently burned areas (every 1–4 years), bison promote tall forbs such as *Solidago rigida* L. (rigid goldenrod) and *Verbena stricta* Vent. (hoary verbena), short annual species, and shorter grasses more typical of drier Great Plains grasslands (e.g., *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths and *Bouteloua dactyloides* (Nutt.) J.T. Columbus) (Ratajczak et al., 2022). The most aggressive encroaching shrubs are functionally diverse (Wedel et al., 2025), but all are deciduous, resprouting, and capable of forming dense shrub thickets: *Cornus drummondii* C.A. Mey. (rough-leaf dogwood), *Rhus glabra* L. (smooth sumac), and *Prunus americana* (American plum).

Between the late 1970s and 1992, KPBS was divided along catchment boundaries into units ranging from 12 to 136 ha. Most replicate catchment units at KPBS have been experimentally burned at 1-, 2-, 3–4-, and 20-year FRI since 1983 (Knapp et al., 1998). Fire suppression began in 1983 for the units used in this study. In 1987, 30 bison were introduced and restricted to under half of their current spatial extent, including catchment N20A. In 1992, the bison herd was given access to its current 1012 ha area, including catchment N20B. The herd increased to an average of 270 adults with the goal of a grazing rate of ~25% removal of aboveground production each year (Towne, 1999, see Appendix S1: Figure S1 for bison stocking rate over time). For this study, we only used catchments burned every 20 years. For this fire frequency, we had two catchments with bison reintroduced and two catchments without bison, referred to as "ungrazed" from here on (see Appendix S1: Figure S2 for treatments used at KPBS).

Vegetation sampling

Between 1983 and 1994, permanent plots were established in each grazing treatment, at two different topographic positions, uplands and lowlands. Plots were evenly spaced along 50-m transects, with five 10-m^2 circular plots per transect and eight transects per catchment, with four transects in uplands and four transects in lowlands. This yields 40 plots per catchment and 80 plots per grazer treatment. Upland soils are shallow, rocky, and cherty silty-clay-loams typified by the Florence soil series. Lowland soils are deeper and less rocky silty-clay-loams typified by the Tully soil series. Since data collection began, the cover of each species has been measured annually in each plot, recording species cover using a modified Daubenmire scale, with cover classes of 0%–1%, 1%–5%, 5%–25%, 25%–50%, 50%–75%, 75%–95%, or 95%–100% aerial coverage (Bailey & Poulton, 1968). Each plot was sampled in the spring (late April to early May) and summer (late August) to capture within-season vegetation dynamics (e.g., some species are much more abundant in the spring and then senesce). For each year-by-plot combination, we used the maximum cover value for each species among these two sampling periods and used the midpoint of the Daubenmire scale ranges to calculate cover values. We used data from 1994 to 2020 to compare the two grazing treatments. We do not report data from 2021 onward because half the catchments became part of a new experiment (see Noble & Ratajczak, In press).

Large-scale woody plant changes: Remote sensing

Quantifying woody vegetation typically uses methods with a larger footprint than herbaceous species because shrubs and trees are much larger than herbaceous plants. For instance, a single tree could cover much of a 50-m herbaceous species transect, whereas the herbaceous community often turns over within much smaller distances (Koerner & Collins, 2013). Therefore, to quantify the extent of woody encroachment, we used remote sensing that categorized the entire study area, pixel by pixel, into grassland, shrub-dominated, evergreen tree-dominated (*Juniperus virginiana* L.), deciduous tree-dominated, and other (water, roads) (Appendix S1: Figure S2). We developed this 2 × 2 m resolution land cover map using a large training dataset (214,065 training pixels), remotely sensed inputs from low-flying planes, and random forest models (Noble & Ratajczak, 2025). Based on a hold-out dataset of 90,113 pixels separate from the samples used to train the model, the overall model accuracy was 97% (Noble & Ratajczak, 2025). We used the package raster in R (Hijmans, 2020) to determine the proportional cover of each land cover class within the bison-grazed and ungrazed catchments. We masked riparian areas within 20 m (as in Dodds et al., 2023; Keen et al., 2022), which have deep soils and a wet microclimate that promotes woody vegetation regardless of fire and grazing.

Seedling trial

J. virginiana is an aggressive encroaching species unburned tallgrass prairies (Briggs et al., 2005; Nippert et al., 2021) and many other Great Plains grasslands (Engle et al., 2008). In November 2020, we transplanted 40 *J. virginiana* seedlings that were 10–30 cm tall and obtained from woodland on a private property 17 km NNE of our study site, with similar soils to KPBS. Across a fence-line contrast, we planted 20 seedlings in a catchment with bison (catchment N4C) and 20 without bison access (catchment 4A) (see Appendix S1: Figure S3 for locations). Each treatment had two 100-m-long transects placed 200 m apart. We planted one seedling every 10 m along each transect.

We measured seedlings in December 2020, January 2021, and February 2021. During each visit, we recorded any mortality and the apparent cause of mortality (browsed, trampling, and ripped out). We planted seedlings in late autumn because most of KPBS was scheduled for prescribed burning in that spring, necessitating that we transplant seedlings beforehand. Also, we hypothesized that the time of most intense browsing by bison would be during the winter, when the quality of grass forage is low (Raynor et al., 2015). Therefore, the sole evergreen tree species (*J. virginiana*) could be a rare high-protein forage site, despite its higher concentration of secondary defense compounds. This made winter an opportune time to track seedling mortality.

Data analysis

We quantified changes in plant community biodiversity using long-term plant community data from 1994 to 2020 to calculate annual species richness, species diversity, and species evenness, all at the plot (alpha) scale. Species richness is the total number of species found in each 10-m^2 plot. For species evenness, we calculated the Shannon's diversity index ($H = \Sigma(p_i \times \ln p_i)$) and then calculated the Shannon equitability index (evenness $= H/\ln(S)$), where S is the total number of species and p_i is the relative abundance of species i. Instead of Shannon's index, we report the exponential Shannon's index, calculated as $e^H = \exp(H' = \Sigma(p_i \times \ln p_i))$. e^H is the number of equivalently abundant species in a sample and is generally a more interpretable measure.

To describe how species richness, evenness, and e^H, changed over time, we used generalized additive models (GAMs). GAMs are flexible models that allow for both nonlinear relationships and/or linear relationships between the response variable and multiple predictor variables using smooth functions. This flexibility is particularly useful for ecological time series, which often exhibit nonlinear patterns over time. For these GAMs, we performed independent analyses for each combination of response variable, grazing treatment, and soil type. We used the "gam" function in the "mgcv" package for GAM analyses (Wood, 2017).

