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J. Boone Kauffman
Oregon State University

Dian Lyn Cummings
Illahee Sciences International

Cimarron Kauffman
Illahee Sciences International

Robert L. Beschta
Oregon State University

Jeremy Brooks
Idaho State University

Keeley MacNeill
University of Nebraska-Lincoln

See next page for additional authors

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Bison influences on composition and diversity of riparian plant communities in Yellowstone National Park

J. Boone Kauffman[1,2] | Dian Lyn Cummings[2] | Cimarron Kauffman[2] | Robert L. Beschta[3] | Jeremy Brooks[4] | Keeley MacNeill[5] | William J. Ripple[3]

[1]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

[2]Illahee Sciences International, Corvallis, Oregon, USA

[3]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA

[4]Department of Biological Sciences, Idaho State University, Pocatello, Idaho, USA

[5]School of Natural Resources, University of Nebraska-Lincoln, Lincoln, Nebraska, USA

Correspondence
J. Boone Kauffman,
Email: boone.kauffman@oregonstate.edu

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Abstract

Riparian zones are among the most biologically diverse ecosystems in the Intermountain West, USA, and provide valuable ecosystem services, including high rates of biotic productivity, nutrient processing, and carbon storage. Thus, their sustainability is a high priority for land managers. Large ungulates affect composition and structure of riparian/stream ecosystems through herbivory and physical effects, via trailing and trampling. Bison (*Bison bison*) in Yellowstone National Park (YNP) have been characterized as "ecosystem engineers" because of their demonstrated effects on phenology, aboveground productivity of grasses, and woody vegetation structure. Bison have greatly increased in numbers during the last two decades and spend large periods of time in the broad open floodplains of the Northern Range of the Park, where they are hypothesized to have multiple effects on plant species composition and diversity. We sampled indicators of bison use as well as riparian vegetation composition, diversity, and structure along eight headwater streams within YNP's Northern Range. Total fecal density ranged from 333 to 1833 fecal chips and/or piles/ha, stubble heights ranged from 7 to 49 cm, and streambank disturbance ranged from 9% to 62%. High levels of bison use were positively correlated with exotic species dominance and negatively correlated with species richness, native species diversity, willow (*Salix* spp.) cover, and wetland species dominance. At three sites, the intensity of bison use exceeded recommended utilization thresholds to avoid degradation of streams and riparian zones on public lands. The influences of large herbivores, principally bison, on vegetation composition and structure suggest the cumulative effects of the current densities on the Northern Range are contributing to biotic impoverishment, representing the loss of ecosystem services that are provided by native riparian plant communities. In addition, contemporary levels of bison use may be exacerbating climate change effects as observed through ungulate-related shifts in composition toward plant assemblages adapted to warmer and drier conditions. However, the resilience of native riparian vegetation suggests that sites currently heavily utilized by bison would have the potential for recovery with a reduction in pressure by this herbivore.

KEYWORDS
American bison, grazing impacts, herbivory, large herbivore disturbance, plant diversity, riparian ecosystems, streambank disturbance, ungulate impacts, Yellowstone National Park

INTRODUCTION

Among the great conservation successes at Yellowstone National Park (YNP) has been the 1995–1996 reintroduction of gray wolves (*Canis lupus*) into the Northern Range and the subsequent trophic cascade, fostering the recovery of riparian zones and quaking aspen (*Populus tremuloides*) communities (Beschta & Ripple, 2016; Ripple & Beschta, 2012). Prior to wolf reintroduction, the loss or decline of apex predators resulted in decades of intensive herbivory by Rocky Mountain elk (*Cervus canadensis*), resulting in a decline in willow, aspen, and other woody species (Barmore, 2003; Chadde & Kay, 1991; Kay, 1990; National Research Council, 2002a; Singer, 1996), as well as contributing to impacts on streambanks and channel structure (Beschta & Ripple, 2019a, 2019b).

Following the reintroduction of wolves, as well as the recovery of other large carnivores (cougars [*Puma concolor*] and grizzly bears [*Ursus arctos horribilis*]), willows (*Salix* spp.), quaking aspen, and thin-leaf alder (*Alnus incana* spp. *tenuifolia*) increased in height and density in some riparian zones. Furthermore, at some sites, quaking aspen recruitment increased and berry-producing shrubs became taller with increased fruit production (Beschta & Ripple, 2012, 2016).

In addition to the trophic effects imposed by apex predators, including humans (Vucetich et al., 2005), the current states and trajectories of riparian zones in the Northern Range are being influenced by a multitude of interacting biotic and abiotic processes. These include the extended, functional absence of beavers (*Castor canadensis*) and their ecosystem engineering effects (Wolf et al., 2007), incision and over-widening of stream channels (Beschta & Ripple, 2019a, 2019b), a warming and drying climate (Beschta & Ripple, 2016; Pederson et al., 2011), changes to landscape-scale water storage and hydrology (Ray et al., 2019), site-specific soil water and nutrient conditions (Marshall et al., 2013), and increased densities and concentrations of American bison (*Bison bison*) (Beschta et al., 2020; Geremia et al., 2019).

While the conservation of bison within the Yellowstone ecosystem has been instrumental in preventing their extinction and supporting their reintroduction in other areas of North America, recent increases in densities and concentration have noticeably altered the Northern Range ecosystem (Beschta et al., 2020; Geremia et al., 2019). Bison have been termed "ecosystem engineers" because they are capable of modifying grasslands through their intense herbivory (Geremia et al., 2019). In the past few decades, bison numbers have substantially increased while there has been a concomitant decrease in elk numbers, partially due to reestablishment of the top predator community (Barber-Meyer et al., 2008; Middleton et al., 2013; Ripple et al., 2010; Tallian et al., 2017) as well as other factors, including climate-induced shifts in food availability, human hunting pressure, and management both within and outside the Park (Greater Yellowstone Whitebark Pine Monitoring Working Group, 2020; Ripple & Beschta, 2012; Taper & Gogan, 2002).

Beschta et al. (2020) and Frank et al. (2016) reported that the current grazing intensity of large ungulates at YNP is at a historical high as bison have replaced elk as the principal large ungulate. Geremia et al. (2019) found that bison grazing in the Northern Range removed more than 50% of available plant tissue (grasses) in the most intensely used areas. They reported that the intense grazing kept plants in low, dense stature, which enhanced forage quality. Intense grazing by bison caused grasslands to green up faster and for a longer duration. Frank et al. (2016) reported the increased bison densities resulted in lower aboveground net primary productivity (ANPP) than when elk dominated the ungulate community of the Northern Range. They also reported ANPP was higher in grazed than in ungrazed sites. However, these studies did not report whether changes in ANPP were due to a change in composition or a change in phenology. Further, these studies are likely underestimates of ecosystem ANPP because they did not measure the productivity of shrubs nor did they specify which plant communities or grass species were sampled in this diverse landscape. In terms of ecosystem management, the success of increasing bison numbers in the Northern Range must be tempered by the probability that large bison herds were likely absent before the mid-1800s and thus may have had no significant role in the ecological processes that shaped YNP's prehistoric landscape (Beschta & Ripple, 2019a, 2019b; Keigley, 2019).

