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# Where the buffalo roam: Ungulate influences on quaking aspen and willow communities in the Greater Yellowstone Ecosystem

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**Abstract**

Quaking aspen (*Populus tremuloides*) and willows (*Salix* spp.) are keystone species of montane and shrub-steppe landscapes of the Western United States. Intact communities dominated by these species provide a wide range of ecosystem services, harboring an exceptional proportion of landscape biodiversity. Land use, especially overgrazing by large ungulates, is among the greatest threats to these ecosystems. To examine the effects of wild ungulates and levels of grazing at Yellowstone National Park (YNP) and the adjacent Gallatin National Forest, we sampled plant community composition and vegetation structure of aspen and willow communities both inside and outside of exclosures. Within the Park, we found that current grazing pressures from large ungulates, principally American Bison (*Bison bison*), have a dramatic effect on community composition and structure, resulting in a shift from a structurally diverse forest or tall shrub dominance to that of a grassland. On heavily grazed sites, shrubs common to semiarid uplands are now relatively abundant, as are exotic grass species, in contrast to an abundance of berry-producing shrubs within exclosures. Finally, large herbivores at unnaturally high densities are resulting in the simplification of landscape diversity outside of exclosures through a decline in the patch diversity of the site (i.e., homogenization of the landscape). Increases in exotic species and those adapted to semiarid environments suggest that current levels of bison use at YNP are amplifying the effects of climate change as well as resulting in a loss of biodiversity values. Inside exclosures, the inherent resilience of these keystone ecosystems was demonstrated by the recovery of plant diversity following decades of large ungulate utilization exceeding natural carrying capacity. This suggests that reductions in current grazing pressures within YNP would have positive feedbacks to beneficial ecosystem processes such as increased species and habitat diversity, increased carbon sequestration, and a greater adaptive capacity to climate change.

**KEYWORDS**
herbivory, National Park management, riparian ecology, species diversity, structural diversity, ungulate effects

## INTRODUCTION

In the montane and semiarid landscapes of the American West, quaking aspen (*Populus tremuloides*) and willow (*Salix* spp.) communities have a disproportionately important role in promoting and sustaining biodiversity, sequestering carbon, limiting the effects of forest disturbances, and providing other ecosystem services (Kauffman et al., 2001; Rogers et al., 2020). Aspen and willows, members of the Salicaceae family, are highly palatable to large herbivores, which often result in overuse that can impair other ecosystem services. Ungulates, both wild and domestic, directly influence ecosystem services by (1) removing vegetation through herbivory, (2) physically disturbing soils, biotic soil crusts, streambanks, and vegetation through trampling, (3) redistributing nutrients via defecation and urination, and (4) dispersing or creating favorable conditions for exotic organisms, including invasive plant species and pathogens (Dwire et al., 1999; Fleischner, 1994; Kauffman, Beschta, et al., 2022; Kauffman, Coleman, et al., 2022).

Riparian zones typically only occupy 0.5%–2% of the landscape but provide habitats for more plant, mammal, avian, and amphibian species than the surrounding uplands (Baril et al., 2011; Kauffman et al., 2001). As much as 53% of the wildlife, including as much as 80% of the local avifauna, breeds in riparian willow habitats (Berger et al., 2001; Kauffman et al., 2001). Given the high biodiversity values associated with aspen and willow communities, their decline in the montane and semiarid landscapes of the Western United States is concerning. For example, at the turn of the century, the extent of aspen loss among states in the Western United States was estimated to range between 49% and 96% (Bartos, 2001). In northern Yellowstone National Park (YNP), a pronounced decline in various deciduous species, including aspen, willows, and cottonwoods (*Populus* spp.), appears to have begun in the early 1900s and became increasingly severe in the mid to late 20th century. By the mid-1900s, Kay (1990) estimated that more than 90% of the area occupied by aspen had declined, and Houston (1982) estimated that willow-dominated communities had declined by about 50%. This decline was largely driven by the intensive herbivory of wintering populations of Rocky Mountain elk (*Cervus canadensis*) that prevented young deciduous plants from growing taller, thus maintaining them in a suppressed state with limited reproductive capacity (Brookshire et al., 2002). Even though the extent to which aspen and willow communities occur across landscapes is limited, they nevertheless serve as biodiversity hotspots and their conservation and restoration recognize critical ecosystem functions.

The increased effects of ungulates, principally elk, on woody plant species in northern Yellowstone began to occur after the 1920s extirpation of gray wolves (*Canis lupus*) and reduction in cougar populations (*Puma concolor*) (Barmore, 2003; Jonas, 1955; Kay, 1990; Lovaas et al., 1966; Ripple et al., 2022; Ripple & Larsen, 2000; Wolf et al., 2007). Following the return of wolves in the mid-1990s, which reestablished the region's large carnivore guild, various studies found increased plant height, stem diameter, establishment, canopy cover, and recruitment in young woody plants—a phenomenon known as a trophic cascade (Beschta et al., 2018, 2023; Brice et al., 2021; Hobbs et al., 2023; Painter et al., 2018; Ripple & Beschta, 2004). During this same timeframe, American bison (*Bison bison*) became the dominant ungulate across much of northern YNP with a nearly 10-fold increase in numbers over the last two decades (National Park Service, 2023). Bison influences on vegetation composition and structure of the Northern Range of the Park are well known (Beschta et al., 2020; Geremia et al., 2019; Kauffman et al., 2023; Painter et al., 2023; Ripple et al., 2011). In addition to historically high current densities, bison influences are different than those of elk as they are considerably greater in size and they utilize the Northern Range all year and not just seasonally. In the Gallatin National Forest (GNF), by contrast, elk are the dominant large ungulate because bison are absent.

The overarching objectives of this study were to quantify how the presence and absence of large ungulates, especially bison and elk, affect the structure, composition, and diversity of quaking aspen and willow-dominated communities in the Northern Yellowstone Ecosystem. To accomplish this, we undertook vegetation measurements inside and outside of long-established exclosures in landscapes with differing histories of the types and intensity of wild ungulate use. Sampling at these sites allowed comparison of the composition and structure of plant communities where large ungulates are excluded to those sites subjected to herbivory, trampling, defecation, and exotic species dispersal (Table 1; Figures 1 and 2). A major advantage of using permanent large ungulate exclosures is that environmental site

**TABLE 1** The sampled exclosures and related communities at Yellowstone National Park and the Gallatin National Forest (2021–2023).

| Exclosure name | Sampled communities | General observations | Latitude | Longitude | Year established |
|---|---|---|---|---|---|
| Yellowstone National Park | | | | | |
| Mammoth | Aspen, willow | Aspen on side slope; willow on level ground | N 44°57′38.0″ | W 110°41′57.6″ | 1957 |
| Junction Butte | Aspen, willow | Level ground, springs originate in exclosure | N 44°54′42.2″ | W 110°22′05.5″ | 1962 |
| Lamar West | Aspen | Toe slope within the Lamar Valley; springs originate in exclosure | N 44°53′01.8″ | W 110°13′03.1″ | 1962 |
| Lamar East | Aspen | Toe slope within the Lamar Valley | N 44°52′19.3″ | W 110°12′17.7″ | 1957 |
| Gallatin National Forest | | | | | |
| Crown Butte | Aspen | Side slope well above the valley bottom | N 45°03′49.1″ | W 111°08′53.9″ | 1945 |
| Snowflake | Willow | Riparian willow along the Gallatin River | N 45°03′41.2″ | W 111°10′10.5″ | 1948 |
| Porcupine | Aspen, willow | Small intermediate headwater riparian zone and aspen | N 45°13′33.00″ | W 111°14′8.79″ | 1945 |

variability (precipitation, geology, climate change, etc.) is held constant between adjacent grazed and ungrazed areas, thus isolating the potential influence of large ungulates (Coles-Ritchie et al., 2007; Sarr, 2002).

Our hypotheses of research were as follows: (1) large ungulates (principally bison and elk) can result in differences in the structural diversity, vegetation composition, species richness, and species diversity within quaking aspen and willow-dominated communities; and (2) composition of the large ungulates herbivores and their current intensity of use will differentially affect how these parameters are now responding.

# STUDY AREAS

The YNP and GNF study areas occur within mountain valleys of the northern Rocky Mountains where mountain big sagebrush (*Artemisia tridentata vaseyana*)–Idaho fescue (*Festuca idahoensis*) is the dominant upland plant community, transitioning into coniferous forests at higher elevations. Quaking aspen stands occur in both upland and riparian settings, whereas willows are commonly found in riparian areas. Both currently occupy <2% of the landscape (Barmore, 2003; Brown et al., 2006).

The National Park Service and the US Forest Service have maintained large herbivore exclosures in the YNP and GNF study areas since establishment between 1947 and 1962 (Table 1). These exclosures were established to ascertain how large ungulates and the management of their population densities affect key plant communities (Barmore, 2003; Singer, 1996). Historical photos of the exclosure sites showed that at the time of ungulate exclusion, the composition and structure were similar inside and outside of the exclosures (Barmore, 2003; Chadde & Kay, 1991; Kay, 1990).

# METHODS

During the growing seasons of 2021–2023, we sampled community composition and structure inside and outside of the YNP and GNF exclosures. A total of six aspen-dominated sites and four willow-dominated sites were sampled in this manner (Table 1).

We identified paired vegetation communities inside and outside of each exclosure. In selecting locations where transects could be established, we also looked for continuity of soils and topography to ensure that we were isolating effects of large ungulates and not inherent site differences. We established transects in each sampled vegetation type (i.e., aspen or willow) to determine fecal density, vegetation composition, and structure (Appendix S1: Figure S1). Two 30-m transects were established both inside and outside of exclosures within each sampled plant community. The starting point of each transect was randomly established.

Our transects inside and outside of the exclosures were as close to each other as was feasible, not sampling within 4 m of the exclosure fences to avoid possible fence-line effects. The global positioning system (GPS) coordinates at the start location of each transect were recorded (Table 1).

## Fecal counts

To index the current large ungulate use, we counted all fecal deposits in $2 \times 30$ m belt transects associated with the vegetation transects ($n = 2$ transects both inside and outside of exclosures at each site). Each ungulate fecal pile (individual defection event) within transects was identified to species (i.e., bison, elk, deer [*Odocoileus* spp.], or pronghorn [*Antilocapra americana*]).