To supplement GAMs, we also conducted fixed-effect ANOVAs comparing the first (1994) and last (2020) years of the plant community dataset for each diversity metric. These ANOVAs included grazing treatment (bison vs. ungrazed), soil type or topographic position (Florence vs. Tully soils), year, and their interactions as fixed effects. Although the GAM results already capture treatment differences over time, the ANOVA maintain continuity with approaches commonly used for shorter datasets (see Appendix S1: Figure S4, Tables S1–S5). We conducted post hoc comparisons using Tukey tests via the multcomp package in R (Hothorn et al., 2008), with an alpha level of 0.05 and honest squares difference adjustment to p values. We performed all analyses in R (v4.0.5; R Core Team, 2021).

To assess changes in plant community composition, we used a nonmetric multidimensional scaling (NMDS) ordination based on a Bray–Curtis dissimilarity metric. Bray–Curtis is one of the most effective distance metrics for ecological data (Beals, 1984; Ricotta & Podani, 2017), and NMDS is a flexible ordination technique suitable for data that deviate from normality, which often includes vegetation data (Dexter et al., 2018). We used species scores to determine what species drove the communities in the bison and ungrazed treatments. For this NMDS, species were selected based on their statistical significance at the $\alpha = 0.05$ level, ensuring a focus on the most influential species. We used the "envfit" function in the package "vegan" (Oksanen et al., 2013) to fit species vectors onto the ordination and test the significance of species–ordination relationships using permutation tests. The fitted vectors only reflect significant patterns in species abundances relative to the NMDS ordination space.

We used permutational multivariate analyses of variance (perMANOVA) with a Bray–Curtis dissimilarity metric using the package "vegan" (Oksanen et al., 2013) to determine whether there were community compositions. We first used a perMANOVA to determine any significant differences between the treatments across all years (1994–2020), with Year, grazing treatment, and soil type as main effects, and included all interaction terms. We used a separate perMANOVA for the first year (1994) to determine whether there were large pretreatment differences, with all previous effects except for "year." We used another perMANOVA of data from 2020 to assess how far communities diverged by the end of available data, again, without a main or interactive effect of "year."

Multivariate community composition gave us species-specific changes in communities, but we also calculated changes in the abundance of functional groups. For each plot, we calculated the total cover of trees, shrubs, and grasses. To model long-term trends in plant functional group cover, we used GAMs implemented with the mgcv package in R (Wood, 2017). For each combination of functional group, grazing treatment (grazed, ungrazed), and soil type (upland, lowland), we fit a separate GAM with Year as the predictor variable and cover as the response variable. GAMs allowed us to assess nontemporal trends in vegetation cover across treatments, capturing gradual and abrupt changes over time.

Remote sensing allowed us to measure wall-to-wall land cover for our treatment units with high accuracy (Noble & Ratajczak, 2025). Ecologists often use statistics because we can only measure a subset of a treatment, and therefore, need to generate a confidence interval for the average value of our measurements. In this case, we know that our measurements encompassed the entire community to ecosystem scale, negating the need for inferential statistical methods typically used in samples to infer about subsamples. Therefore, we used a descriptive and comparative approach. We calculated the land cover for each vegetation type as a proportion, such that Shrub area = area with shrub land cover/total catchment area. This conversion allows for straightforward comparisons of vegetation patterns across treatments, with direct insights into the landscape composition without the assumption of sampling error or variability. We recognize that this approach comes at the expense of replication. However, we argue that ecosystem-scale experiments, like this one, have an added benefit of being much more realistic than plot-based experiments, where the experimental treatments alter small locations but not the surrounding meta-community. Others have made similar arguments (Carpenter, 1996, 1998; Schindler, 1998). In the case of megafauna manipulations and the effects on trees, large treatment areas are critical, which often means that replication is difficult.

For the seedling trial, we used a two-sample proportion test to determine whether there were differences in mortality between the two treatments as of the final sampling.

RESULTS

Species diversity

In bison-grazed upland plots, species richness, evenness, and exponential Shannon diversity increased over time (Figure 1A–C, Appendix S1: Table S6). Species richness increased substantially (adjusted $R^2 = 0.62$, $p < 0.001$), evenness increased slightly and was variable (adjusted $R^2 = 0.07$, $p < 0.001$), and exponential Shannon diversity increased substantially (adjusted $R^2 = 0.31$, $p < 0.001$). In contrast, ungrazed upland plots saw only a minor increase in species richness with minimal variance explained (adjusted $R^2 = 0.06$, $p < 0.001$; Figure 1A). Evenness remained relatively static and variable across plots (adjusted $R^2 = 0.04$, $p = 0.002$; Figure 1B). Exponential Shannon diversity did not change significantly, remaining relatively low ($p = 0.06$; Figure 1C). As of the final year of data (2020), all three diversity metrics were greater in grazed uplands than in ungrazed uplands, based on confidence intervals of GAMs and a corresponding ANOVA (Appendix S1: Tables S1–S6).

In lowland plots with bison grazing, species richness decreased at first but increased sharply in the last decade (adjusted $R^2 = 0.356$, $p < 0.001$; Figure 1D). Evenness oscillated at first and then decreased, resulting in a statistically significant but small decrease overall (adjusted $R^2 = 0.06$, $p < 0.001$; Figure 1E). Exponential Shannon diversity decreased at first and then increased for the last eight years, resulting in a small but significant net increase (adjusted $R^2 = 0.05$, $p = 0.001$; Figure 1F). Ungrazed lowland plots showed a significant but small net gain in species richness (adjusted $R^2 = 0.20$, $p < 0.001$; Figure 1D). Evenness generally decreased for the first 17 years, then remained low but variable for the final 12 years (adjusted $R^2 = 0.105$, $p < 0.001$; Figure 1E). Exponential Shannon diversity generally decreased, although with a small increase in the last six years (adjusted $R^2 = 0.11$, $p < 0.001$; Figure 1F). As of the final year of data, compared to the ungrazed lowlands, lowlands with bison had 38% higher species richness, similar evenness, and higher exponential Shannon diversity (all based on confidence intervals of GAMs and a corresponding ANOVA, Appendix S1: Tables S1–S6).

Multivariate composition

Initially, the grazed and ungrazed plant communities were close in NMDS space (stress = 0.139 for the NMDS model), with slight differences along NMDS axis one based on soil type (Figure 2). Over time, the bison-grazed communities shifted upward along NMDS axis two, primarily toward shorter plant species, which loaded heavily on this axis. Grazed uplands shifted slightly to the left along NMDS axis one, primarily toward more grass- and forb-dominated communities, which were heavily loaded along NMDS axis one. This included a shift toward greater abundance of shorter grasses such as *Bouteloua* spp. and a perennial bunchgrass *Schizachyrium scoparium*, indicative of a grazing lawn community. These species had high loading on NMDS axis one. Grazed lowland plots, however, moved toward increases in tall shrubs such as *P. americana* (a thorny shrub species) and *Symphoricarpos orbiculatus* (coral berry), a subshrub.