Riparian areas are zones of contact between land and water ecosystems, represented by mesic, productive environments that border streams, rivers, lakes, and springs (Naiman et al., 2005). Whereas riparian zones typically comprise only 1%–2% of landscapes in the western United States, they provide habitat for more wildlife species than any other habitat type (Knopf & Sampson, 1994). They are also crucial factors affecting aquatic habitats for fish, amphibians, and other organisms (National Research Council, 2002b). Riparian zones are the most important ecosystems on the landscape with respect to the sustained management of threatened and endangered species, biological diversity, and water quality and for addressing climate change (Goss & Roper, 2018).

Riparian zones are susceptible to shifts in composition, structure, and productivity due to large animal herbivory. Most studies on the ecosystem effects of large ungulates on riparian composition and structure have examined the effects of domestic livestock grazing (Kauffman et al., 2004; Kauffman, Coleman, et al., 2022). Fewer studies have quantified how wild ungulates affect riparian zones with respect to vegetation composition, diversity, and structure (Averett et al., 2017; Brookshire et al., 2002; Case & Kauffman, 1997). Our principal research questions centered around the hypotheses that the current high densities of bison significantly influence ecosystem composition and structure, primarily through grazing, trampling, and streambank disturbance. Our objectives were to quantify how the effects of varying levels of bison grazing intensity (as described through fecal density, streambank disturbance, and stubble heights) affect riparian vegetation composition, diversity, and structure.

METHODS

Study areas

The Northern Range comprises ~1500 km^2 of low- to mid-elevation mountainous terrain, of which approximately two thirds lies within YNP. Big sagebrush (*Artemisia tridentata*)/Idaho fescue (*Festuca idahoensis*) represents the dominant plant communities in the uplands adjacent to the riparian zones. We sampled riparian vegetation composition and indicators of large herbivore use along eight independent headwater streams in the Northern Range within YNP (Lamar and Yellowstone watersheds). Streams were considered "independent" when their closest network connection to other streams was the mainstems of the Yellowstone or Lamar Rivers. There are few such independent streams found in the Northern Range, therefore the eight we selected represent a near census. In the process of site selection, we identified potential study reaches that, based on field observations and historical photographs (Beschta & Ripple, 2019a, 2019b; Beschta et al., 2020), currently supported or had the potential to support willow/alder communities. Further, we selected study sites located in alluvial floodplain segments where over-bank flows promote the recruitment and growth of riparian plants (e.g., Bendix & Hupp, 2000). While individual willows were present at all sites, composition and structure greatly varied among the headwater streams ranging from grass-/sedge-dominated streambanks to those dominated by willows and alder. As such, the selected study reaches reflected a gradient of the variation in riparian vegetation composition and structure of the Northern Range (Appendix S1: Figure S1).

There were four riparian areas where streambanks were largely dominated by willow/alder communities. These included West Fork (WF) Antelope, East Fork (EF) Blacktail Deer, Geode, and Crystal Creeks. Four riparian areas had streams dominated by herbaceous vegetation: Rose, Lost, Jasper, and Chalcedony Creeks. Three of the four herbaceous-dominated sites, Rose, Jasper, and Chalcedony Creeks, supported primarily grassland species, whereas the Lost Creek was dominated by sedges.

The sampled riparian zones were associated with streams reflecting broad physical and hydrological characteristics of the headwater streams of the Northern Range. Mid-summer discharge across streams ranged from 2 to 346 L s^{-1}; three of the sampled streams (Jasper, Chalcedony, and Crystal Creeks) became intermittent between mid-July and early August. Average bankfull widths ranged from 1.4 to 3.8 m and average bankfull depths ranged from 0.14 to 0.48 m. The ratio of bankfull width to bankfull depth was 9.4 and 6.9 for the herbaceous-dominated sites and willow-dominated sites, respectively. All streams were either first or second order (Strahler, 1952). Elevation of the selected riparian zones ranged from 1768 to 2132 m.

Vegetation sampling

At each selected stream reach, we established four 90-m transects parallel with the channel. Two transects were established at the land/water interface along each side of the stream (hereafter the "greenline") and two transects were established midway between the edge of the active channel edge and the edge of the riparian/upland ecotone (hereafter the "historical floodplain"). The greenline is defined as the transitional point at the aquatic margin where terrestrial vegetation dominates (ground cover). It is the ecotone between dominance by aquatic and terrestrial vegetation. It has also been described as the first perennial vegetation that forms a lineal grouping of community types at or near the water's edge (Winward, 2000). For each transect, 25 vegetation plots at a 3-m spacing were established and measured, thus providing a total of

50 greenline plots and 50 historical floodplain plots per sampled stream reach.

Plant composition and diversity

Vegetation community composition and the relative abundance of species were determined from nested frequency and plant canopy cover measurements. We determined plant frequency through detection 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 second largest nested plot, and finally in the entire plot. Species encountered in the smaller nested plots are included in the frequency determination of the larger plots in which they are a part of. Cover measurements included all plant species with a canopy cover ≥5% within the 25 × 25 cm plots.

From the nested frequency data, we calculated relative abundance, species richness (number of species per experimental reach), 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. 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 4 while occurrence in the middle-sized nested plot was given a score of 2 (i.e., the square root of 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 score 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). Evenness or the distribution of abundance among different species was determined by dividing diversity (H') by the natural log of species richness (S). When all species are present in equal abundance, $J' = 1$. If one species strongly dominates, J' will be close to zero.

The similarity between the floodplain and streamside communities within each sampled stream reach was calculated using Sorenson's quantitative measure of similarity (Magurran, 1988). Similarity ranges from 0 (no species in common) to 1 (all species and their relative abundance are identical). Similarity (C_N) was calculated using the following formula:

$$C_N = 2j_N/(a_N + b_N),$$

where j_N is the sum of the lower of the two abundances (relative abundance) of all species occurring in the floodplain and streamside transects; a_N is the sum of relative abundance in the streamside transects; and b_N is the sum of relative abundance in floodplain transects.

The wetland species prevalence index, also referred to as the wetland indicator score, was calculated for greenline communities, floodplain communities, as well as for all transects combined to determine the predominance of hydrophytic (wetland) vegetation at each sampled stream reach (Wentworth et al., 1988). The wetland indicator score was computed by weighting the relative abundance of each species with index values for wetland indicator categories (Appendix S1: Table S1).

Wetland indicator values were assigned to each species using the national list of plant species that occur in wetlands (Appendix S2: Table S1; USDA, NRCS, 2016). By assigning the composition to the wetland indicator scores, we derived a wetland score for each stream reach of the study. Wetland scores can range from 1 (all species wetland obligate) to 5 (all species upland obligate).

Wetland indicator scores were calculated as follows:

$$\text{Wetland score or prevalence index} = \sum A_i W_i / \sum W_i,$$

where A_i is the relative abundance of species i and W_i is the indicator index value for species i.

Streambank disturbance

We determined the amount of streambank alteration due to large herbivores (e.g., bison, elk, and deer) walking along or crossing the greenline during the current grazing season. Streambank alteration is an annual or short-term indicator of the effect of trampling/grazing impacts on long-term streambank stability (Burton et al., 2011). To ascertain the percent of streambanks altered by ungulate use, we used a greenline disturbance technique similar to that described by Heitke et al. (2008) and modified by Burton et al. (2011). At each sampled reach, two 90-m transects were established along the greenline where we sampled streambank alteration and stubble heights of grass and sedge species in 30 plots spaced every 3 m ($n = 60$ plots for each sampled reach).