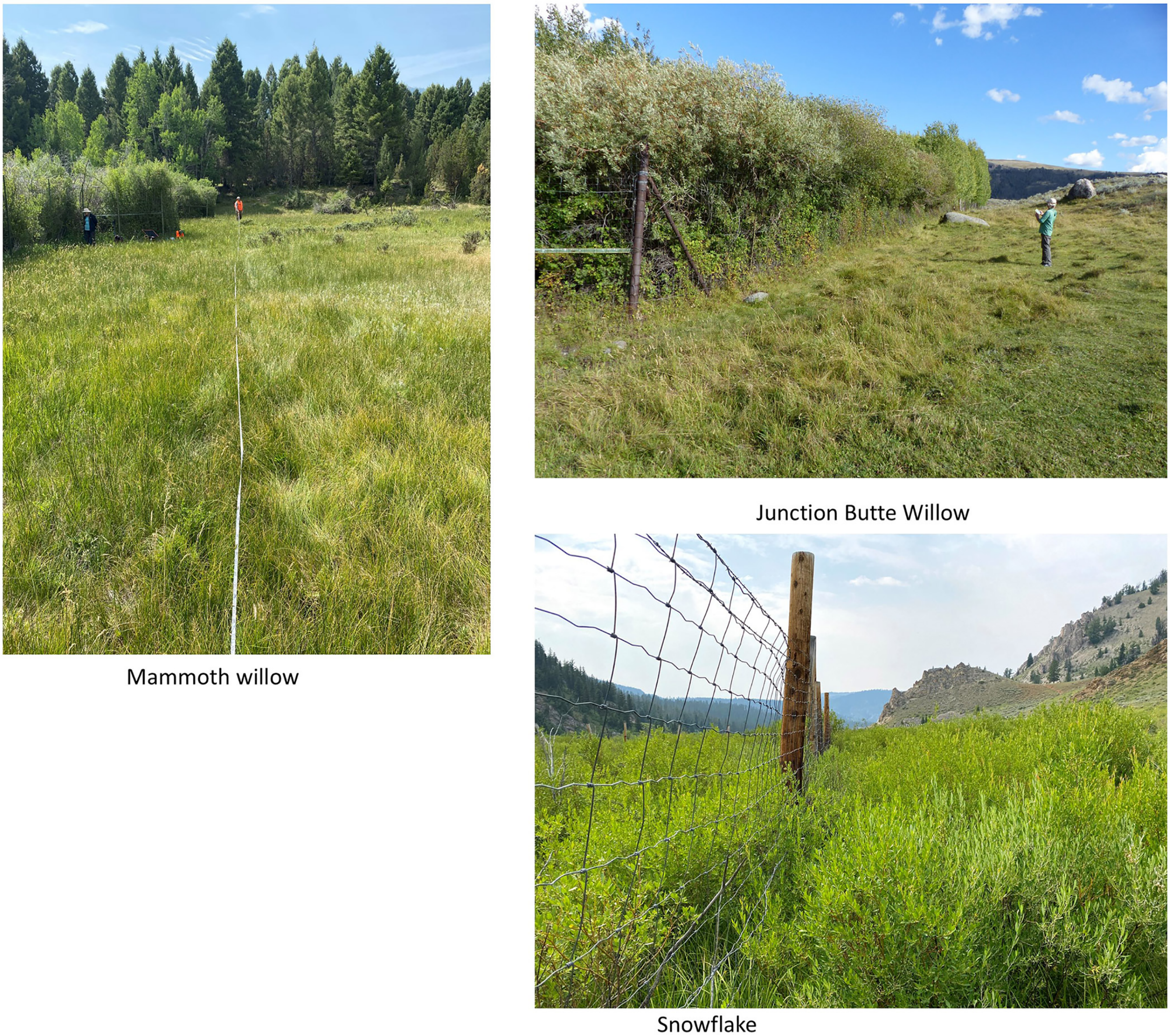


**FIGURE 1** Fence-line contrasts of sampled willow communities at the Mammoth, Junction Butte, and Snowflake exclosures. All exclosures are on the left side of each photo. Photo credits: J. Boone Kauffman and Robert L. Beschta.

## Vegetation sampling

Canopy cover of the overstory was digitally measured every 5 m along each transect ($n = 5$/transect) using a camera on a cell phone with the CanopyApp (University of New Hampshire, 2025). A wide-angle photo was taken of the overstory at 30 cm above the soil surface, and tree and shrub canopy was then determined with this application.

Vegetation community composition and the relative abundance of species were determined from nested frequency and plant canopy cover measurements following methods outlined by Kauffman et al. (2023). We determined plant frequency through the identification of plant species occurrence within each of three different plot sizes. The largest plot size was 50 × 50 cm, with nested plots 25 × 25 cm and 12.5 × 12.5 cm. For nested frequency measurements, each plant species that occurred in the plots was identified to the most specific taxonomic unit possible (Hitchcock & Cronquist, 2018). Species in the smallest nested plot were first identified and recorded, followed by the next largest nested plot and finally in the entire plot. Species encountered in the smaller nested plots are thus necessarily included in the frequency determination of their respective larger plots. Cover measurements included all plant species with a canopy cover ≥5% within the 25 × 25 cm plots.


**FIGURE 2** Fence-line contrasts of the aspen communities sampled at the Junction Butte, Lamar West, Porcupine, and Lamar East exclosures. At Lamar West, the exclosure is behind the transect outside of the exclosure; also note the dead aspen outside of the exclosure on the left. For the Porcupine site, the sampled willow is in the foreground and the aspen is behind. Photo credit: J. Boone Kauffman.

From the nested frequency data, we calculated relative abundance, species richness (number of species per site), species diversity, evenness, and similarity. The relative abundance of each species was determined by calculating the adjusted relative frequency scores for each species in each transect (Kauffman et al., 2023). The adjusted relative frequency of each species was calculated by adjusting scores for occurrence in the nested (smaller) plots. Occurrence in the smallest nested plot was given a score of 16, while occurrence in the middle-sized nested plot was given a score of 4 (i.e., the difference in plot area between the nested plot and the largest plot). Occurrence only in the largest plot was given a score of 1. Relative abundance is the sum of adjusted frequency scores for the individual species divided by the total adjusted frequency scores for all species encountered along the transect.

Species diversity was calculated using the Shannon index:

$$H' = -\sum p_i \ln(p_i).$$

The quantity $p_i$ is the proportion of relative abundance of the $i$th species relative to the sum of relative abundance for all species. We also report species diversity as the exp $H'$, which is equivalent to the number of equally common species required to produce the value of $H'$ (Magurran, 1988).

The similarity ($C_N$) between the sampled communities inside and outside of each exclosure was calculated using Sorenson's quantitative measure of similarity (Magurran, 1988). We also determined the similarity in species composition between all sampled aspen and willow communities both inside and outside of exclosures to determine how ungulates may influence heterogeneity in the landscape. Similarity ranges from 0 (no species in common) to 100 (all species and their relative abundance are identical) and was calculated using the formula:

$$C_N = 2jN/(aN + bN) \times 100,$$

where $jN$ is the sum of the lower of the two abundances (relative abundance) of all species inside or outside of an exclosure (or between any two communities being compared), $aN$ is the sum of relative abundance for a transect within an exclosure, and $bN$ is the sum of relative abundance for a transect outside of an exclosure.

## Shrub and tree overstory

Shrub and tree composition, density, and structure were measured in three 2 × 5 m plots in each transect (Appendix S1: Figure S1). In 2021, tree and shrub density and structure of individuals >1.3 m in height were measured by identifying them to species and measuring their diameter at 1.3 m in height (dbh). For multitrunked species (e.g., willows), the diameter (in centimeters) of each rooted stem within the plot was measured. From these data, we determined overstory plant density and basal area. In 2022 and 2023, we returned to the sites in YNP to measure the heights of all woody species in the plots. Heights of each individual plant encountered in the plots were measured to the nearest cm with either a tape measure or stadia rod. From these data, we determined the mean height and density of all trees and shrub species both inside and outside of the exclosures.

## Components of structural diversity

Structural diversity is an important vegetation metric as it influences such features as biodiversity, microclimate, resilience to disturbance, and resistance to climate change. This plant community characteristic requires identification and measurement of the frequency of occurrence of all layers of vegetation structure in the sampled stand. A total of 34 potential vegetative layers including surface layers, shrubs, deciduous trees, and conifers were defined for the sampled plant communities (Appendix S1: Table 2). At each 50 × 50 cm plot along the transect, all vegetation layers present above their vertical projection were identified. This provided a measure of the number of vegetation layers and their relative abundance of vegetation layers in the sampled stand.

Structural diversity was calculated using the Shannon index, where the quantity $p_i$ is the proportion of frequency of the $i$th vegetative layer (Appendix S1: Table S2) relative to the sum of frequency for all vegetative layers. We also report structural diversity as the exp $H'$, which is equivalent to the number of equally common vegetative layers required to produce the value of $H'$ (Magurran, 1988).

Another metric of assessing differences in structural diversity of willow communities entails measurement of crown area and volume. For the two willow-dominated stands in YNP (Mammoth and Junction Butte), we determined the crown area (in square meters) and crown volume (in cubic meters) of willows inside and outside of exclosures using regression equations presented in Kauffman and Cummings (2024) that estimate crown area and crown volume based on plant height (in meters).

We tested for differences in vegetation abundance, structure, and diversity inside and outside of exclosures using simple paired comparison tests (paired $t$-tests). Further, we tested for differences among plant communities at the landscape level using sites as replicates.

# RESULTS

## Grazing history and fecal densities outside of exclosures

The vegetation composition outside of exclosures reflects the grazing histories in the decades since their construction. At the time when the exclosures were built, elk were the dominant large ungulate on the Northern Range; in 1968, there were about 4000 elk and 100 bison in YNP (Allin, 2000). However, about two decades following exclosure construction their populations had increased to nearly 20,000 elk and 1000 bison (Beschta et al., 2020). Following the recovery of the Park's large carnivore guild in the mid-1990s, the Northern Range's elk population has declined to ~5000 animals in recent years, with most of these wintering outside the Park. In contrast, bison numbers inside the Park have now increased to historical highs of approximately 4000 animals (YNP annual ungulate counts reported by Beschta et al., 2020).