Changes in ungrazed treatments were strongly dependent on soil type. Upland plots changed very little along

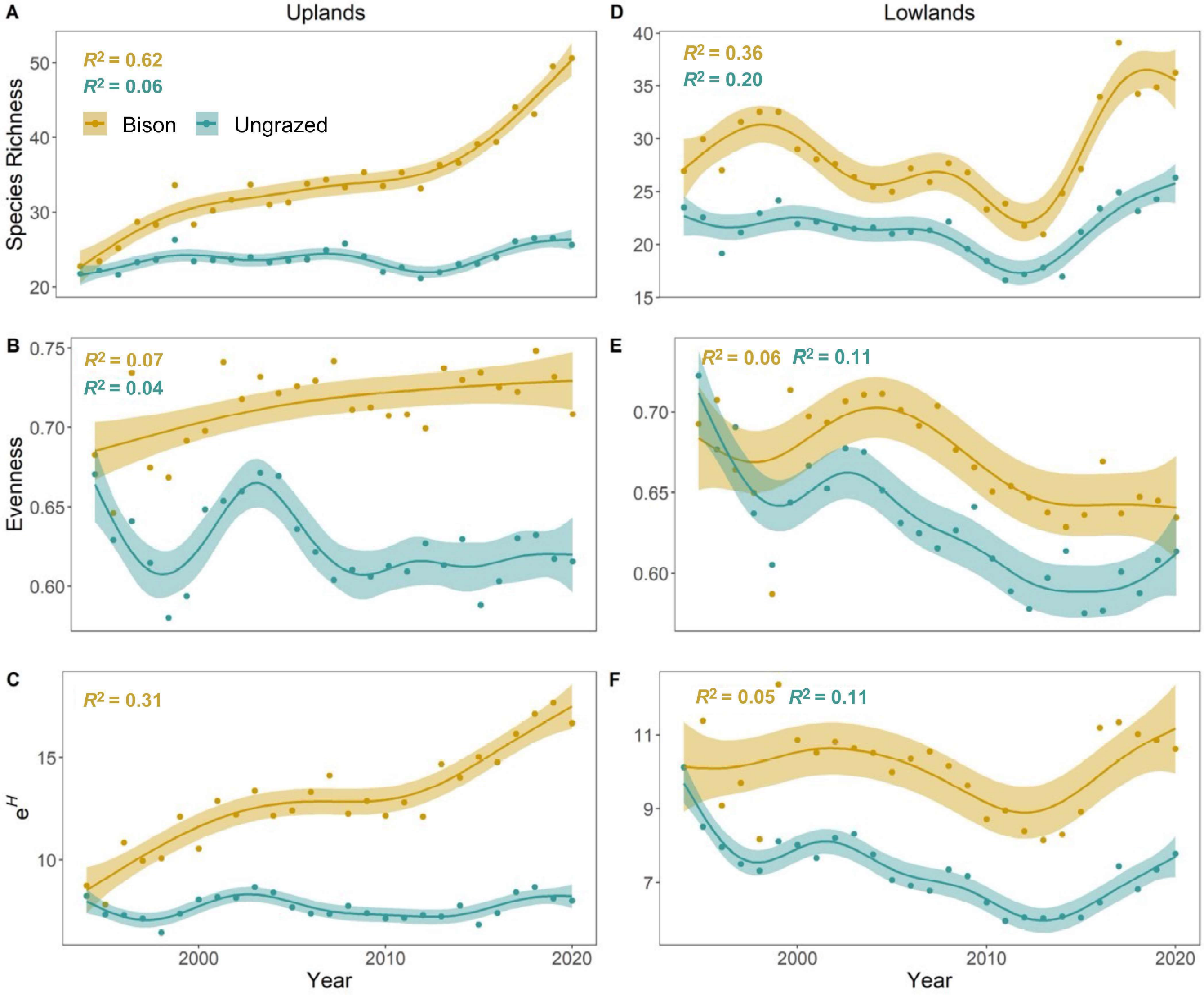


FIGURE 1 Time series of mean plant species richness per 10-m^2 plot (A), evenness (B), and mean equivalent species richness (e^H) (C) in upland (left panel) and lowland (right panel) soils in bison grazed and non-grazed woodlands from 1994 to 2020 (orange = grazed, blue = ungrazed). Points are annual averages and shaded areas span the 95th confidence interval of Generalized Additive Models (GAMs). All R^2 values are the adjusted R^2 and shown only for significant models ($p < 0.05$).

either NMDS axis. Ungrazed lowlands moved far to the right along NMDS axis one (Figure 2). This followed an increase in tree species abundance, such as *J. virginiana* and *Gleditsia triacanthos* (a native deciduous tree). Most ungrazed plots showed little movement along the second NMDS axis. Instead, shifts in composition were due to gains from other woody plants and declines by herbaceous species, especially tall grasses. Unlike grazed plots, shorter grasses did not increase substantially. Both grazed and ungrazed lowland plots moved toward greater cover of *C. drummondii* and *P. americana*, native thicket-forming shrubs.

In 1994, grazing accounted for 5.4% of the variation ($R^2 = 0.05$, $p = 0.001$), soil type for 11.15% ($R^2 = 0.11$, $p = 0.001$), and their interaction for 4.4% ($R^2 = 0.04$, $p = 0.001$). In 2020, the influence of grazing increased to explain 10.8% of the variation ($R^2 = 0.108$, $p = 0.001$), soil type explained 18.1% ($R^2 = 0.18$, $p = 0.001$), and their interaction accounted for 6.1% ($R^2 = 0.06$, $p = 0.001$). The increase in the proportion of variation explained by these factors from 1994 to 2020 suggests that the impact of grazing and soil type on plant community composition became more pronounced. A perMANOVA that included all years of data (1994–2020) found that year explained ~28% of the variance, grazing treatment explained ~19%, soil type ~11%, and grazing treatment and soil interaction ~8%, with all other interactions