At each sampling point, we determined whether there was mechanical streambank alteration due to large herbivores (e.g., apparent evidence of shearing, trampling, or trailing damage). With the possible exception of trailing damage, we assumed all disturbance was this year's disturbance as vegetative regrowth/weathering effects of freeze/thaw cycles, rain events, and erosion by stream flow would normally mask the effects of previous years.

A 50×50 cm plot was used for these measurements. The middle of the 50-cm length of the plot was placed at the greenline parallel to the channel. Within this plot were five 50-cm cross-plot lines, 12.5 cm apart on the sampling frame, where occurrences of alteration were detected (Burton et al., 2011). We determined which of the five 50-cm lines of each plot had apparent disturbance. The count for each plot ranged from zero to five, depending upon the number of lines where disturbance was detected. We varied sampling somewhat from Burton et al. (2011) in that our line sample length was 25 cm on each side of the greenline (vs. 21 cm). Further, we thoroughly examined each line in each plot both visually and by touch when vegetation obstructed the sight of the streambank. From our experience, we have found that both sight and touch are necessary to obtain accurate data and to minimize sampler error.

Stubble heights

Stubble height is a measure of the residual leaf length of key herbaceous vegetation species remaining after grazing. Determination of utilization and stubble heights were similar to methods outlined in Burton et al. (2011). For both greenline and floodplain transects, we measured the stubble height (i.e., leaf length) of the nearest perennial grass or sedge located closest to the inside corner of the plot frame (Burton et al., 2011). These were identified to their most specific taxonomic unit possible. If there was no herbivory, we measured the total leaf length and denoted it as ungrazed. This methodology provided a measure of total ungrazed leaf length and facilitated determination of the percent utilization of herbaceous species.

Fecal counts

We sampled fecal density of large ungulates in each of the sampled riparian reaches. The plot size for the fecal counts was 2×90 m and they were located in the same transects as the historical floodplain vegetation transects. Each fecal unit (individual defecation event) within transects was identified to animal species (i.e., bison, elk, deer [*Odocoileus* spp.] or pronghorn [*Antilocapra americana*]).

Data analysis

Relationships of plant composition metrics (e.g., species richness, diversity, evenness) with ungulate disturbance metrics were described through regression analyses. The specific regression model (curve of best fit) was determined as those with the highest coefficient of determination and lowest standard error. Similarly, we examined relationships of the abundance of exotic species with metrics of ungulate using regression analyses. Kruskal–Wallis tests were used to test for differences in the parameters of large animal use as well as composition, diversity indices, and wetland indicator scores between willow-dominated and herbaceous-dominated streams.

RESULTS

Composition

There are about 1350 plant species in the entirety of YNP (8991 km^2) and we recorded a total of 123 plant species within the eight sampled riparian zones (Appendix S2: Table S1). The area of all plots sampled in this study was only 200 m^2, yet within that area, we identified about 9.2% of all vascular plant species that occur in the Park. Of the plants encountered in the plots, 13% were obligate-wetland species, 26% were facultative-wetland species, and 28% were facultative species, indicating that 67% of the riparian vegetation composition was classified as hydrophytic whereas 33% was classified as nonwetland (facultative upland or obligate upland).

The composition of riparian vegetation varied between reaches (Table 1). Three sites (Rose, Chalcedony, and Jasper Creeks) did not have a shrub layer and were dominated by exotic perennial grasses, principally Kentucky bluegrass (*Poa pratensis*) and meadow timothy (*Phleum pratense*) in both streamside and floodplain communities. Lost Creek was rather unique in that it was the only study stream dominated by sedges (*Carex* spp.) along the greenline. Streamside communities at four sites (Crystal, EF Blacktail, Geode Creeks, and WF Antelope) were dominated by willow species and/or thin-leaf alder with a predominantly sedge understory. The mean cover of riparian shrubs was 79% in willow-dominated sites and absent in herbaceous-dominated sites ($p = 0.01$). The overall species richness was significantly higher in the willow-dominated streams ($p = 0.02$). Species richness

TABLE 1 The total species richness of floodplain and greenline communities and the most abundant species in terms of plant cover (%), Northern Range, Yellowstone National Park.

Stream	Species richness			Dominant cover (%)	
	Total	Floodplain	Greenline	Floodplain	Greenline
Rose	29	20	28	**POPR(50), PHPR(13), TAOF(13), TRRE(7), CIAR(5), BRIN(5)**	**POPR(38), TRRE(15), CIAR(14), TAOF(10)**
Chalcedony	44	28	34	**POPR(31), PHPR(14), TAOF(7)**	**POPR(25), TAOF(19), PHPR(8)**, CAUT(7), **BRIN(5)**
Jasper	56	41	45	**POPR(52), PHPR**(7), ROWO(7), GEVI(6)	**POPR(21)**, ROWO(16), ARLU(13), CAPE(7), SEIN(7), **PHPR(6)**, SAEX(5)
Lost	52	38	42	**POPR(16)**, JUBA(12), SEIN(9), **PHPR(8)**, Carex-Ovales(5), CAPE(5)	CAAQ(47), CACA(20), CAUT(17)
Crystal	70	57	54	**POPR(39)**, ROWO(19), GEVI(9), SABE(7), SOCA(7), **PHPR(6)**, SYAL(5)	SALU(44), SABE(30), ROWO(19), SEIN(8), ALIN(8), CAPE(8), **POPR(7)**, EQAR(7), SOCA(6), JUBA(5)
WF Antelope	75	49	49	**PHPR(31)**, FRVI(27), **TRRE(24)**, POGR(5)	ALIN(37), SALU(35), CAAQ(22), SAGE(19)
EF Blacktail Deer	63	51	37	**TRRE(23), POPR(16), PHPR(11)**, POGR(6), FRVI(6), POGR(6)	CAUT(34), SALU(34), SAGA(33), CAPE(8), SOCA(7), TRRE(5)
Geode	60	48	45	Agrostis sp(29), CAAQ(14), POGR(13), SAGE(10), **PHPR(8)**, CACA(6), EPAN(5)	SALU(45), SAGE(31), CAAQ(31), CACA(11), CAUT(8), Agrostis sp(5)
Herbaceous-dominated	45 (6)	32 (5)	37 (4)		
Willow-dominated	67 (3)	51 (2)	46 (4)		
p	0.02	0.02	0.11		

Note: Exotic species are denoted in boldface. Species are reported in alpha codes and the full species name can be found in Appendix S2: Table S1. Means with standard errors in parentheses are reported for herbaceous- and willow-dominated streamsides.
Abbreviations: EF, East Fork; WF, West Fork.

ranged from 60–75 in the willow-dominated reaches to 29–56 in herbaceous-dominated stream reaches (Table 1).