The measured fecal densities reflect the current grazing pressures in the Northern Range (Figure 3). Comparing the sample sites at YNP and GNF, it is apparent that there are differences in large ungulate composition and hence influences on community composition between the two management areas. Mean fecal density outside of the YNP exclosures was over 100-fold greater than outside of exclosures at GNF (2922 piles/ha compared to 21/ha; $p = 0.002$; Appendix S1: Table S3). With the exception of the Mammoth exclosure area, the vast majority of animal use in YNP was that of bison. Bison feces comprised 81% of all fecal piles encountered in transects outside of exclosures at YNP but were nonexistent at GNF, where only elk scat was encountered. Within

**TABLE 2** Total understory plant cover (in percentage), exotic species cover (in percentage), and dominant understory species of plant communities inside (ungrazed) and outside of exclosures (grazed) in the Northern Range of Yellowstone National Park and the Gallatin National Forest.

| | Total cover (%) | | Exotic cover (%) | | Dominant understory species (% cover) | |
|---|---|---|---|---|---|---|
| Site | Inside | Outside | Inside | Outside | Inside | Outside |
| Yellowstone National Park | | | | | | |
| Lamar East—Aspen | 61.4** | 39.3 | 12.4 | 13.5 | **ARUV (15.6)**, POPR (11.0), **POTR (8.4), BERE (6.0)**, GEVI (3.9), MAST (3.0) | FEID (18), POPR (13.0), **ARTR (2.3)** |
| Lamar West—Aspen | 79.3*** | 32.2 | 4.9** | 11.4 | **SYAL (43.2), BERE (13.2), ROWO (9.6), POTR (5.5)**, POPR (4.6) | BRIN (7.3), **SYAL (4.2)**, SYAD (4.1), POPR (2.9) |
| Mammoth—Aspen | 40.3** | 26.8 | 0.0*** | 22.1 | **BERE (11.7), SPLU (10.8), SYAL (9.8)**, GATR (2.8), Agrostis (2.0) | POPR (15.9), PHPR (5.2) |
| Junction Butte—Aspen | 29.3*** | 50.9 | 6.1*** | 23.1 | MAST (12.3), **POTR (6.6)**, POPR (4.2), **ROWO (2.4)** | POPR (21.9), ANMI (16.2), GEVI (2.7), **DAFR (2.4)**, SYAD (2.1) |
| Junction Butte—Willow | 40.9** | 62.3 | 0.5*** | 42.3 | **Salix spp. (16.0), RIIN (5.0)**, GATR (4.0) | POPR (42.2), CAREX-Ball (5.7), SYAD(2.6) |
| Mammoth—Willow | 71.9* | 83.8 | 14.2* | 21.7 | **Salix spp. (12.2)**, Agrostis sp. (17.1), POPR (9.6), MAST (8.5), GATR (5.4), **ROWO (2.6)** | JUBA (23.0), POPR (20.0), SYAD (17.5), POHI (4.6), **Salix spp. (4.0)** |
| Gallatin National Forest | | | | | | |
| Crown Butte—Aspen | 61.2 | 50.4 | 0.1*** | 11.6 | **SYAL (30.2), RIIN (7.5)**, MAST (5.7), FRVI (4.6), **ROWO (3.6), POTR (3.3)** | GEVI (15.7), POPR (10.4) |
| Porcupine—Aspen | 45.9** | 67.6 | 2.0*** | 15.4 | **BERE (22.6), SYAL (4.7), POTR (4.3), RIIN (3.7)**, THOC (2.7) | **POTR (24.1)**, POPR (14.2), **SYAL (4.0), BERE (2.5)** |
| Porcupine—Willow | 64.4** | 46.7 | 13.9 | 10.9 | **Salix spp. (17.3)**, POPR (13.4), **DAFR (6.2)**, SYFO (5.2) | **Salix spp. (6.6)**, POPR (10.6), JUBA (8.7), **DAFR (6.2)**, SYFO (4.4) |
| Snowflake—Willow | 75.9 | 89.7 | 2.2 | 1.1 | Caut (41.6), **Salix spp. (15.8)**, Agrostis sp.(7.2), CARO (4.2) | CAUT (47.9), **Salix spp. (30.8)**, CARO (7.9) |
| Summary data | | | | | | |
| Mean Yellowstone Aspen | 52.6 ± 11.1 | 37.3 ± 5.2 | 5.8 ± 2.6* | 17.5 ± 3.0 | ... | ... |
| Mean Gallatin Aspen | 53.6 ± 7.6 | 59.0 ± 8.6 | 1.0 ± 0.6* | 13.6 ± 1.8 | ... | ... |
| Mean Yellowstone Willow | 56.4 ± 15.5 | 73.0 ± 10.7 | 7.4 ± 6.4 | 32.0 ± 10.3 | ... | ... |
| Mean Gallatin Willow | 70.2 ± 20.8 | 68.2 ± 28.0 | 8.0 ± 4.1 | 6.0 ± 3.9 | ... | ... |
| Mean Aspen | 52.9 ± 7.3 | 44.5 ± 6.1 | 4.2 ± 1.9** | 16.2 ± 1.1 | ... | ... |
| Mean Willow | 63.3 ± 7.8 | 70.6 ± 2.2 | 7.7 ± 3.7 | 19.0 ± 8.8 | ... | ... |

*Note*: Species are reported as alpha codes, and the scientific and common names of all species names can be found in Appendix S1: Table S6. Shrub species appear in boldface while herbaceous species are in normal font. *$p$ = 0.1–0.05; **$p$ = 0.05–0.001; ***$p \geq 0.001$ when testing inside and outside of exclosures.

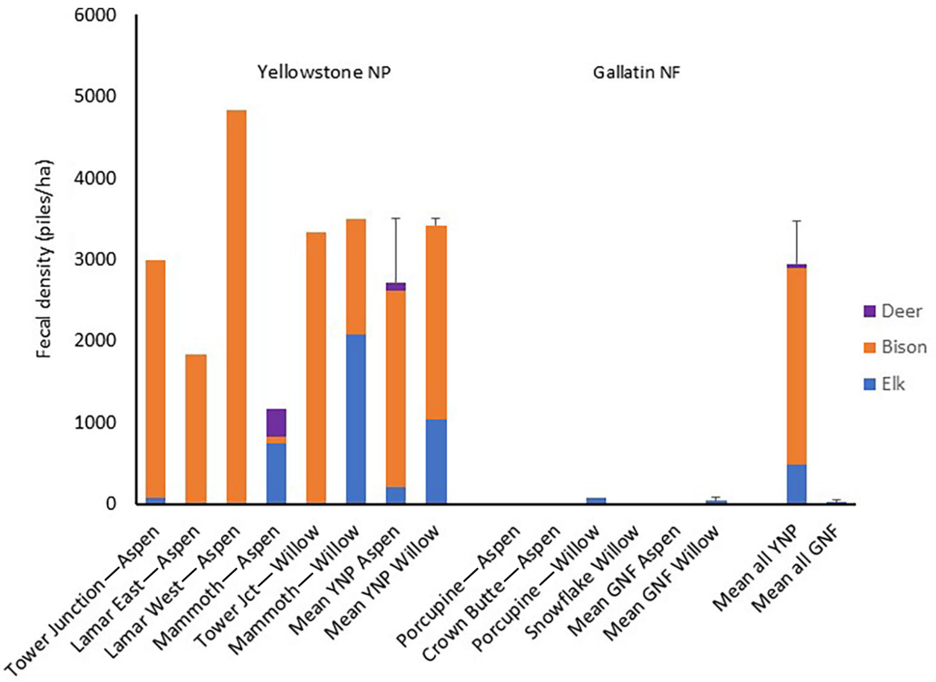


**FIGURE 3** Mean fecal density in sampled aspen and willow communities in Yellowstone National Park (YNP) and the Gallatin National Forest (GNF). Capped vertical lines above the means represent 1 SE.

YNP, high densities of elk scat were only encountered outside the Mammoth exclosure, an area close to a human population center within the Park and likely with a lower predation risk by wolves (Beschta & Ripple, 2016).

As expected, exclosures were effective in eliminating large ungulates, and we only encountered mule deer scat in one exclosure (i.e., the Mammoth exclosure). However, smaller herbivores such as rodents as large as yellow-bellied marmots (*Marmota flaviventris*) as well as small-medium carnivores such as coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) were observed inside the exclosures.

## Plant overstory cover

In general, there were dramatic and apparent differences in the structure and composition of plant communities inside and outside of exclosures (Figures 1 and 2). The largest and most obvious difference was the presence of an overstory canopy of aspen or willows inside the exclosures compared to a dominance of grasses or low shrubs on the outside. The mean canopy cover of aspen communities inside exclosures was 63% (range: 40%–76%) while mean overstory canopy cover outside of exclosures was 16% (range: 0%–48%; Figure 4). The only grazed aspen site with substantial overstory canopy was at the Mammoth site (48%). But here the composition differed such that the overstory was largely coniferous in the grazed sites and largely aspen in exclosures. The overstory cover outside of the Porcupine exclosure (GNF) was 26% and was largely comprised of young regenerating aspen.

The mean overstory cover within the willow-dominated stands was 40% (range: 29%–70%) inside exclosures and 6% outside of exclosures (range: 0%–23%; Figure 4). At YNP, overstory cover outside of exclosures was essentially absent (<1%) in the willow stands. Only the GNF Snowflake site had a similar overstory cover inside and outside the exclosure (Figure 1) with a mean overstory cover of 31% and 23% in the exclosed and grazed treatments, respectively.

## Species composition and species diversity

Species composition differences in grazed compared to exclosed sites were quite apparent (Table 2). While there were no significant trends in the total cover of understory vegetation, there were significant differences in the cover of exotic species. The mean cover of exotic species at YNP was fourfold greater in grazed aspen stands compared to excluded stands (16% vs. 4%, respectively; $p = 0.01$).