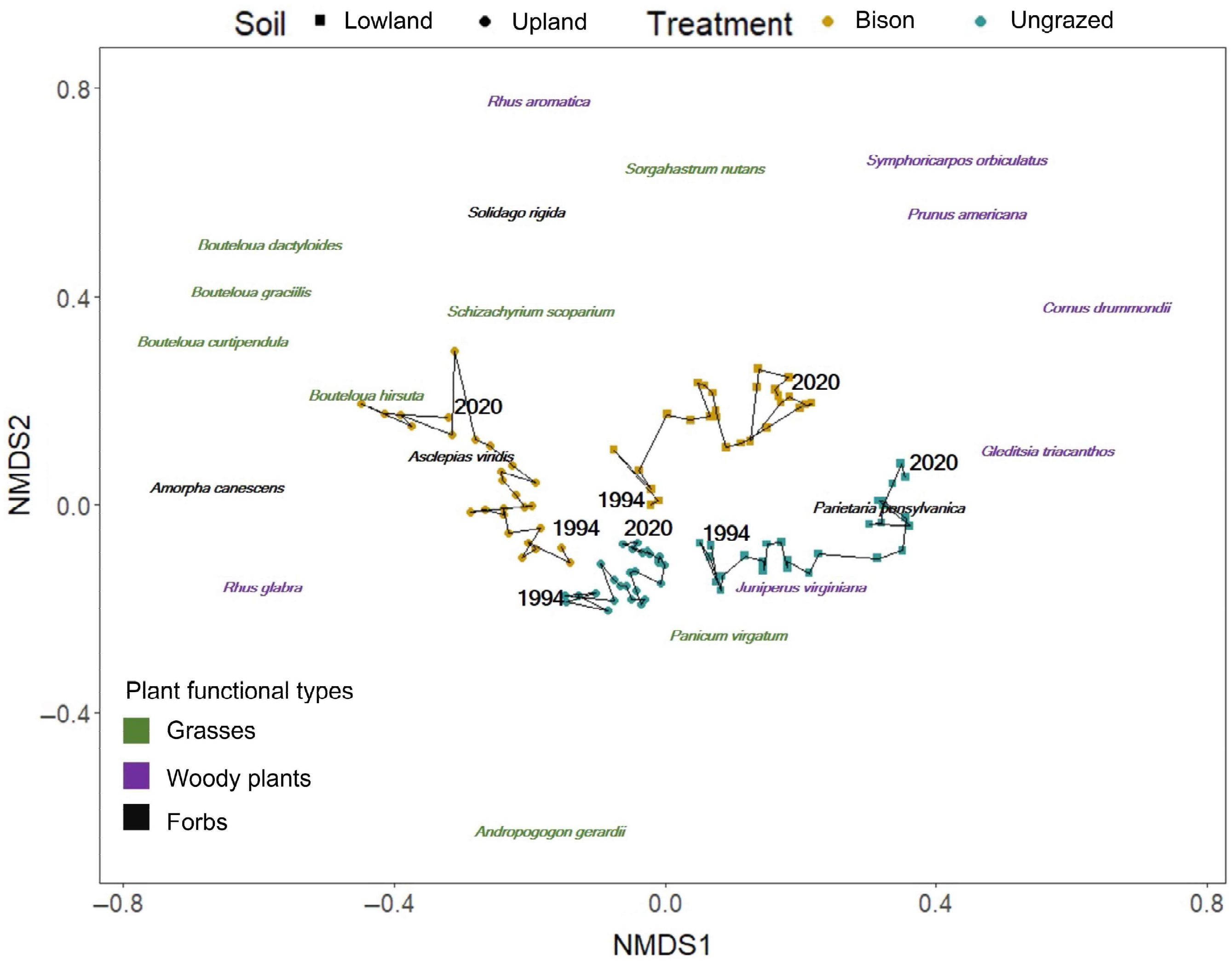


FIGURE 2 Nonmetric multidimensional scaling (NMDS) with a Bray–Curtis distance of the plant community composition data over time (1994–2020) across soil types in the grazed and ungrazed treatments. Ungrazed are blue and grazed are orange with lowland soils being represented by squares and upland soils by circles. Species are colored by functional group with purple representing forbs, green representing grasses, and brown representing woody plants.

explaining ~8% of the variance (Appendix S1: Tables S7 and S8).

Plant functional group cover over time

The GAM model of tree cover with bison in the uplands had a nonsignificant smooth term for Year ($p = 0.056$) because tree cover remained near zero (~0%–1%) (Figure 3A). In contrast, tree cover in ungrazed uplands increased from 0% to ~15% by 2020 ($p < 0.001$, $R^2 = 0.78$). In lowlands, tree cover in grazed plots remained low (~0%–3%) throughout the study ($p = 0.316$, $R^2 = 0.13$), whereas in ungrazed plots, tree cover went from 0% to ~50% ($p < 0.001$, $R^2 = 0.70$; Figure 3B).

Shrub cover in both treatments increased over time. In uplands, shrub cover increased in both grazed ($p < 0.001$, $R^2 = 0.78$) and ungrazed plots ($p < 0.001$, $R^2 = 0.74$), peaking between 60% and 90% in both cases by 2020 (Figure 3C). In the lowlands, grazed plots showed the steepest increase in shrub cover, reaching ~110% cover around 2012 before declining slightly and stabilizing ($p < 0.001$, $R^2 = 0.90$). Shrub cover in ungrazed lowlands increased gradually, plateauing near 90% cover by 2020 ($p < 0.001$, $R^2 = 0.68$; Figure 3D).

Grass cover fluctuated substantially. In uplands, grass cover ranged from ~90% to 170% over time. Both grazed ($p < 0.001$, $R^2 = 0.65$) and ungrazed ($p < 0.001$, $R^2 = 0.74$) had a temporary increase in the middle of the study, but then fell to approximately the same cover as at the beginning of the study (Figure 3E). In lowlands, grass cover was still variable, but followed a stronger directional trend. Grazed plots oscillated at first, ranged from ~70% to 160% ($p < 0.001$, $R^2 = 0.82$), while ungrazed plots ranged from