Large ungulate use

The degree of use and effects of large herbivores varied dramatically between riparian zones (Figure 1). For example, total fecal density ranged from 333 to 1833 chips and/or piles/ha and stubble heights ranged from 7 to 49 cm. At sites with the lowest stubble heights and highest degree of streambank disturbance (e.g., Chalcedony, Jasper, and Rose Creeks), 72%–99% of sampled plots had been grazed. At sites with taller stubble heights and lower levels of streambank disturbance (e.g., EF Blacktail, Geode, and WF Antelope Creeks), only 9%–26% of sampled plots showed any level of herbivory. Indices of ungulate disturbance were anomalous at Lost Creek. Here, fecal density was quite high but streambank disturbance was low and stubble heights were high (Figure 1). Low disturbance and high stubble heights suggest that the current year's herbaceous growth at Lost Creek had been lightly grazed, while the high fecal counts suggest that heavy levels of herbivory had occurred, but prior to the current growing season (late summer–winter periods of the previous year). There were few differences in the stubble heights between the floodplain and streamside sections of the stream reaches.

The degree of streambank alteration by trailing and trampling of ungulates also varied greatly between streams, ranging from 9% to 62% (Figure 1). There were relatively low levels of streambank disturbance (<12% of streambank disturbance) at the willow-dominated EF Blacktail and Geode Creeks, moderate levels of streambank disturbance (16%–19%) at WF Antelope, Lost, and Crystal Creeks, and high levels of disturbance

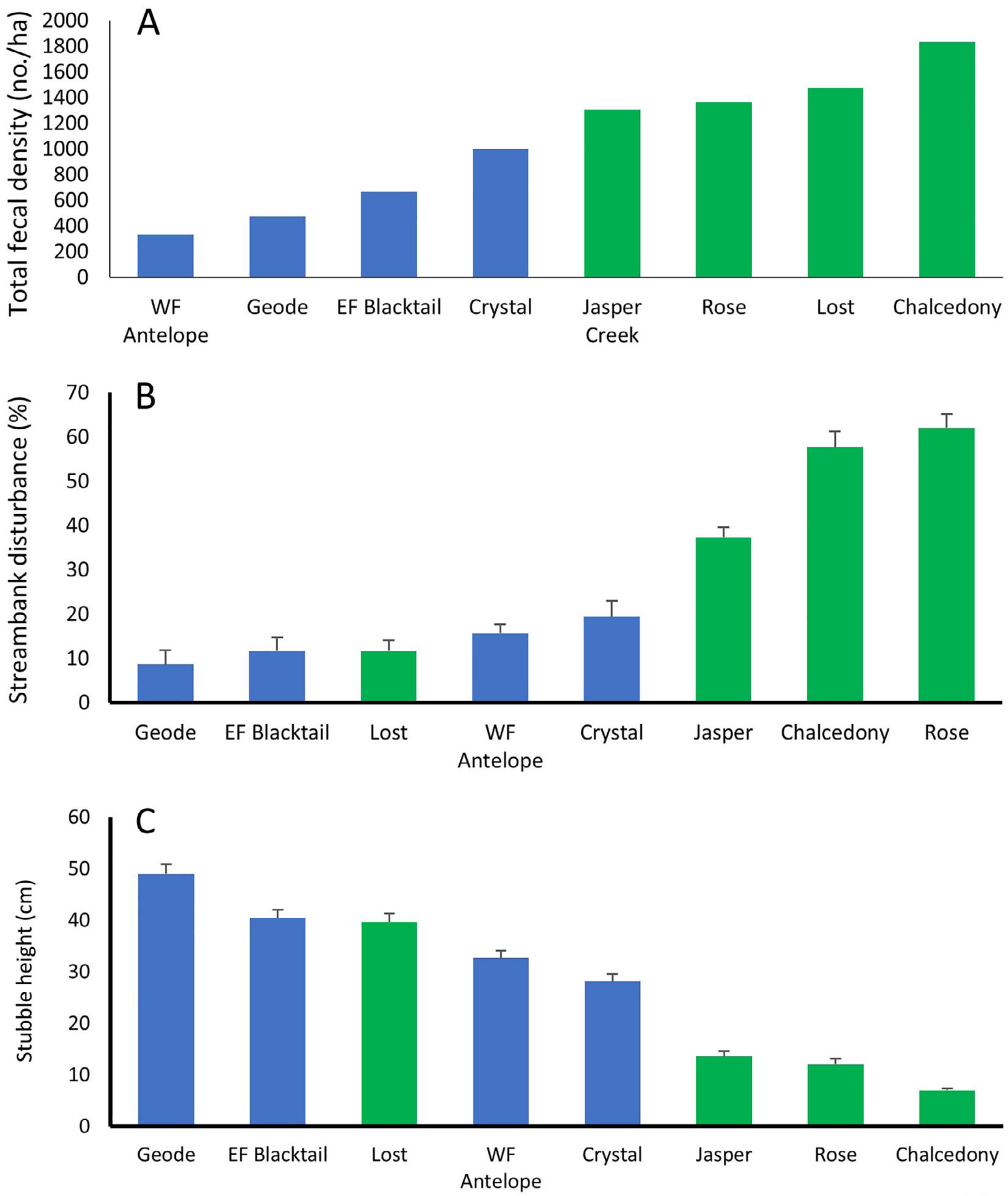

FIGURE 1 (A) The mean fecal density, (B) streambank disturbance ($N = 60$), and (C) stubble heights ($N = 120$) of selected riparian/stream ecosystems in the Northern Range, Yellowstone National Park. All data were collected in July 2020 and therefore do not reflect the total utilization or disturbance occurring during the growing season. Blue bars are willow-dominated stream reaches and green bars are herbaceous-dominated stream reaches. Vertical bars over figures (B) and (C) are 1 SE. The p values, when testing for differences between willow- and herbaceous-dominated communities, were 0.02 for fecal density, 0.11 for streambank disturbance, and 0.08 for stubble heights. EF, East Fork; WF, West Fork.

(37%–62%) at the grass-dominated Chalcedony, Rose, and Jasper Creeks.

Fecal counts suggest that bison were the dominant large herbivore influencing all streams except for Geode Creek (Appendix S1: Table S3). Bison feces comprised 90% of all fecal piles measured and elk accounted for the remainder. Only bison feces were encountered along Chalcedony, Lost, and Rose Creeks, which had bison fecal pile densities >1361 piles/ha. Relatively low levels of fecal density (i.e., 333–667 fecal piles/ha) were measured in the willow-dominated stream reaches.

Reaches lacking willows tended to have high levels of animal use, while willow-dominated riparian areas tended to have lower levels of use. Comparing differences in ungulate use between herbaceous- and willow-dominated riparian sites, we found significant differences in stubble heights ($p = 0.08$), fecal density ($p = 0.02$), and streambank disturbance ($p = 0.11$) (Figure 1). A notable exception was Lost

Creek, which had less streambank disturbance and lower stubble heights, but streambanks were dominated by sedges rather than grasses. Crystal Creek was dominated by willows (Appendix S3: Table S1; Appendix S4: Table S1), but levels of herbivory exceeded that of the other willow-dominated stream reaches.

Large ungulates effects on riparian vegetation composition and structure

At the heavily utilized Rose Creek, exotic species overwhelmingly dominated the composition of riparian vegetation, with a combined average cover of 87%. The cumulative cover of the exotic grasses—*P. pratensis* and *P. pratense*—was quite high in the grassland-dominated riparian reaches (39%–53%; Figure 2). The dominance of these exotic grasses was most pronounced in the floodplain communities of these sites where total cover ranged from 45% to 63%. Crystal Creek, which had the highest utilization parameters of any of the willow-dominated reaches (Figure 1), had a comparatively high cover of *P. pratensis* (27%) compared with other willow-dominated sites (Table 1; Appendix S3: Table S1). Along the greenline, the cover of these two abundant exotic grasses was 28%–43% in the grass-dominated sites but only 0.8%–8% at willow-dominated sites (Appendix S3: Table S1). There was a very strong correlation between the prevalence of exotic grasses and stubble heights ($r^2 = 0.88$; $p = 0.0006$) and streambank disturbance ($r^2 = 0.93$; $p = 0.0001$; Figure 3).