We also found that the dominant understory cover was largely shrubs (or herbaceous dicots) within exclosures and grasses (often exotic grasses) in the grazed sites (Table 2). For example, the understory shrub cover

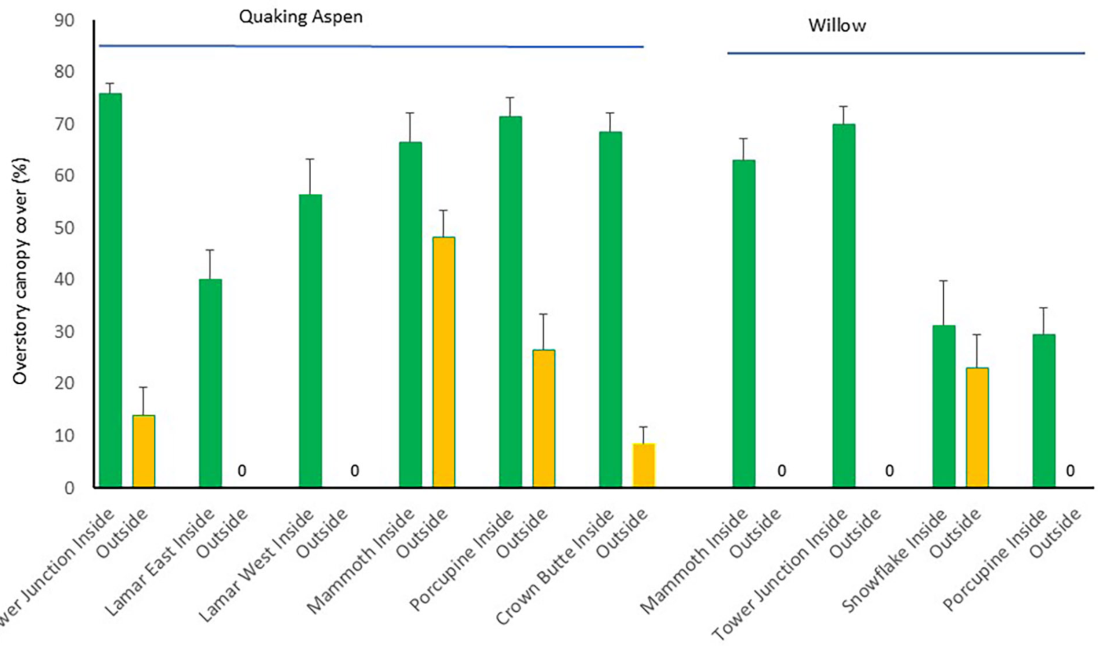


**FIGURE 4** The overstory canopy cover (mean + 1 SE) of sampled aspen and willow communities inside and outside of exclosures, Northern Range of Yellowstone National Park (YNP), and the Gallatin National Forest (GNF). Differences inside and outside of exclosures were significantly different ($p < 0.01$) at all sites except the Mammoth aspen ($p = 0.03$) and the Snowflake willow sites ($p = 0.46$).

at the Lamar West aspen was 71% in the exclosure and 7% in the grazed stand. Similarly, in the Mammoth willow site, understory shrub cover was 18% in the exclosure and 4% in the grazed stand.

The dominance of shrubs in the understory of exclosures and of grasses in grazed areas is also apparent in examining the relative abundance of understory species (Table 3). The relative abundance of shrubs was significantly greater ($p < 0.05$) in the exclosures compared to the grazed stands. For example, at the Lamar West aspen site the relative abundance of shrubs was 51% of the composition in exclosures but only 8% in grazed sites.

Species richness (S) was significantly higher in exclosed willow stands compared to grazed sites (a mean of 35 and 30, respectively, $p < 0.05$; Table 3). In contrast, S tended to be lower in the aspen exclosures compared to the grazed stands (a mean of 31 and 38, respectively; Table 3) although the difference was not statistically significant ($p > 0.10$). Similarly, we found that species diversity ($H'$ and exp $H'$) tended to be higher in grazed aspen stands but lower in grazed willow stands. This was largely reflective of an increase in exotic species and increases in species adapted to upland drier conditions in the grazed site (Appendix S1: Tables S4 and S5).

A total of 142 vascular plant species were identified in the transects (Appendix S1: Table S6). There was a relatively low degree of similarity of the species composition ($C_N$) when comparing the understory composition inside and outside of exclosures at all of the aspen sites as well as the willow sites in YNP (i.e., 13.9–39.6; Table 3). In contrast, we found a higher degree of similarity in the composition of the recovering Porcupine and Snowflake willow sites in the GNF (57.7 and 66.9, respectively). The higher degree of similarity reflects the resilience and recovery of native species in these ecosystems where grazing pressure is now lower than in the past.

We also calculated the similarity of aspen and willow stands within the different exclosures and found reasonably low degrees of similarity of the understory composition, reflecting that across the landscape there is a high degree of heterogeneity of species composition in intact plant communities. For example, we found that the composition within the exclosed Junction Butte and Mammoth willow communities was somewhat dissimilar with a $C_N$ of 32.2. In contrast, the composition of the willow stands outside of exclosures was quite similar with a $C_N$ of 52.3 (Appendix S1: Table S4; Kauffman, 2025). We also described unique species compositions with a low degree of similarity, comparing aspen and willow stands within both the Junction Butte and Mammoth exclosures. In contrast, the unique compositions were lost in grazed sites in that the degree of similarity between the grazed willow and aspen sites was quite high. For example, at Junction Butte, the $C_N$ of the aspen compared to willow stands was 29.4 inside exclosures and 78.5 outside of the exclosure. This suggests a loss of patch diversity/landscape heterogeneity due to current levels of ungulate use.

**TABLE 3** Understory species richness, species diversity indices ($H'$ and exp $H'$), cumulative relative abundance (in percentage) of exotic species and shrub species, and similarity index ($C_N$) of sampled exclosures in the Northern Range of Yellowstone National Park and the Gallatin National Forest.

| | Species richness (S) | | $H'$ | | Exp $H'$ | | Exotics (%) | Shrubs (%) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Site** | **Inside** | **Outside** | **Inside** | **Outside** | **Inside** | **Outside** | **Inside** | **Outside** | **Inside** | **Outside** | $C_N$ |
| Aspen | | | | | | | | | | | |
| Mammoth | 24 | 31 | 2.43 | 2.62 | 11.40 | 13.69 | 2.7 | 50.6 | 43.1 | 14.0 | 24.1 |
| Lamar East | 37 | 29 | 2.78 | 2.42 | 16.04 | 11.27 | 21.0 | 27.3 | 29.2 | 1.6 | 24.2 |
| Lamar West | 33 | 46 | 2.48 | 2.97 | 11.99 | 19.48 | 17.5 | 33.2 | 50.7 | 8.1 | 36.4 |
| Junction Butte | 27 | 38 | 2.25 | 2.74 | 9.45 | 15.48 | 29.3 | 23.2 | 7.8 | 1.4 | 39.6 |
| Crown Butte | 30 | 42 | 2.62 | 3.07 | 13.74 | 21.49 | 7.4 | 26.1 | 30.2 | 3.71 | 37.5 |
| Porcupine | 34 | 40 | 2.49 | 2.83 | 12.06 | 16.95 | 16.6 | 29.3 | 42.8 | 21.2 | 37.8 |
| Willow | | | | | | | | | | | |
| Junction Butte | 33 | 30 | 2.96 | 2.62 | 19.25 | 13.76 | 7.6 | 25.6 | 39.4 | 6.1 | 13.9 |
| Mammoth | 31 | 26 | 2.64 | 2.36 | 14.06 | 10.54 | 28.1 | 25.6 | 6.9 | 4.7 | 26.5 |
| Porcupine | 46 | 42 | 2.63 | 2.88 | 13.88 | 17.81 | 26.5 | 24.3 | 7.9 | 3.4 | 57.7 |
| Snowflake | 28 | 22 | 2.32 | 2.06 | 10.16 | 7.88 | 21.3 | 11.9 | 6.6 | 10.1 | 66.9 |
| Mean All sites | 32.2 ± 1.4 | 34.6 ± 2.5 | 2.56 ± 0.04 | 2.66 ± 0.10 | 13.20 ± 0.92 | 14.84 ± 1.34 | 17.8 ± 2.7* | 27.7 ± 3.1 | 26.5 ± 5.6** | 7.4 ± 2.0 | |
| Mean Aspen | 30.8 ± 2.0 | 37.7 ± 2.7 | 2.51 ± 0.07 | 2.78 ± 0.10 | 12.45 ± 0.91 | 16.39 ± 1.53 | 15.8 ± 3.8* | 31.6 ± 4.0 | 34.0 ± 6.2** | 8.3 ± 2.2 | |
| Mean Willow | 34.5 ± 4.0** | 30.0 ± 4.3 | 2.64 ± 0.13 | 2.48 ± 0.18 | 14.34 ± 1.87 | 12.50 ± 2.14 | 20.9 ± 4.7 | 15.2 ± 8.1 | 15.2 ± 8.1 | 6.1 ± 1.5 | |

*Note*: For combined sites, values are mean ± 1 SE. Individual species frequency and relative abundance may be found in Appendix S1: Table S4. For the combined sites, *$p$ = 0.1–0.051; **$p$ = 0.05–0.001.

## Overstory composition and structure

Total shrub density, height, and structure inside and outside at the four exclosures and six sites sampled at YNP were dramatically different (Figures 5–8). Aspen density was consistently greater inside exclosures compared to sampled sites outside of exclosures (Figure 5). For example, at Lamar East, the density of aspen was 20,500/ha and 833/ha inside and outside of exclosures, respectively. Densities of shrubs most common to aspen understories (e.g., Wood's rose [*Rosa woodsii*] and snowberry [*Symphoricarpos albus*]) were also consistently higher in exclosures compared to grazed areas. In contrast, shrubs more common to semiarid uplands were most abundant in the grazed aspen sites. For example, at YNP we encountered Mountain big sagebrush in all of the grazed sites. Big sagebrush was the most abundant shrub in the grazed sites at Lamar East with a density of 9833 plants/ha.