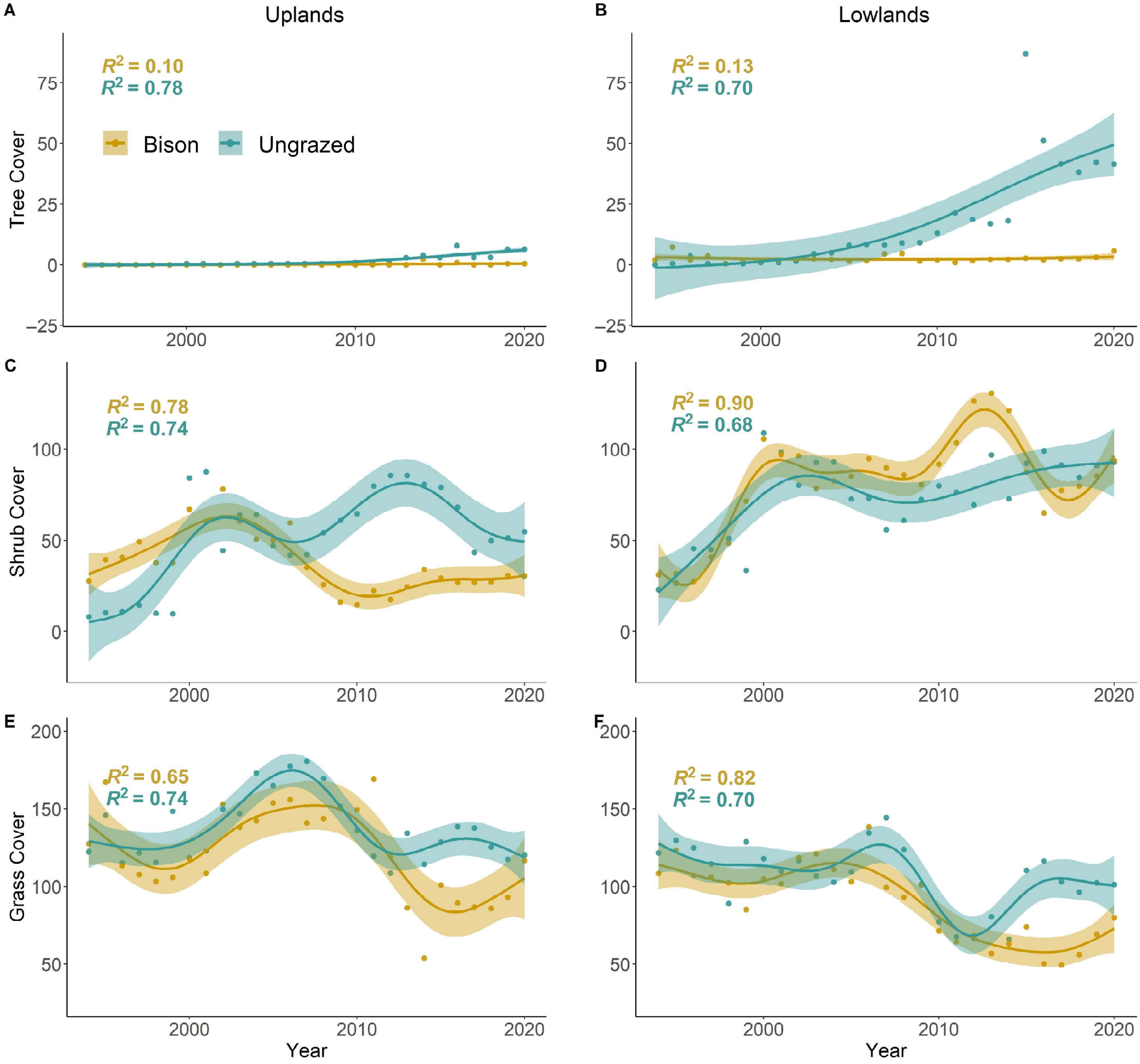


FIGURE 3 Tree cover, shrub cover, and grass cover as a function of time and grazing treatment (orange = grazed, blue = ungrazed) in upland (left panel) and lowland (right panel) soils. Points are annual averages and shaded areas span the 95th confidence interval of generalized additive models (GAMs). Adjusted R^2 values are only shown for the significant GAMs ($p < 0.05$).

~100% to over 175% ($p < 0.001$, $R^2 = 0.70$; Figure 3F). Both treatments experienced marked declines in grass cover between 2008 and 2013, with grazed plots showing some recovery (see Appendix S1: Table S9 for model summaries).

Large-scale, remote sensed woody cover

When available, remote sensed land cover is a better indicator of large-scale land cover changes than plot-based assessments, especially in ecosystems with large plants such as trees. The land cover of herbaceous-dominated vegetation was 51% in the grazed treatment and 40% in the ungrazed plots (Figure 4). Shrub land cover was 42% and 41% for the grazed and ungrazed treatments, respectively. The grazed treatment had effectively no *J. virginiana* (~0%) cover and lower deciduous tree land cover (6%). In contrast, the ungrazed treatment had 4% *J. virginiana* land cover and 16% deciduous tree land cover. This lower amount of tree cover corresponds to 11% higher herbaceous land cover in the grazed treatment.

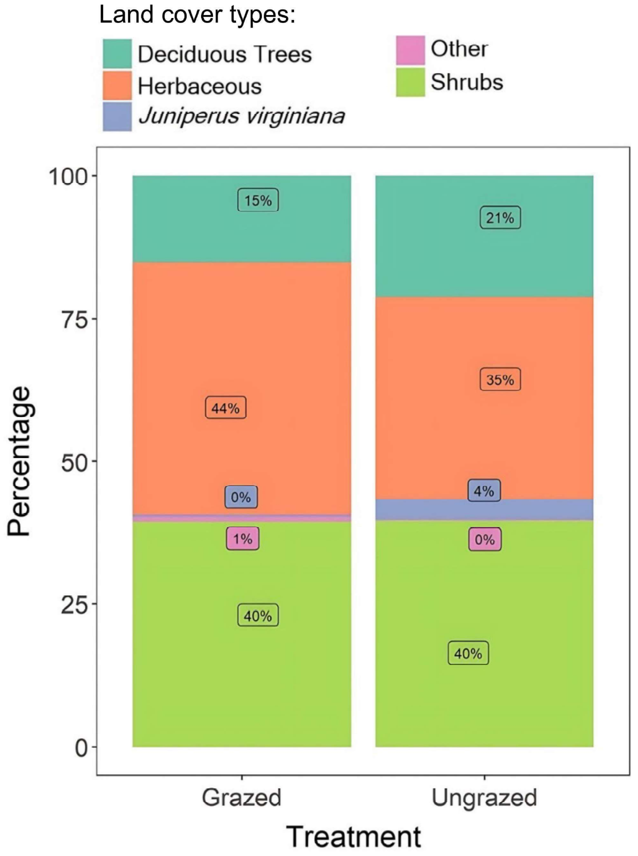


FIGURE 4 Stacked bar plot of the different vegetation covers in the bison-grazed and ungrazed treatments. The other category represents bare ground and water.

FIGURE 5 Photo of one of *Juniperus virginiana* seedlings ripped out in the bison-grazed area at Konza Prairie Biological Station (Photo Credits: Sidney Noble).