In addition to significant relationships between indicators of ungulate disturbance and the abundance of exotic grasses, there were also significant relationships between levels of ungulate use and species diversity. Similar to species richness, species diversity indices were lowest in the herbaceous-dominated stream reaches (exp $H' = 10.0$–19.1 in floodplain communities) and higher in willow-dominated communities (exp $H' = 20.1$–27.0; $p = 0.02$; Table 2). We found a significant inverse relationship between greenline species diversity and streambank disturbance ($r^2 = 0.72$; $p = 0.008$; Figure 4). Ungulate use also appeared to affect species composition to the detriment of wetland-obligate/hydrophytic species. There was a highly significant relationship between streambank disturbance and wetland indicator scores of the riparian composition ($r^2 = 0.90$; $p = 0.0003$; Figure 4). Higher levels of ungulate use tended to result in a composition dominated by species adapted to drier conditions.

A wetland prevalence index below 3 suggests that vegetation composition is dominated largely by wetland and facultative-wetland species. The streamside communities of the sedge- and willow-dominated sites had wetland prevalence indices that ranged from 2.52 to 2.82

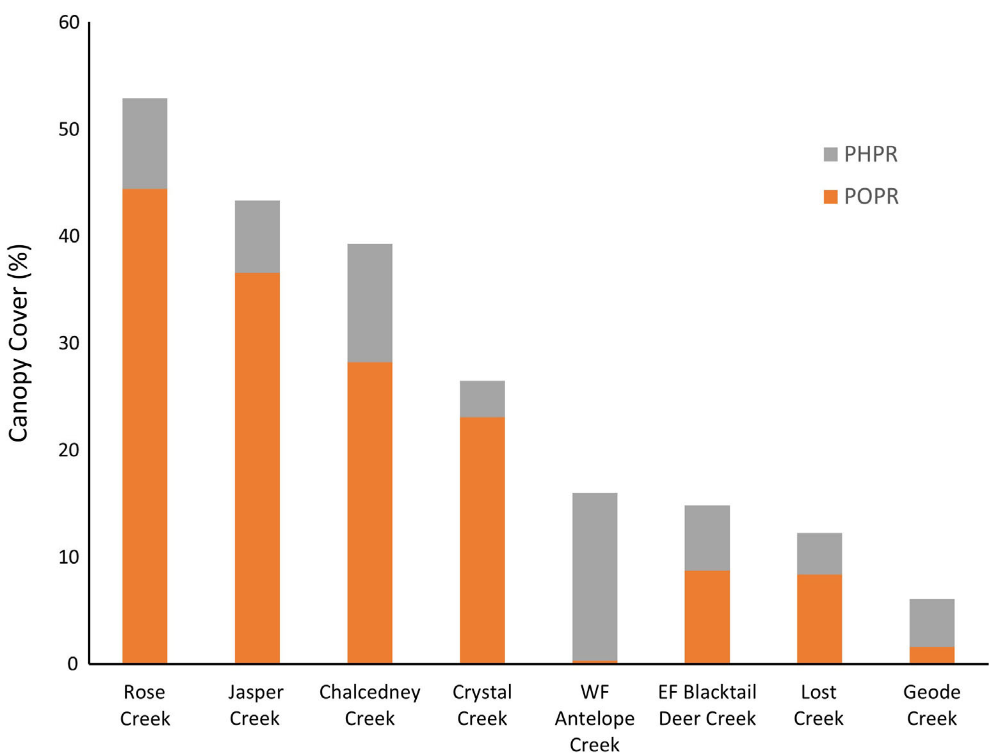

FIGURE 2 The mean cover of exotic grasses, meadow timothy (PHPR, *Phleum pratense*) and Kentucky Bluegrass (POPR, *Poa pratensis*), in riparian zones of the Northern Range, Yellowstone National Park. EF, East Fork; WF, West Fork.