There was a rich and diverse composition of shrubs and trees within the exclosures; a total of 16 species were encountered in aspen stands within exclosures, compared to 10 species encountered in grazed sites. The influences of large ungulates on the woody plant composition were quite apparent. The mean height of quaking aspen within the exclosures ranged from 346 cm at Lamar East to 619 cm at Mammoth (Figure 6). In contrast, the mean height of aspen in the grazed sites was only 18 cm. Other shrub and tree species encountered both inside and outside of the exclosures were consistently taller within the exclosures. The notable exception was big sagebrush, which was the tallest woody plant in the grazed sites associated with the Lamar East, Lamar West, and Junction Butte sites. At Mammoth, another upland species of dry habitats, Rocky Mountain juniper (*Juniperus scopulorum*) was the tallest tree encountered in the grazed aspen site.

There were 11 shrub and tree species encountered in the exclosed willow-dominated communities compared to 6 species encountered in grazed sampled stands (Figure 7). Total shrub densities were quite high for both

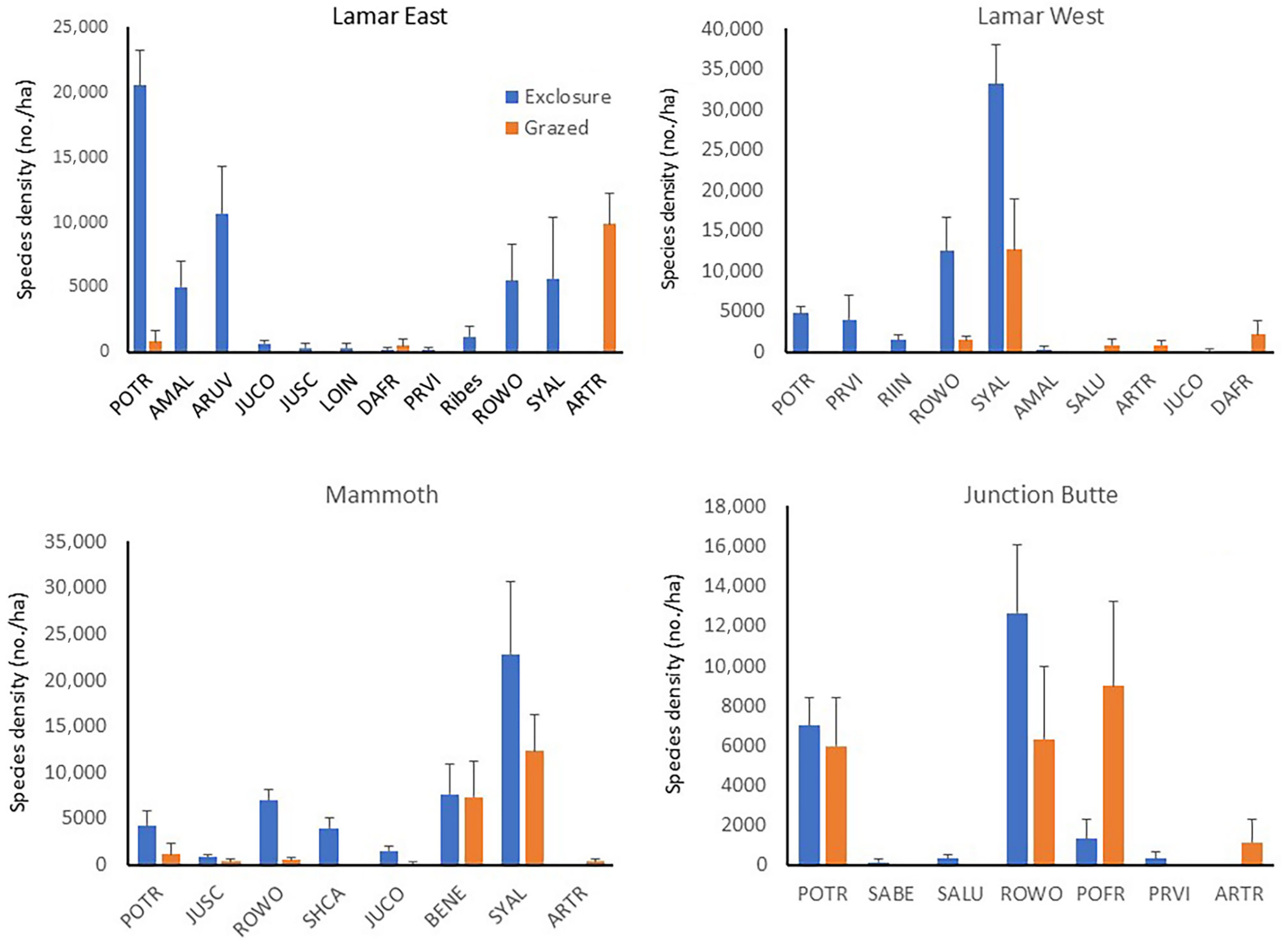


**FIGURE 5** The density of all tree and shrub species encountered inside and outside of exclosures in quaking aspen communities, Northern Range of Yellowstone National Park (mean + 1 SE). The species are POTR, *Populus tremuloides*; AMAL, *Amelanchier alnifolia*; ARUV, *Arctostaphylos uva-ursi*; JUCO, *Juniperus communis*; BERE, *Berberis repens*; JUSC, *Juniperus scopulorum*; LOIN, *Lonicera involucrata*; DAFR, *Dasiphora fruticosa*; PRVI, *Prunus virginiana*; RIIN, *Ribes inermis*; Ribes, *Ribes* spp.; ROWO, *Rosa woodsii*; SHCA, *Shepherdia canadensis*; SABE, *Salix bebbiana*; SALU, *Salix lutea*; SAGE, *Salix geyeriana*; SYAL, *Symphoricarpos albus*; and ARTR, *Artemisia tridentata*.

exclosed and grazed sites, with mean densities exceeding 10,000/ha at Mammoth and 22,667/ha at Junction Butte. However, there were dramatic structural differences. The mean height of willows within the exclosures was 303 cm for Yellow willow (*S. lutea*), 306 cm for Geyer's willow (*S. geyeriana*), and 371 cm for Bebb's willow (*S. bebbiana*). In contrast, mean heights of willows in grazed sites were <35 cm at Mammoth and <12 cm at Junction Butte. Less palatable species adapted to drier habitats (i.e., shrubby cinquefoil [*Dasiphora fruticosa*]) were the tallest species in the grazed sites. While the height differences in willows between grazed and exclosed sites were striking, willow seedlings and stunted plants were abundant in the grazed sites, suggesting that recovery to shrub dominance would still be possible with lower levels of large ungulate use.

The resilience of willow stands following a diminution of ungulate pressure can be evidenced at the Snowflake willow site on the GNF (Figure 8), a location with current low levels of herbivory. At this location, there was no difference in the stem density of willows ≥1.3 m in height between the grazed and exclosed sites (Figure 8). For all other willow sites, stem densities of tall willows were significantly greater within the exclosures compared to adjacent grazed areas ($p = 0.07$). There were no willows exceeding 1.3 m in height in the heavily grazed willow sites outside of the exclosures at YNP.

In aspen communities, there also were significant differences ($p = 0.003$) in the mainstem densities of trees and shrubs (≥1.3 m height) when comparing inside and outside of exclosures. In the sampled grazed aspen stands, we only encountered woody species ≥1.3 m