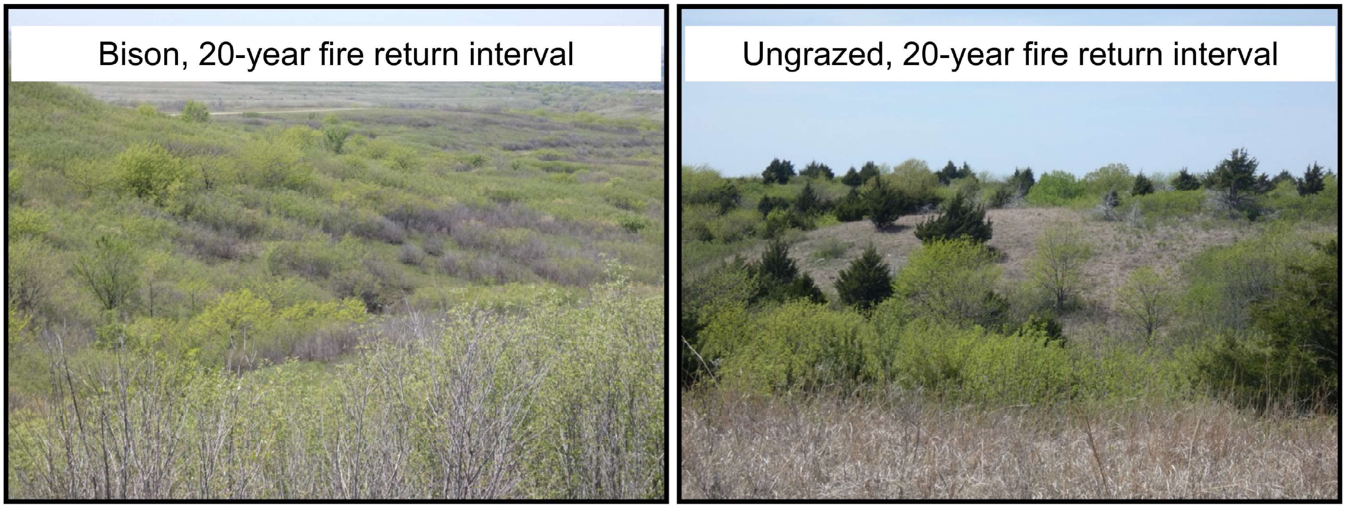
Seedling trial

Mortality of planted *J. virginiana* seedlings was significantly higher in the bison treatment ($\chi^2 = 6.5333$, $p = 0.01$), where 45% died. Eight seedlings showed signs of browsing and uprooting, and one was trampled (see Figure 5). In contrast, only one out of twenty (5%) *J. virginiana* seedlings died in the ungrazed treatment.

DISCUSSION

Plains bison have been reintroduced to more than 1000 locations across North America (USDA, 2016), ranging from mountain grasslands and woodlands in the west to Great Plains grasslands and parts of Appalachia in the east (Freese et al., 2007; Sanderson et al., 2008). Our work supports work from ecosystems like Yellowstone National Park, USA, where bison have also had an outsized impact on woody plant communities (Kauffman et al., 2023; Painter et al., 2023). Finding that these results potentially extend to the Great Plains was surprising because (A) grazers typically favor the expansion of woody species by reducing grass dominance (Anderies et al., 2002; Archer et al., 2017), and (B) based on biomass consumed and the chemistry of bison tissues, multiple studies have found that bison diet is overwhelmingly comprised of warm season graminoids in the Central Great Plains (Griffith et al., 2017; Raynor et al., 2016). Yet, we found that bison inhibited tree expansion, based on two separate measures of woody plant expansion—plot-based data and remote sensing (Figure 6). Our results suggest that bison can have a particularly adverse effect on *Juniperus virginiana*, which is one of the most widely distributed trees in North America (Thompson et al., 1999) and is one of the most impactful woody encroaching species in the Great Plains (Engle et al., 2008). We also found that bison increased plant diversity and altered the plant community composition.

How bison and other grazers increase diversity is often in the context of frequent fires, which otherwise shift plant communities to a homogenous state of high grass dominance in the absence of grazers (Bookout et al., 2025; Collins & Calabrese, 2012; Fuhlendorf et al., 2009). A tallgrass prairie landscape consisting of frequently burned areas would probably be better for



Bison, 20-year fire return interval

Ungrazed, 20-year fire return interval

FIGURE 6 Photos of the bison-grazed (left) and ungrazed (right) treatments burned approximately every 20 years. The ungrazed treatment contains *Juniperus virginiana* (the coniferous tree) while it is virtually absent in the bison-grazed treatment (Photo Credits: Sidney Noble).

reducing woody encroachment, conserving grasslands, increasing grassland biodiversity, and maintaining grazer production in the Central Great Plains (e.g., Fuhlendorf et al., 2009; Ratajczak et al., 2014; Silber et al., 2024). However, much of the Central Great Plains is currently burned infrequently (Chen et al., 2023; Ratajczak et al., 2016; Scholtz & Twidwell, 2022) compared to estimates of fire frequency since the Last Glacial Maximum (Allen & Palmer, 2011; Guyette et al., 2012; Stambaugh et al., 2013). This reflects a decline in burning culture in many areas (Twidwell, Rogers, et al., 2013) and other impediments to using prescribed fire (Wonkka et al., 2015).

It was unclear whether bison would increase diversity at low fire frequencies, but 29 years of reintroducing bison increased plant species richness in two distinct soil types, shallow uplands and deep lowlands (Figure 1). Our results support the finding that bison and many other grazer species can increase plant diversity in mesic grasslands, potentially across a range of fire frequencies (Bookout et al., 2025; Collins et al., 1998; Collins & Calabrese, 2012; Koerner et al., 2018; Ratajczak et al., 2022). Moreover, this increase in diversity could mitigate the loss of diversity due to woody encroachment (Ratajczak et al., 2012; Wieczorkowski & Lehmann, 2022). Although bison had less of an effect on exponential Shannon diversity (e^H) in lowlands, probably because some of the species in the bison-grazed communities are small plants that do not reach high cover (Bookout et al., 2025; Ratajczak et al., 2022), the ability of bison to limit *J. virginiana* expansion could have long-term effects on species diversity, as *J. virginiana* expansion can reduce plant species richness by 95% under its canopy (Briggs et al., 2002; Van Els et al., 2010). For instance, in one meta-analysis *J. virginiana* decreased herbaceous plant species richness more than any other encroaching species in North American grasslands at the time (Ratajczak et al., 2012).