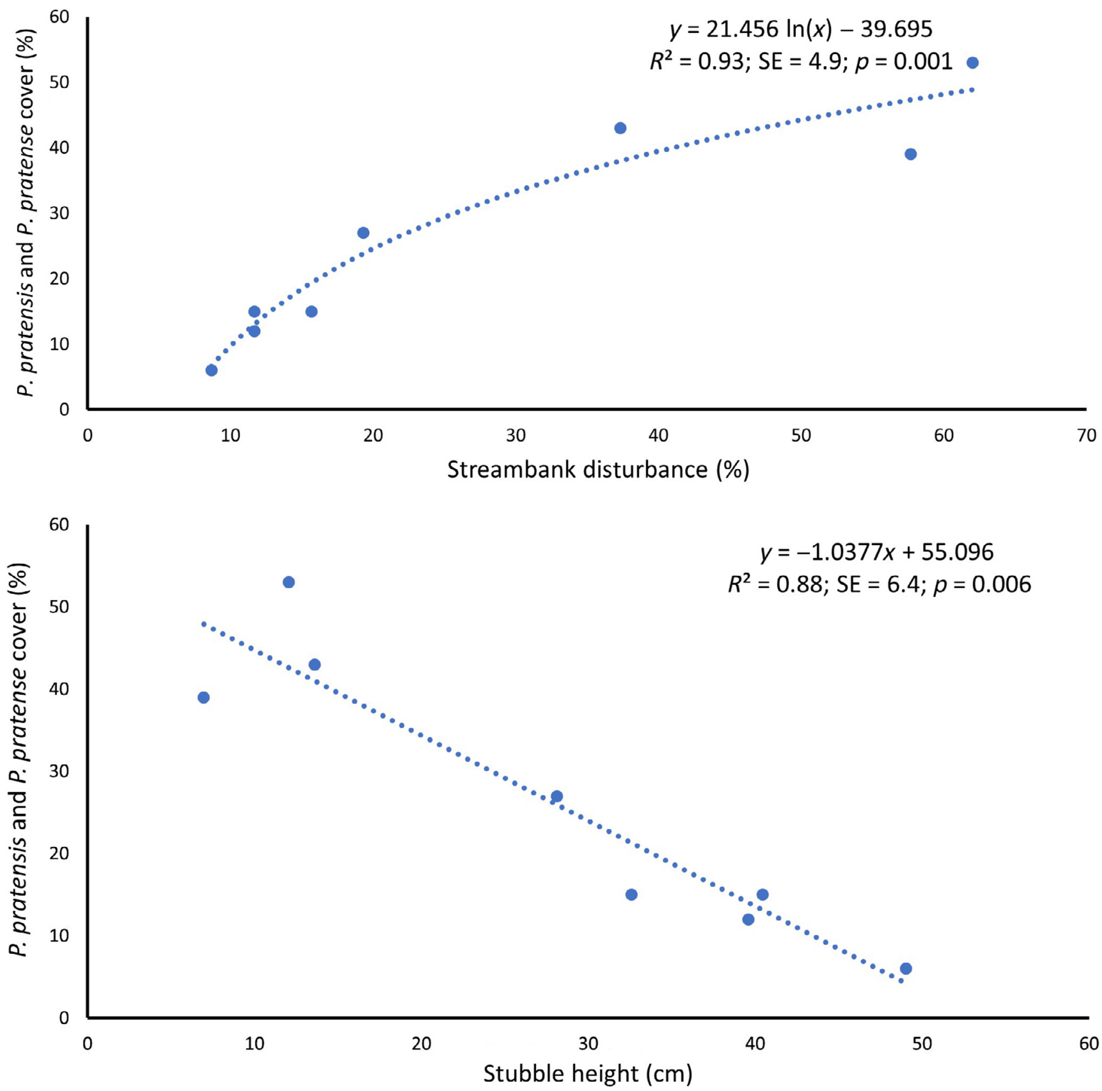

FIGURE 3 The relationships between the abundance of the exotic perennial grasses Kentucky bluegrass (*Poa pratensis*) and meadow timothy (*Phleum pratense*) with the degree of streambank disturbance and stubble heights in the Northern Range, Yellowstone National Park.

(Figure 5). In contrast, the wetland prevalence index of the three grassland-dominated sites exceeded 3.11. At all sites, the floodplain communities had higher wetland prevalence indices compared with their adjacent greenline communities.

Species richness and diversity of the greenline and floodplain communities were significantly related to levels of ungulate disturbance (Table 2; Figure 4). In addition, there was a clear effect of levels of herbivore disturbance on differences in the wetland prevalence indices between floodplain and greenline communities. Sites with higher degrees of streambank disturbance and lower stubble heights had smaller differences in wetland indicator scores between floodplain and greenline communities than sites with lower levels of ungulate disturbance (Table 2). The homogenization of vegetation composition for sites with high levels of ungulate use was also reflected in the similarity indices of the relative abundance of species between floodplain and greenline communities (Figure 6). Similarity in composition of the four sites with the highest degrees of streambank disturbance was 0.58–0.78. In contrast, the similarity indices at sites with the lowest levels of streambank disturbance were 0.24–0.54. This suggests that higher levels of ungulate disturbance lower the compositional diversity of riparian reaches by creating warmer and drier conditions along streambanks, resulting in greenline plant assemblages that are relatively similar to their adjacent floodplain communities.

DISCUSSION

With the exceptions of Geode and WF Antelope Creeks, fecal counts in riparian zones were overwhelmingly that of bison (Appendix S1: Table S3) and consistent with that reported by Beschta et al. (2020) and Frank et al. (2016)

TABLE 2 Wetland indicator scores, species diversity (H' and exp H'), evenness (J'), and similarity indices comparing floodplain to greenline composition for sampled riparian zones in the Northern Range of Yellowstone National Park.

	Wetland indicator score				Floodplain		Greenline		Evenness		
Stream	Total riparian	Floodplain	Greenline	Differences	H'	exp H'	H'	exp H'	Floodplain	Greenline	Similarity
Herbaceous-dominated streamside communities											
Rose	3.33	3.39	3.27	0.12	2.31	10.03	2.52	12.37	0.77	0.76	0.78
Chalcedony	3.19	3.27	3.12	0.16	2.48	11.92	2.63	13.86	0.74	0.75	0.58
Jasper	3.23	3.36	3.11	0.25	2.91	18.27	3.10	22.26	0.78	0.81	0.73
Lost	2.58	2.90	2.25	0.65	2.95	19.07	3.09	21.86	0.81	0.83	0.40
Mean	3.08 (0.017)	3.23 (0.11)	2.94 (0.23)	0.29 (0.12)	2.66 (0.16)	14.82 (2.26)	2.84 (0.15)	17.59 (2.60)	0.78 (0.01)	0.79 (0.02)	0.62 (0.09)
Willow-dominated streamside communities											
WF Antelope	2.82	3.38	2.27	1.11	3.00	20.08	3.15	23.26	0.77	0.81	0.24
EF Blacktail	2.79	3.23	2.35	0.88	3.17	23.70	3.13	22.82	0.81	0.87	0.48
Crystal	3.04	3.17	2.92	0.25	3.29	26.97	3.45	31.49	0.81	0.86	0.66
Geode	2.65	2.90	2.41	0.49	3.23	25.29	3.18	24.16	0.83	0.84	0.54
Mean	2.82 (0.08)	3.17 (0.10)	2.48 (0.15)	0.68 (0.19)	3.17 (0.06)	24.01 (1.47)	3.23 (0.07)	25.43 (2.04)	0.81 (0.01)	0.84 (0.01)	0.48 (0.09)
p	0.24	0.45	0.14	0.11	0.02	0.02	0.02	0.02	0.18	0.06	0.06

Note: Streams are separated by herbaceous and willow dominance. Values in parentheses are standard errors and the *p* values are the results of comparing herbaceous- to willow-dominated riparian zones based upon Kruskal–Wallace tests.
Abbreviations: EF, East Fork; WF, West Fork.

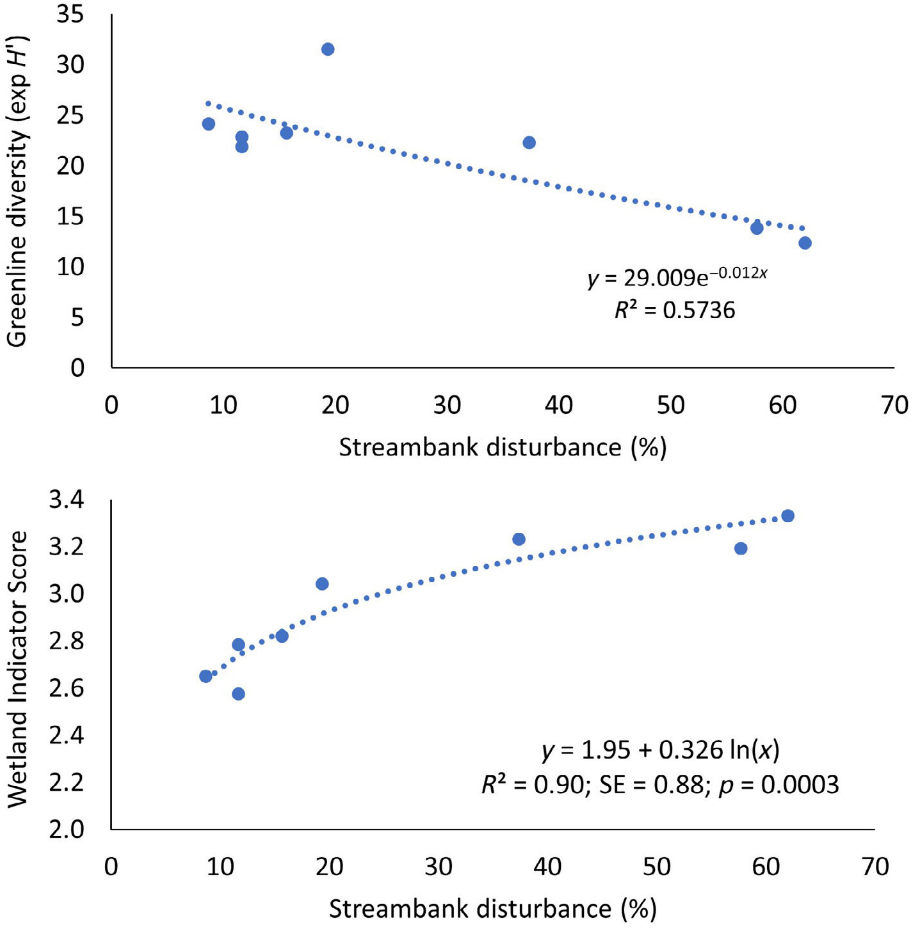

FIGURE 4 Relationships of streambank disturbance with greenline species diversity (exp H') and wetlands species indicator scores for study streams, Northern Range, Yellowstone National Park.