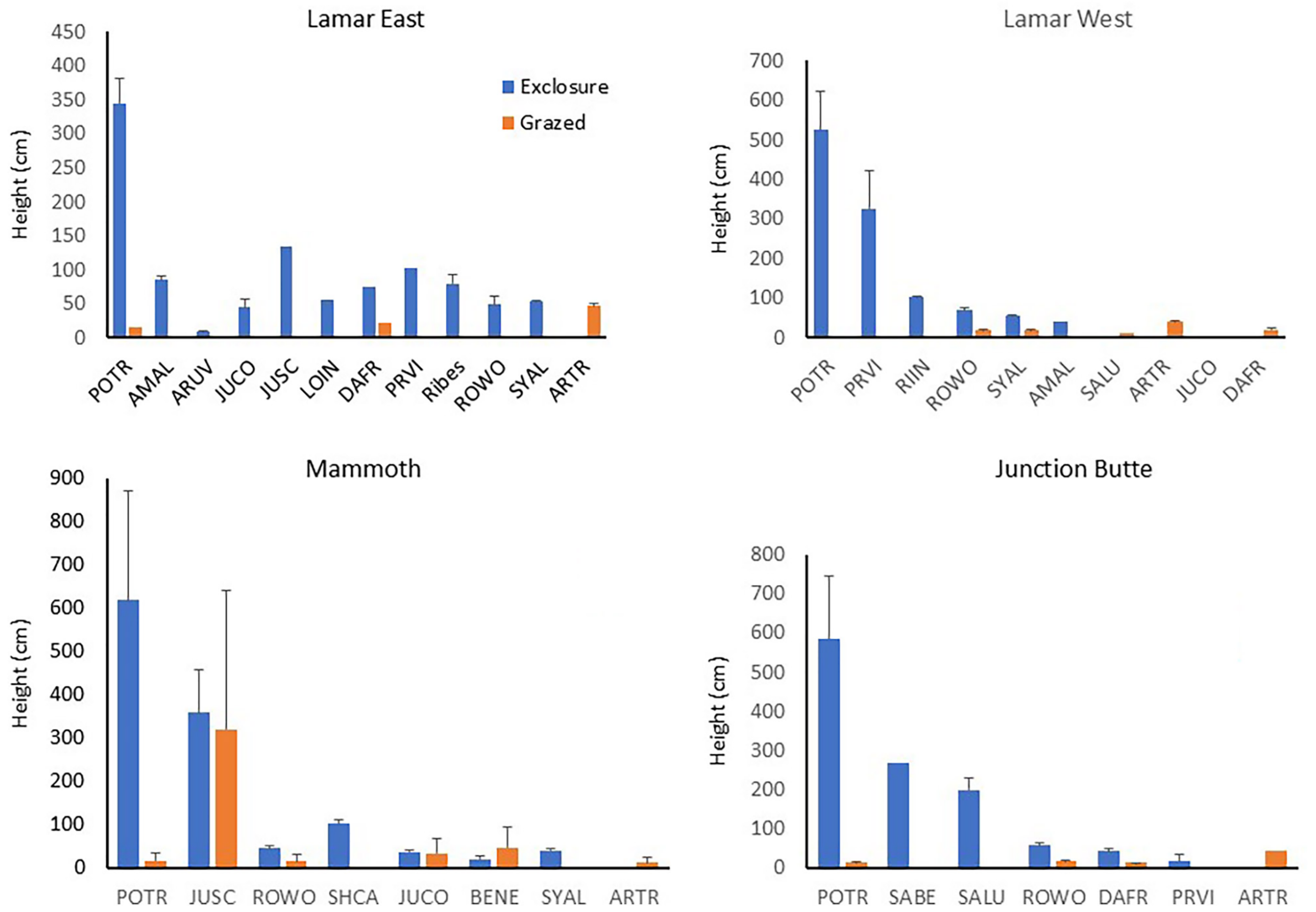


**FIGURE 6** The heights of tree and shrub species in exclosed and grazed aspen communities, Northern Range of Yellowstone National Park (mean + 1 SE). The species are POTR, *Populus tremuloides*; AMAL, *Amelanchier alnifolia*; ARUV, *Arctostaphylos uva-ursi*; JUCO, *Juniperus communis*; JUSC, *Juniperus scopulorum*; BERE, *Berberis repens*; LOIN, *Lonicera involucrata*; DAFR, *Dasiphora fruticosa*; PRVI, *Prunus virginiana*; RIIN, *Ribes inermis*; Ribes, *Ribes* spp.; ROWO, *Rosa woodsii*; SHCA, *Shepherdia canadensis*; SABE, *Salix bebbiana*; SALU, *Salix lutea*; SAGE, *Salix geyeriana*; SYAL, *Symphoricarpos albus*; and ARTR, *Artemisia tridentata*.

height at the Mammoth and Porcupine sites (Figure 8). The composition of the overstory was largely coniferous at the Mammoth site (Figure 6). In contrast, at the grazed Porcupine site (GNF) the taller vegetation was comprised of young aspen that had recently attained these heights (≥1.3 m) following a recent diminution of grazing pressure (Appendix S1: Figure S2).

## Structural diversity

Most of the grazed sites were limited to possessing vegetation layers of herbaceous, dead wood, and low shrubs. In contrast, sampled stands in exclosures also had mid to tall shrub and tree layers containing both living and dead components. This is reflected in significant differences ($p < 0.001$) in the structural diversity (exp $H'$) when testing for differences between grazed and exclosed sites for both aspen and willow communities (Figure 9). Structural diversity of aspen stands within exclosures was almost three times greater than that in grazed sites; the mean exp $H'$ for the exclosed and grazed aspen stands was 15.2 and 5.9, respectively. Differences in the structural diversity in sampled willow stands were even greater; the exp $H'$ was 11.1 within exclosures and 3.3 in grazed sites.

Another indicator of differences in structural diversity associated with herbivory is examination of willow structure within and outside of the two YNP exclosures with willow communities (Table 4) where we found major differences in heights, crown area, and crown volume. For example, at the Junction Butte site the mean height of willows was 428 cm inside of exclosures and 13 cm outside of the exclosures (a 33-fold difference). Differences in mean crown area and crown volume were even more dramatic. The mean crown area of willows at Junction Butte was 15.3 $m^2$ and 0.01 $m^2$ inside and outside of exclosures, respectively (a 1500-fold difference). Further,

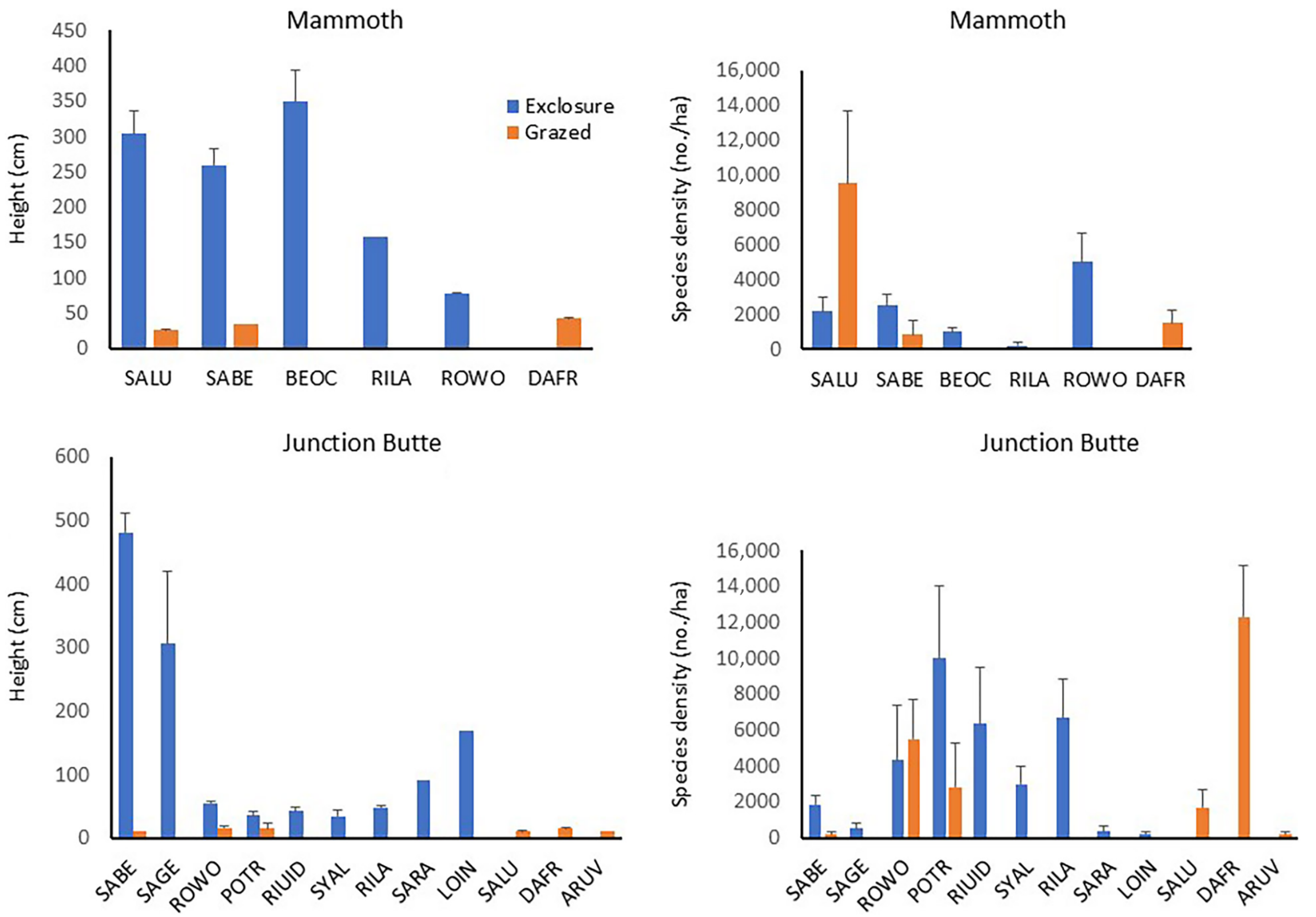


**FIGURE 7** The height and density of tree and shrub species in exclosed and grazed willow-dominated communities, Northern Range of Yellowstone National Park (mean + 1 SE). The species are SABE, *Salix bebbiana*; SAGE, *Salix geyeriana*; SALU, *Salix lutea*; ROWO, *Rosa woodsii*; BEOC, *Betula occidentalis*; RILA, *Ribes lacustre*; DAFR, *Dasiphora fruticosa*; LOIN, *Lonicera involucrata*; POTR, *Populus tremuloides*; RUID, *Rubus idaeus*; SARA, *Sambucus racemosa*; SYAL, *Symphoricarpos albus*; and ARUV, *Arctostaphylos uva-ursi*.

the mean crown volume of willows at this site was 56.0 $m^3$ inside, compared to 0.001 $m^3$ outside of the exclosure (a 55,000-fold difference; Table 4).

## DISCUSSION

Although willow- and aspen-dominated communities currently only occupy a small fraction of the Northern Range landscape (Brown et al., 2006; Chadde & Kay, 1991), their importance in terms of biological diversity is well known (DeByle & Winokur, 1985; Kauffman et al., 2001). Within ungulate exclosures, the return of aspen forest and tall willow dominance demonstrates the resilience and capacity for recovery of these keystone communities in the Greater Yellowstone Ecosystem. The shift in structural diversity and composition within exclosures suggests that positive feedbacks to other beneficial ecosystem processes are underway, including increased species and habitat diversity, increased carbon sequestration, and a greater adaptive capacity to climate change.