When bison were first reintroduced at KPBS, plant communities had a similar composition, structure, and diversity in the grazed and ungrazed treatments (Figure 2). However, community composition has diverged over time, and these treatments now represent two distinct plant communities mediated by soil type. While the extent of shrub encroachment in both treatments was similar—albeit slightly lower with bison—in the remaining herbaceous matrix, bison have created a unique community with more abundant short grasses (e.g., *Bouteloua* spp.) and forbs, such as rigid goldenrod (*Solidago rigida*). Short grass species were prevalent in grazed uplands, whereas grazed lowlands were a mix of short grasses, tall grasses, forbs, and subshrubs (Figure 3). The remaining grassland matrix in areas without bison is much different, with tall grass, such as big bluestem (*A. gerardii*), remaining dominant (Figure 3), despite a substantial litter layer (personal observations). This change in structure resembles many other grazed grasslands, where the response is often an increase in more grazing-tolerant short grasses and/or unpalatable "sour" grasses and forbs (Hempson et al., 2015).

Grazers are widely assumed to favor woody vegetation because they reduce grass abundance and, thereby, the intensity of fires and the ability of grasses to exclude other species through competition (Bond, 2008; Scholes & Archer, 1997). For instance, conventional cattle grazing in tallgrass prairie increases tree establishment and decreases tree mortality from fires (Briggs et al., 2002; Fuhlendorf et al., 2008). However, grazers have also reduced tree height due to browsing in some locations (Capozzelli et al., 2020). Although carbon isotopes indicate that bison overwhelmingly rely on grasses for forage (Griffith et al., 2017; Raynor et al., 2016), tree species' DNA has been found in bison dung and other large grazers (Craine et al., 2015). This matches work from African savannas, where some species considered grazers still have a proportion of woody plants in their diet (e.g., Guyton et al., 2020; Kartzinel et al., 2015). Although bison are unlikely to consume large amounts of woody vegetation, incidental browsing plus mechanical impacts such as trampling, horning, and scratching (i.e., Coppedge & Shaw, 1997) could have an outsized effect on tree recruitment if they are mostly damaging or killing small seedlings. The result would be a demographic bottleneck that prevents adult trees from becoming established (as in Higgins et al., 2000), which is the behavior that allows browsers and mixed-feeders to limit woody vegetation in some African savannas (Sankaran et al., 2008; Staver et al., 2012). Results from this study suggest that bison may prevent tree establishment by killing a large proportion of small seedlings, and we hypothesize that this is one of the mechanisms by which bison inhibit *J. virginiana* woodland recruitment in infrequently burned areas (~20 years). In addition to small juveniles, bison also affect adult trees by horning, scratching on trees to remove their winter fur coats, and potentially scratching on trees to remove ectoparasites and/or coat their fur in secondary compounds that deter ectoparasites (Berman, 2008; Coppedge & Shaw, 1997; Mooring & Samuel, 1998). For instance, bison in the Greater Yellowstone Ecosystem in the United States are suppressing aspen (*Populus tremuloides*) recruitment via a full suite of herbivory, trampling, and breaking of aspen saplings (Beschta et al., 2020; Painter et al., 2023). Anecdotally, we have directly observed bison killing or damaging woody vegetation, especially *J. virginiana*. In extreme cases, we have seen bison push through approximately 40 m of shrub thicket and browse and rub on a mature *J. virginiana* (personal obs. S. Noble, Z. Ratajczak).

While our data suggest that bison may significantly impact the survival of young tree seedlings, we should consider the limitations of our *J. virginiana* transplant experiment. With a sample size of only 20 saplings per treatment, the results are indicative rather than conclusive. The mortality rate of *J. virginiana* was substantially higher in the bison-grazed plots (8/20 vs. 1/20 died). But we did not directly observe bison browsing or killing our planted saplings. On the other hand, our results potentially undercount the difference between grazed and ungrazed treatments. In 2017, one of the ungrazed treatments underwent a prescribed burn where over half of the *J. virginiana* trees—758 out of 1406 trees—suffered mortality (Nippert et al., 2021). This further reinforces that bison probably inhibit *J. virginiana*, as the cover comparison between the grazed and ungrazed treatments would have been higher if not for the prescribed burn. The distinction between seedling and adult mortality is important in this case. If bison-induced tree mortality is largely confined to small trees, then bison may effectively prevent future woodland formation but are unlikely to reverse existing tree encroachment on human timescales.

Bison in the context of alternative states in the Central Great Plains

In the absence of grazers, there is evidence of fire frequency thresholds that regulate the transition of grasslands to shrublands or woodlands (Briske et al., 2008), especially within the Central Great Plains of North America (Ratajczak et al., 2014). Mesic grasslands receive enough precipitation to support shrubs and trees, but fire and grass competition often limit woody plant recruitment (Briggs et al., 2005; Ratajczak et al., 2014; Twidwell, Fuhlendorf, et al., 2013). Without frequent fire, shrub plants can become established and cement their dominance by suppressing grasses and lowering fire intensity (Fuhlendorf et al., 2008; Ratajczak et al., 2011; Twidwell, Fuhlendorf, et al., 2013). This transition from a mesic grassland to shrublands potentially represents a shift to a new self-reinforcing stable state (Briske et al., 2008; Ratajczak et al., 2014), which is difficult to reverse (Collins et al., 2021; Miller et al., 2017; Ratajczak et al., 2017). With further fire suppression and time, *J. virginiana* and deciduous trees can form closed woodlands (Briggs et al., 2002; Nippert et al., 2021). These trees, especially *J. virginiana*, have strong negative effects on surface fuels and herbaceous species, and can even exclude shrubs (Briggs et al., 2005; Ratajczak et al., 2014).

The decreased tree cover, especially *J. virginiana*, within the bison-grazed treatment has implications for the viability of "woodlands" as an end state. In this experiment, bison promoted a shrub-dominated system with sparser trees and decreased the likelihood that a shrubland would transition to a tree-dominated system or greatly increase the time for a woodland transition. We argue that bison break the transition from shrubland to woodland due to decreased tree recruitment, or at a minimum, drastically slow the transition to a closed woodland. For instance, after thirty years of fire suppression we are still far from seeing the formation of a closed woodland in the bison treatment. In contrast, areas in