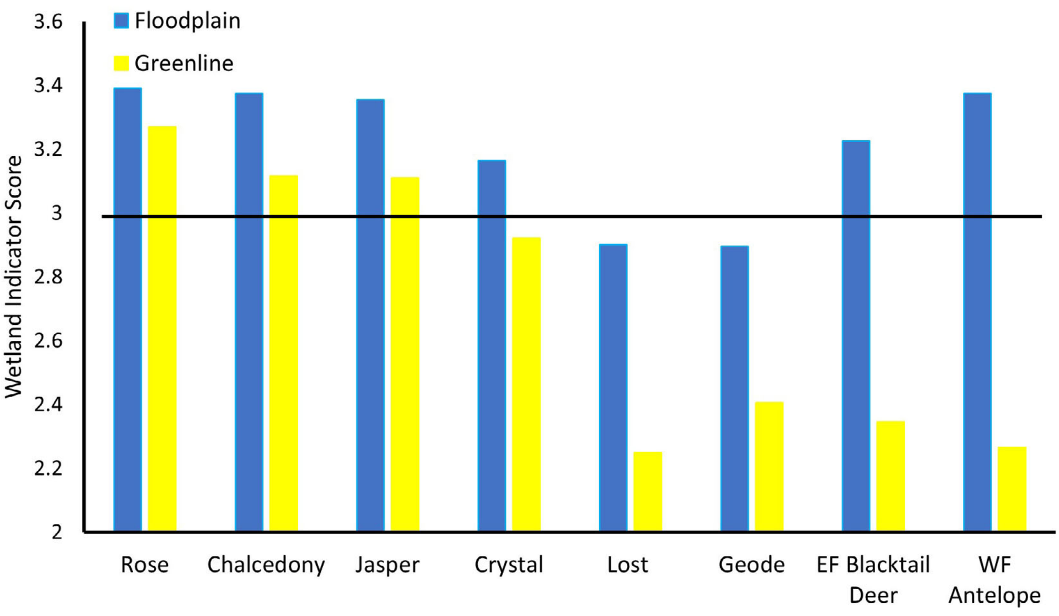

FIGURE 5 Average wetland indicator scores of vegetation communities in riparian zones of the Northern Range, Yellowstone National Park. The horizontal line at the wetland indicator score of 3 suggests that communities with scores below the line are dominated largely by wetland species while those above the line are predominantly dominated by upland species. EF, East Fork; WF, West Fork.

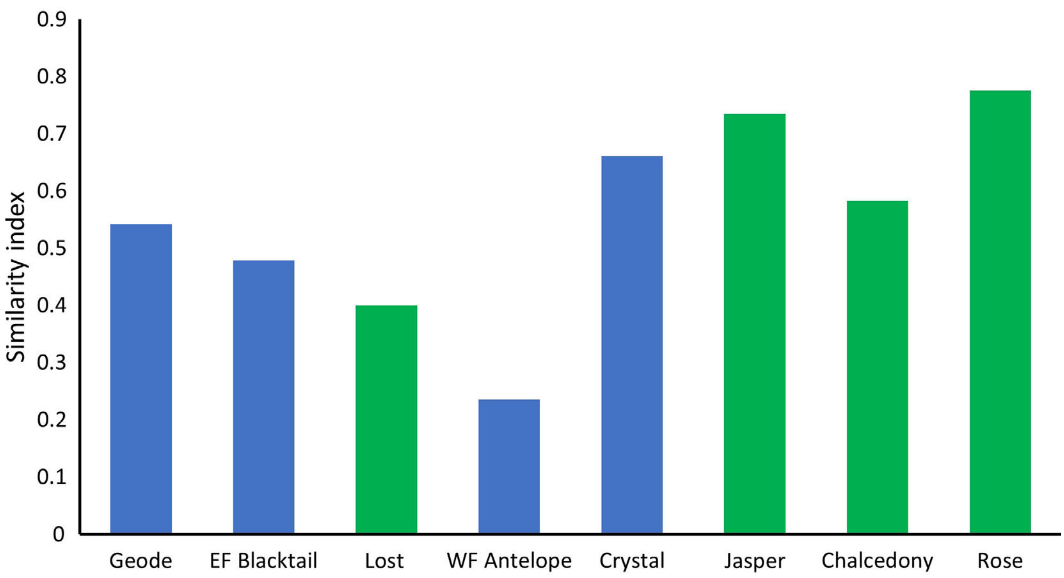

FIGURE 6 Similarity indices of the greenline and floodplain compositions in riparian zones of the Northern Range, Yellowstone National Park. High similarity suggests few differences in composition between these geomorphic surfaces. Green bars are sites dominated by grasses or sedges while blue bars are willow-dominated sites. EF, East Fork; WF, West Fork.

for the entirety of the Northern Range. The decline in habitat use by elk following the reestablishment of the Park's large carnivore guild, low levels of predation on bison, and lack of opportunity for migration and range expansion may be factors contributing to a high concentration of bison in the Northern Range in recent years, and the resulting effects on plant communities and biodiversity (Painter & Ripple, 2012; Ripple et al., 2010).

Utilization indicators compared with recommended grazing thresholds on public lands

This study provided an opportunity to quantify riparian plant composition and structure along broad gradients of utilization and disturbance by native ungulates and to compare this use and impacts with that of domestic livestock on other public lands. There was almost a sevenfold difference in streambank disturbance (9%–62%) and a sixfold difference in fecal density (333–1833 fecal piles/ha) for the sampled riparian zones. Mean stubble heights in the heavily utilized riparian zones of Chalcedony, Jasper, and Rose Creeks were <15 cm (Figure 1) and streambank disturbance in these stream reaches ranged from 37% to 62%. In terms of sustaining riparian/stream habitats, Goss and Roper (2018) recommended limiting stubble heights to ≥15 cm because exceeding this grazing level can degrade conditions important to salmonids. They also recommended a conservative limit of 25% for streambank disturbance. Both the stubble height and streambank alteration criteria were exceeded at Chalcedony, Jasper, and Rose Creeks, suggesting that aquatic habitats in these Northern Range streams would be degraded under these conditions. In other words, the level of use by bison in these riparian zones exceeds the recommended utilization levels for domestic livestock on public lands, which is necessary to avoid degradation of riparian zones.