We found considerable differences in ungulate effects between the YNP and GNF study areas. In YNP, bison are now the most prevalent large herbivore at sampled sites in the eastern portion of the Northern Range (i.e., Junction Butte, Lamar West, and Lamar East), with elk locally abundant around Mammoth, in the western portion of the Northern Range. Results from these four YNP sites, which are located in areas of exceptionally high ungulate use, suggest a continuing loss of aspen- and willow-dominated communities. In general, these communities are being replaced by grasslands dominated by exotic species or species adapted to semiarid environments. The overall effect is a simplification and desertification of the Park's most biologically diverse plant communities, as well as a decline in food resources and physical habitats for numerous species of wildlife. In contrast, results from the GNF Snowflake and Porcupine exclosures indicate

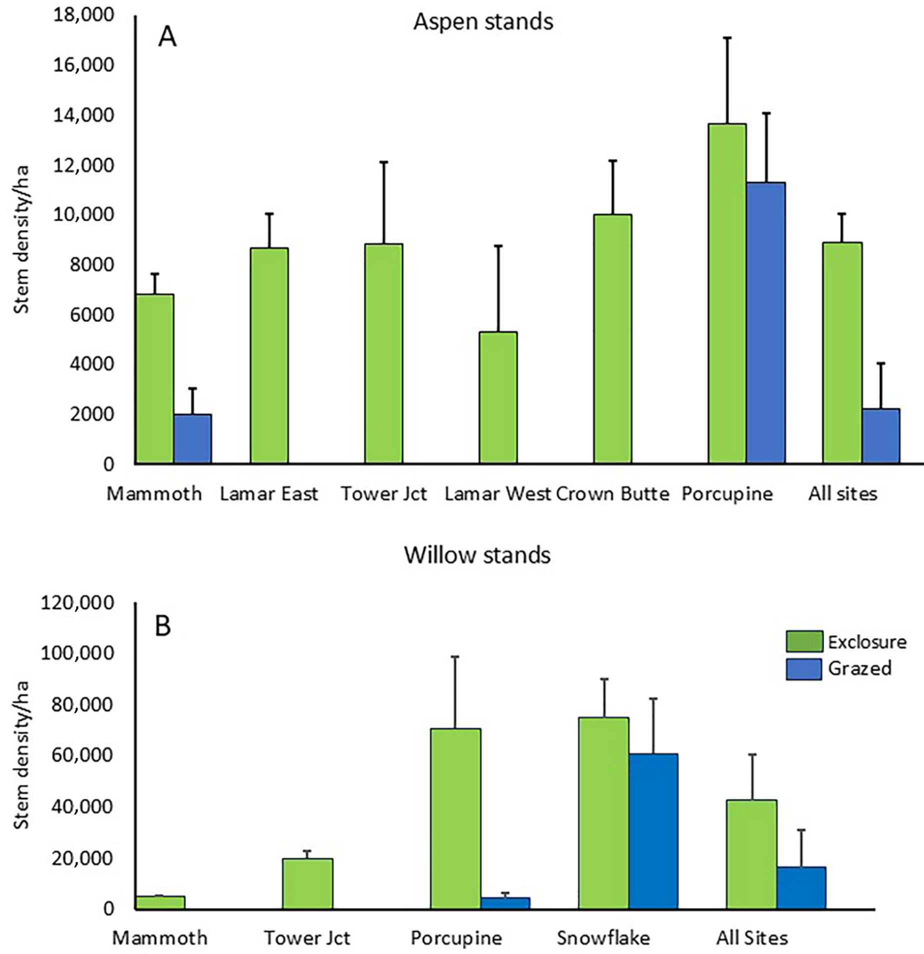


**FIGURE 8** Total rooted stem density (number/hectare; mean + 1 SE) of all woody species combined that were ≥1.3 m in height in (A) aspen and (B) willow communities inside and outside of exclosures, Northern Range of Yellowstone National Park and Gallatin National Forest.

willow and aspen communities outside of exclosures are in various stages of recovery.

## Understory composition and structure

A number of studies have quantified how large ungulates in unnaturally high numbers affect ecosystem composition and structure in western montane riparian ecosystems (Chadde & Kay, 1991; Coles-Ritchie et al., 2007; Kauffman, Beschta, et al., 2022; Kauffman, Coleman, et al., 2022). At least in portions of YNP's Northern Range, where the exclosures are situated, bison appear to be exerting effects similar to those associated with overgrazing by domestic livestock such as has been identified on public lands in the west (Beschta et al., 2013; Kauffman, Beschta, et al., 2022). Similar to the compositional response at YNP, Kauffman, Coleman, et al. (2022) found that domestic cattle grazing maintained the presence of exotic dominants and the diminution of native and wetland obligate species in montane riparian zones of the American West.

At the Junction Butte, Lamar West, and Lamar East exclosures, >97% of fecal piles encountered in sampling transects were those of bison (Figure 3). These findings are consistent with those of Beschta et al. (2020) who found that the overall foraging pressure from bison in the Northern Range began to exceed that of elk in 2007 and is currently ~10 times greater than that of elk. The notable exception to this is outside of the Mammoth exclosure, where the presence of large numbers of visitors tends to create a region of low predation risk for elk from wolves and other large carnivores—a situation known as human shielding (Beschta et al., 2018). At this exclosure, ≈60% of the overall fecal density was that of elk.

In riparian zones of YNP, Kauffman et al. (2023) found significant declines in species diversity and willow cover with increasing levels of bison use. They also found a strong inverse relationship between bison use and the prevalence of wetland vegetation. These results suggest that current densities of bison in YNP's Northern Range may be contributing to: (1) desertification; (2) a lowered

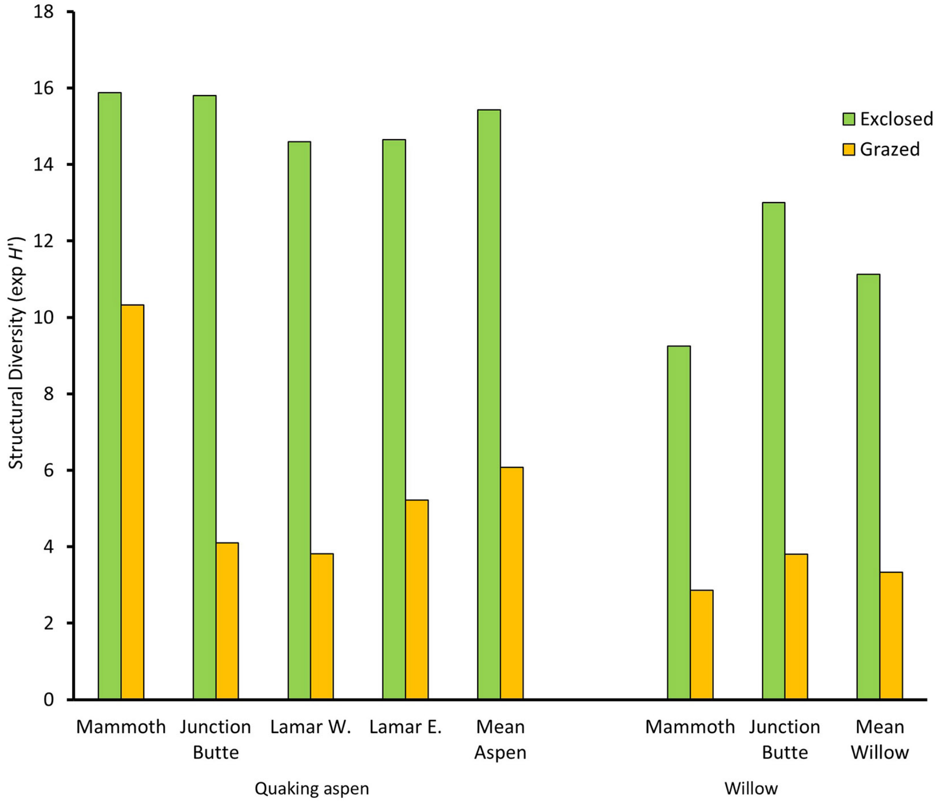


**FIGURE 9** The structural diversity (exp $H'$) of aspen and willow stands inside and outside of exclosures, Yellowstone National Park. The differences in exp $H'$ between exclosure and grazed sites were significant for both aspen and willow communities ($p < 0.001$).

**TABLE 4** Height, crown area, crown volume, and density of willows inside and outside of exclosures, Northern Range of Yellowstone National Park (mean ± 1 SE).

| Location | Height (cm) | Crown area ($m^2$) | Crown volume ($m^3$) | Density (no./ha) |
|---|---|---|---|---|
| Mammoth | | | | |
| Inside | 268 ± 38 | 4.98 ± 2.04 | 11.80 ± 8.47 | 4667 ± 803 |
| Outside | 27 ± 2 | 0.025 ± 0.005 | 0.005 ± 0.001 | 10,333 ± 4387 |
| Ratio Inside: outside | 10 | 199 | 2360 | 0.45 |
| Percent Increase | 893 | 16,500 | 235,900 | −55 |
| Junction Butte | | | | |
| Inside | 428 ± 79 | 15.34 ± 4.3 | 55.95 ± 18.29 | 2333 ± 558 |
| Outside | 13 ± 2 | 0.01 ± 0.002 | 0.001 ± 0.001 | 1833 ± 980 |
| Ratio Inside: outside | 33 | 1534 | 55,950 | 1.27 |
| Percent Increase | 3192 | 153,300 | 5,594,900 | 27 |

*Note:* Crown area is elliptical crown area (in square meters) and crown volume is the ellipsoidal crown volume (in cubic meters).

resistance to the stresses associated with a changing climate; (3) a shift from net carbon sinks to sources of greenhouse gases; (4) biotic impoverishment; and (5) the loss of ecosystem services provided by native plant communities. The species composition and structure in exclosed compared to grazed aspen and willow communities strengthen these conclusions.

## Effects of overuse by large ungulates and resilience of aspen and willow communities

Our composition and similarity data show there is considerable heterogeneity among the willow and aspen stands within the YNP exclosures (Table 3). Geremia et al. (2019) detailed how current densities of bison, as "ecosystem engineers," are creating additional grasslands in the Northern Range. This conversion of willow, aspen, and other plant assemblages to grasslands is homogenizing the landscape, thus contributing to losses in structural diversity, species diversity, and wildlife habitat. The vegetation response within exclosures at YNP and outside of exclosures at the Snowflake and Porcupine exclosures at GNF suggests that a reduction in herbivore pressure in the Northern Range would restore losses in landscape diversity that have occurred as a result of management decisions leading to overuse by large ungulates.

Although exotic grasses and plants are typically more suited to dry upland communities, they tended to dominate the grazed aspen and willow sites at YNP (Table 2). In contrast, berry (fruit)-producing shrubs were a dominant feature within ungulate exclosures. Berry-producing shrubs and herbs were >15% cover in all exclosed aspen stands, but ≤4% in grazed stands (Table 2). In some instances, these differences were striking, such as for aspen stands at the Lamar West exclosure where the cover of fruit-producing understory shrubs was 66% inside the exclosure and only 4% on the outside. In portions of the YNP Northern Range with low bison use and that have had a decline in elk use following the reintroduction of wolves, Beschta and Ripple (2012) found increases in heights and fruit production for berry-producing shrubs. A wide range of terrestrial faunal species in YNP benefit from the food-web support provided by berry-producing shrubs, including bears, birds, small mammals, and invertebrates (Beschta & Ripple, 2012). The general reduction in berry-producing shrubs that continues to occur outside of YNP exclosures underscores one of the important pathways that contemporary levels of ungulate use, principally from bison, are exerting on the biodiversity of the Northern Range.