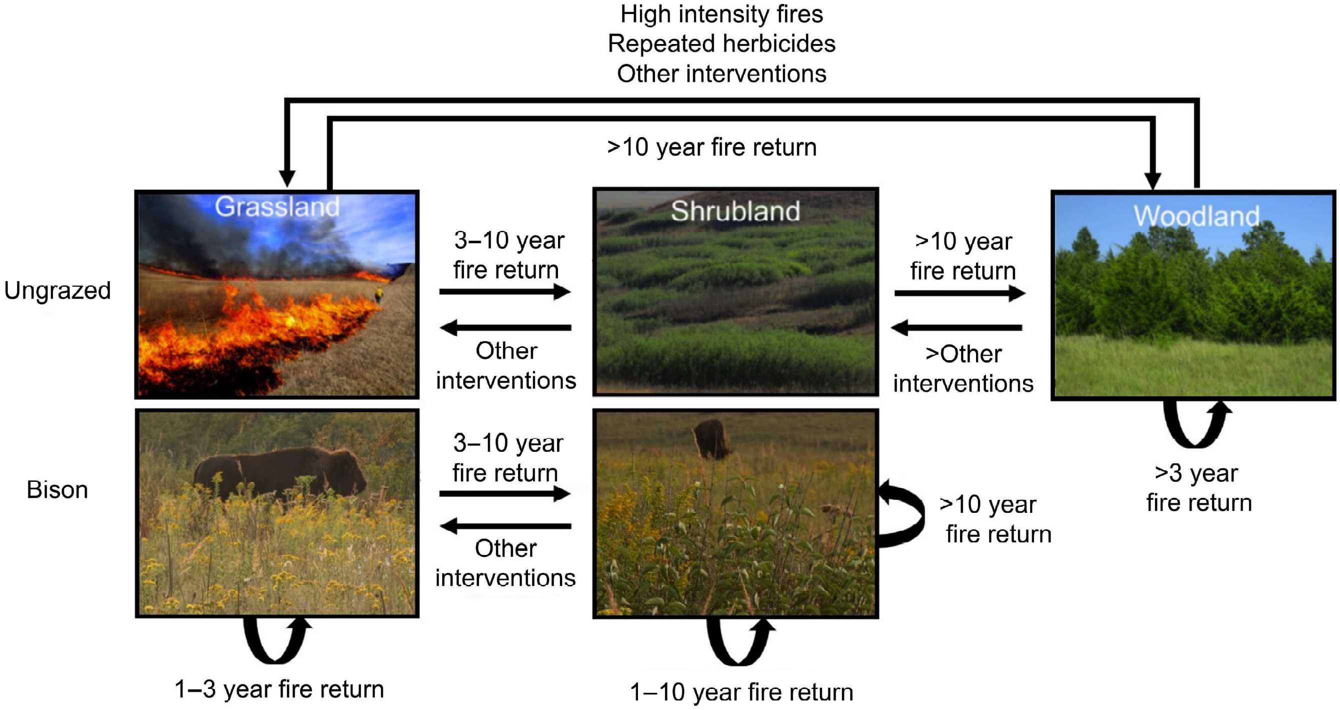


FIGURE 7 State and transition model of grassland, shrubland, and woodland states including the presence and absence of bison adopted from Ratajczak et al. (2014). Square photos represent states and arrows represent processes that may allow a transition to another state. Selfing arrows represent hysteresis, where reintroducing conditions that maintained a grassland do not return the shrubland or woodland back to grassland. High-intensity fires may transition an *Juniperus virginiana*-dominated woodland back to a grassland (Bielski et al., 2021). The presence of bison prevents the transition of shrubland to *Juniperus virginiana*-dominated woodland. Photo Credits: (Grassland: Eva Horne, Grassland with bison: Sidney Noble, Shrubland: Zak Ratajczak, Shrubland with bison: Sidney Noble, Woodland: John Blair).

the region without bison can converge on a closed woodland in 40 years (Bragg & Hulbert, 1976; Briggs et al., 2002). Therefore, we propose an alternative conceptual model that takes our original state and transition model from Ratajczak et al. (2014) and includes bison (Figure 7). In the revised model, bison-grazed grasslands exhibit community composition and structure that differ markedly from ungrazed grasslands. Additionally, with bison we do not depict a transition to woodland or at least that transition occurs much more slowly. Instead, at long FRIs bison maintain a shrub-dominated system with sparse trees. This state is more like the mosaic of grasses, shrub thickets, and tree clusters seen in some subtropical savannas (e.g., Charles-Dominique et al., 2015; Roques et al., 2001).

One key feature of transitions to shrubland and woodlands is that they are difficult to reverse frequently due to increases in resistance to fire (Twidwell, Fuhlendorf, et al., 2013) and the breaking feedback loops that reinforce a fire-prone grass-dominated state (Archer et al., 2017; Ratajczak et al., 2014). A major unknown is how bison affect the reversibility of woody encroachment (several key arrows in Figure 7). Starting in the spring of 2021, the bison-grazed catchments used in this study have been burned every year, which will allow us to assess the long-term influence of bison on reversing woody encroachment (see Noble and Ratajczak, in press for early results).

CONCLUSION

We found that bison have decreased and altered the composition of tree species in a mesic grassland while continuing to increase plant diversity in the Central Great Plains. This decrease is surprising because grazers are generally thought to facilitate woody plant expansion by reducing the dominance of grasses. The possible mechanism behind this removal may relate to bison behavior, where bison will kill tree seedlings via browsing and mechanical disturbance (e.g., ripping, trampling, and horning). Even small decreases or increases in tree cover can have large implications for grassland conservation and the maintenance of ecosystem services. For instance, many grassland obligate birds, such as lesser prairie chickens, are sensitive to tree encroachment (Engle et al., 2008; Silber et al., 2024). In the Gypsum Hills to the southwest of our study site, areas with a tree density of just two trees per hectare see almost no usage by lesser prairie chickens—an iconic and threatened grassland bird species (Lautenbach et al., 2017). Similar patterns have been seen for grassland birds in southern tallgrass prairie, where an increase in *Juniperus* cover from 0% to 10% reduced grassland bird abundance by 50% (Engle et al., 2008). However, bison's impact on areas already dominated by mature trees may be limited. In such cases, additional management strategies, such as cutting or burning, might be necessary to complement the grazing impact of bison. Therefore, bison may be most effective in preventing the expansion of species like *Juniperus* spp. or hindering their initial recruitment rather than reversing well-established woodlands.

AUTHOR CONTRIBUTIONS

Sidney Noble and Zak Ratajczak developed the research questions, hypotheses, and performed statistical analyses. Brynn Noble, Sidney Noble, and Zak Ratajczak collected training data for the remote sensing product. Zak Ratajczak created the final remote sensing product used in this study. Sidney Noble and Brynn Noble conducted the fieldwork for the juniper seedling trial. All authors contributed to drafting and editing the manuscript. The authors have no conflict of interest to report.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available on the Environmental Data Initiative's Data Portal as follows: plant community data (Hartnett et al., 2022), https://doi.org/10.6073/pasta/b768b10f9b17bafc68194a4aaa8e53c2; data from the *J. virginiana* seedling trial (Noble et al., 2024), https://doi.org/10.6073/pasta/27bc74e40a7abdedbe1f868c3bac95e2; remote sensing product (Noble & Ratajczak, 2023), https://doi.org/10.6073/pasta/7bc9d89762cb02ad9dc98bdfb95abde2.

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SUPPORTING INFORMATION

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

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