## Shrub species height and density

Since their establishment in the late 1950s and 1960s, several studies have reported dramatic increases in the height and density of willows within the YNP exclosures (Barmore, 2003; Chadde & Kay, 1991; Painter et al., 2023; Singer, 1996). When these exclosures were initially constructed, Barmore (2003) reported that average willow heights were about 46 cm at the Mammoth site and 41 cm at the Junction Butte site. Singer (1996) reported that by 1986, the crown area of individual plants had increased by 200%–500% and that by 1989, willows were 200%–400% taller inside exclosures compared to outside. This trend has apparently continued to the present (Figures 6 and 7). While different methodologies complicate comparisons, the mean crown areas of willows were 200%–2600% greater by 2023. Even more demonstrative of changes in structural diversity and habitat availability are the estimated increases in willow crown volume, where we found crown volume was 2400-fold (Mammoth) and 55,000-fold (Junction Butte) greater in exclosures compared to grazed areas (Table 4). These results are significant as Baril et al. (2011) found that increased structural complexity of willow communities allowed for greater bird richness, abundance, and diversity in the Northern Range.

In 2022, the mean heights of willows outside of exclosures at the Mammoth and Junction Butte sites were 23 and 13 cm, respectively. Incredibly, these heights were lower than those measured some 63 and 60 years previously, when the exclosures were constructed. Additionally, photos taken inside and outside of the Mammoth exclosures in 1956–1958 (see Barmore, 2003) clearly show heavily browsed willows 1–3 m in height that were no longer present when we sampled these sites in 2022; another example of the declines in willow structure that have occurred on heavily grazed areas of the Northern Range.

Singer (1996) reported that height-suppressed willows, subjected to intensive browsing pressure by elk in communities outside of the YNP exclosures, persisted for three decades as part of the vegetation understory. Our sampling, which occurred six decades after the earliest exclosure measurements, indicates that willows continue to be present as a component of the grass/herb layer with a mean density of approximately 10,000/ha at the predominately elk-grazed Mammoth site and approximately 2000/ha at the predominately bison-grazed Junction Butte site (Figure 5). Willows ≥1.3 m tall are now nonexistent outside the Junction Butte and Mammoth exclosures, compared to stem densities of 5000–20,000/ha for this height class inside the exclosures (Figure 8). This persistence of browsing-suppressed willows suggests that recovery to a willow-dominated site would be possible with a significant reduction in grazing pressure. Such a recovery is also indicated by tall willow stem densities outside the Porcupine and Snowflake exclosures on the GNF, where herbivore pressure has moderated since the introduction of wolves (Ripple & Beschta, 2004). At the Snowflake site, riparian willow stem densities exceed 60,000/ha both inside and outside of the exclosure (see also Figure 1).

In examining the shrub component outside of the YNP exclosures, Singer (1996) reported a shift to unpalatable shrubs adapted to drier environments. At that time, the density of shrubby cinquefoil, a less palatable shrub for elk, was three times greater outside of exclosures than inside the exclosures. We found that this trend toward a dominance of an unpalatable species adapted to drier (semiarid) environments is continuing outside of exclosures, but not inside. For example, the density of shrubby cinquefoil was 9000/ha at grazed sites outside of Junction Butte, versus 1333/ha inside the exclosure. Further, we found densities of big sagebrush (a species adapted to semiarid upland environments) had densities of 800–9833/ha outside of the exclosures aspen sites (Figure 5) but absent inside the exclosures. This would indicate an ongoing and long-term trend toward desertification of aspen and willow communities to upland semiarid shrub-steppe communities as a result of persistently high levels of ungulate herbivory, mostly bison. This further suggests that contemporary management of YNP's bison herd appears to be amplifying the effects of climate change as well as loss of biodiversity values.

The establishment of the YNP exclosures occurred when the aspen were already in a degraded state, with only a few remaining overstory trees present inside and outside of exclosures (Barmore, 2003; Kay, 1990; Painter et al., 2023). At all of the sampled exclosures, the remnant mature aspen had disappeared by the time of our sampling (e.g., see Appendix S1: Figure S2 of the Porcupine exclosure though time). The mean height of aspen sprouts at the time of exclusion was 64 cm at the Lamar East site, 58 cm at the Mammoth site, and 25 cm at Junction Butte. Seven years after exclusion, the mean aspen height inside the Mammoth exclosures was 109 cm (Barmore, 2003), increasing to 619 cm by 2023 (Figure 6).

Similar to willows, mean aspen heights and stem densities outside of YNP exclosures are now lower than they were in 1958. For example, at the Mammoth site aspen height outside the exclosure was 38 cm in 1958 and had decreased to 18 cm in 2022 (Figure 6; Barmore, 2003). Aspen densities outside of exclosures have also decreased, from about 11,000 stems/ha in 1958 to 1167 stems/ha in 2022 (Figure 5).

## Ecological roles of bison

Limited archaeological evidence suggests that bison have been present in the Greater Yellowstone Ecosystem for >10,000 years (Cannon et al., 2020). Further, historical accounts suggest that bison were present in some Intermountain valleys of the Rocky Mountains in the first half of the 19th century (Bailey, 2016). How does archaeological and historical evidence support or conflict with ecological evidence? Historical observations cannot be used to estimate population sizes, relative abundances, seasonal movements, migration routes, or periods of occupancy with certainty (Whittlesey et al., 2018). Based largely on a review of the historical accounts of bison inside and outside of YNP, Keigley (2019) concluded that bison played no significant role in the ecological processes that shaped the Park's prehistoric landscape. Interpreting historical and current photos coupled with measurements of recent shifts in the geomorphic structure of the rivers and streams in the Lamar valley, Beschta and Ripple (2019) also concluded bison were not an important factor shaping ecosystems of the Northern Range prior to Park establishment in 1872.

This study reports dramatic differences in the composition and structure of plant communities inside and outside of exclosures. Other studies have quantified bison influences on aspen structure, streambank structure, channel sinuosity, and riparian ecosystems of YNP (Beschta et al., 2020; Kauffman et al., 2023; Painter et al., 2023). Collectively, these studies demonstrate that the historic vegetation composition and geomorphic structure of the Lamar valley could not have formed with current bison densities and that these densities are now resulting in widespread declines in ecosystem structure and biodiversity.

The likelihood that bison could not have played a significant evolutionary role is also manifested in the vegetation composition of the uplands surrounding riparian areas and aspen stands communities of the Park. The dominant plant assemblage across the uplands of the Northern Range is predominately Mountain big sagebrush/Idaho fescue. These are shrublands with an understory largely dominated by caespitose grasses (e.g., Idaho fescue), as opposed to grassland communities on the Great Plains that are dominated mainly by rhizomatous/stoloniferous species (e.g., blue grama [*Bouteloua gracilis*]). Unlike rhizomatous/stoloniferous grasses, the caespitose grasses in the Park did not co-evolve with significant populations of large ungulates and thus are more susceptible to degradation and exotic replacement when intensive ungulate herbivory occurs (Mack & Thompson, 1982). For shrub-steppe vegetation at the moist end of the precipitation gradient (annual precipitation >450 mm), such as is the situation for the Northern Range (Beschta & Ripple, 2016), the rhizomatous Kentucky bluegrass (*Poa pratensis*) increases in abundance with high levels of ungulate use. This effect is reflected in our results where Kentucky bluegrass cover was consistently higher in grazed compared to exclosures sites (Tables 2 and 3).

## Is there any evidence of a trophic Cascade?

When a top trophic-level predator significantly affects the behavior or density of a prevalent herbivore, and this interaction in turn significantly alters or influences vegetation, a "trophic cascade" occurs (Ripple & Beschta, 2004). If a trophic cascade were to occur, we would expect there to be few differences inside and outside of the exclosures in affected environments. Even though various studies have documented changes in woody plant communities across various portions of the Park's Northern Range following the reintroduction of wolves (e.g., see synthesis by Beschta & Ripple, 2016), our results indicate that large ungulate use outside of YNP's exclosures, principally bison, is masking, reversing, and/or preventing the demonstration of a trophic cascade. While the reintroduction of wolves has mainly affected elk populations, their primary prey, they have not affected, to any measurable degree, bison populations in the Park.

In contrast to the exclosures at YNP, a different scenario exists at the Snowflake and Porcupine exclosures on the GNF, where bison are absent and wolves returned to the upper Gallatin basin in the mid-1990s after approximately seven decades of absence (Ripple & Beschta, 2004). At the Snowflake site, there are currently few differences in willow height and species composition inside and outside of the exclosure (Figure 1; Table 3). Furthermore, exotic cover was quite low (≤2%) and the abundance of native grasses and sedges (*Carex* spp.) was similar inside and outside of these exclosures (Tables 2 and 3). This is a relatively recent shift as photos from recent decades clearly show large differences in community structure with tall willows inside the exclosure and grass-dominated vegetation outside of this exclosure (Ripple & Beschta, 2004). The composition and structure of vegetation outside of the Snowflake and the Porcupine exclosures on the GNF suggest ongoing recovery of riparian and aspen vegetation that is consistent with the occurrence of a trophic cascade (Ripple & Beschta, 2004).

The American bison is one of YNP's iconic wildlife species (Keigley, 2019). The majestic experience of observing vast numbers of bison across areas in YNP must be tempered by the fact that their current densities are not a natural component of the landscape (Beschta & Ripple, 2019; Keigley, 2019). If bison densities continue to be managed at the current historically high numbers in the Park's Northern Range (USDOI NPS, 2024), they will do so at great ecological cost: continued suppression of biological diversity, losses of aspen and willow communities, a simplification of landscape heterogeneity, degraded riparian/stream ecosystems, and the amplification of climate change effects on the ecosystems.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Raw data (Kauffman, 2025; Kauffman & Cummings, 2024) are available from Figshare: https://doi.org/10.6084/m9.figshare.27905172.v2 and https://doi.org/10.6084/m9.figshare.28135685.

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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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