High levels of utilization are of concern given their potential to affect terrestrial and aquatic habitats, as well as biological diversity. 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 (Kauffman et al., 2001). As much as 53% of the biota, including as much as 72% of avian species, are dependent upon riparian zones (Kauffman et al., 2001). We found that as streambank disturbance increased, or stubble heights decreased, there were decreases in willow cover, species richness, species diversity, and wetland species abundance (Figure 4). Concomitantly, there were increases in the abundance of exotic species associated with the increases in streambank disturbance and declines in stubble height.

The high degree of streambank disturbance at Chalcedony, Jasper, and Rose Creeks (Figure 1B) is similar to observations of Beschta et al. (2020) who reported streambank collapse from bison trampling along Chalcedony and Rose Creeks, likely contributing to accelerated bank erosion during high flows. Of additional concern, Goss and Roper (2018) found that various stream habitat attributes (i.e., width-to-depth ratio, streambank angle, percent undercut banks, streambank stability, residual pool depth, percent pools, percent pool-tail fine sediments <2 mm, and wood frequency) trended toward lower quality salmonid habitat as streambank disturbance increased or as stubble height decreased.

Large ungulate influences on riparian ecosystems

Geremia et al. (2019) termed bison in northern Yellowstone as "ecosystem engineers" because they are capable of modifying grasslands through their intense herbivory and migratory life history. Bison and other large ungulates influence ecosystems in four direct ways: (1) by removing vegetation through herbivory; (2) by trampling soils, biotic soil crusts, streambanks, and vegetation; (3) by redistributing nutrients via defecation and urination; and (4) by dispersing or creating favorable conditions for the establishment and dominance of exotic organisms, including noxious plant species and pathogens (Dwire et al., 1999; Fleischner, 1994; Kauffman, Beschta, et al., 2022; Kauffman, Coleman, et al., 2022). Large ungulate grazing also decreases the protective litter layer and the quantity of organic matter (and carbon) that can be incorporated into soils. Physical damage through trampling occurs from soil compaction and physical damage to biotic soil crusts and vegetation. For stream ecosystems, intense use by bison has been linked to increased sedimentation (e.g., Grudzinski et al., 2018; Larson et al., 2013), which in turn can have negative consequences for the diversity and function of fish, aquatic invertebrate, primary producer, and microbial communities (Fritz et al., 1999; Kominoski & Rosemond, 2012; Louhi et al., 2017). Defecation and urination by ungulates can lead to stream eutrophication and increases in fecal coliform concentrations (James et al., 2007; Meays et al., 2006; Scrimgeour & Kendall, 2002). Finally, large ungulates facilitate dominance by exotic species (Figures 2 and 3; Kauffman, Coleman, et al., 2022).

Unlike the native bunchgrasses of the Northern Range, many exotic plant species that now dominate the heavily utilized riparian zones (*P. pratensis* and *P. pratense*) evolved under continuous grazing pressure and are well adapted to the altered conditions associated with high densities of large ungulates (Mack & Thompson, 1982). Thus, it would appear that the high densities of bison in Yellowstone's Northern Range exert similar environmental impacts to those quantified for high levels of domestic livestock (cattle) use on other public lands.

Exotic species dominance

We hypothesized that increasing disturbance from large ungulates would affect riparian species composition, whereby exotic species adapted to herbivory would be favored over native species that evolved with minimal large animal herbivory. Exotic grasses and herbs were most abundant at sites with the highest metrics of ungulate use (Figures 2 and 3). Are these results due to site characteristics or the potential effects of animal use? *P. pratensis* is a grazing-tolerant non-native species in the United States (Gasch et al., 2020; Mack & Thompson, 1982; Toledo et al., 2014) and is currently a dominant in many riparian zones across the western United States. Furthermore, the dominance of *P. pratensis* has been shown to be maintained by large ungulates and will decrease with their reduction or elimination (Kauffman, Coleman, et al., 2022). In the absence of domestic livestock grazing (and with low levels of wild ungulate use) in riparian zones of Northeastern Oregon, native graminoids and dicots increased in abundance while there was a concomitant decrease in the exotics—*P. pratensis* and Dutch clover (*Trifolium repens*). In northern Yellowstone's riparian areas, a similar pattern of exotic species dominance occurs in heavily grazed sites. Furthermore, a dominance of native willows and sedges occurs in sites that have been lightly grazed, suggesting that large ungulate herbivory by bison represents a dominant influence on composition.

Species diversity

Species richness and species diversity indices were lowest in the grassland and sedge-dominated riparian zones and highest in willow-dominated riparian zones (Tables 1 and 2). Species diversity of streamside communities was inversely correlated with the metrics of grazing disturbance (Figure 4). These results are similar to the pattern of plant diversity in riparian zones that have been grazed (and ungrazed) by domestic livestock (Kauffman, Coleman, et al., 2022). They found that species richness and diversity were higher in riparian reaches ungrazed by cattle. In addition, the abundance of native sedges (*Carex* spp.) and native broad-leaved forbs was also significantly greater in ungrazed riparian areas compared with adjacent grazed areas.

Current low levels of herbivory at some of the willow-dominated riparian reaches is a relatively recent phenomenon that followed the 1995–1996 reintroduction of wolves in YNP (Beschta & Ripple, 2019a, 2019b). For example, they found that willows along the west and east forks of Blacktail Deer Creek in YNP averaged <50 cm in height in 1995, but by 2017 had attained heights of ≥300 cm. Similarly, canopy cover over the streams, which was <5% in 1995, had increased to 43%–97%. In this study, we found that there was a 67% cover of willows along the EF Blacktail Creek, indicating a relatively intact willow community. The resilience of native riparian vegetation suggests that sites currently heavily utilized by bison would also have the potential for recovery with a reduction in herbivore pressures.

Climate change and wetlands prevalence

Two general hypotheses have been proposed to explain the large declines in willows on Yellowstone's Northern Range. The first suggests that willow declines were due to an overabundance of large ungulates, initially elk but more recently by bison, exceeding the carrying capacity of their habitats (Beschta et al., 2020; Chadde & Kay, 1991; National Research Council, 2002a), while the second suggests conditions favoring growth and establishment of willows have changed as Yellowstone's climate has become drier and warmer (Pederson et al., 2011; Tercek et al., 2012). Notably, Chadde and Kay (1991) considered both of these hypotheses when they evaluated willow growth inside and outside of Northern Range ungulate exclosures. They found dramatic increases in willow cover and density inside ungulate exclosures while those on the outside continued to be heavily browsed. They further observed that the climate, as well as any ongoing changes in climate, would be the same for adjacent sites inside and outside the exclosures. However, while the climate is changing similarly across northern Yellowstone, wetland habitats within the Northern Range seem to have varying sensitivities to change (Ray et al., 2019). Ray et al. (2019) evaluated wetland drying across the regions of Yellowstone and Grand Teton National Parks and found that wetland sensitivity to changing climate varied between and within these regions. Subbasin characteristics, such as topography, groundwater connectivity, and soil characteristics, influenced the sensitivity of wetlands to precipitation and runoff. In turn, these subbasin characteristics interacted with varying air temperature, evapotranspiration, precipitation, and runoff such that individual wetlands within the Northern Range responded to climate change quite differently over the eight-year study (Ray et al., 2019).

Our stream-riparian study sites are similarly distributed across multiple subbasins within the Northern Range, necessitating a consideration of the influence of subbasin characteristics. Though we did not collect the same types of measurements as Ray et al. (2019), we can use patterns in stream intermittency and apparently anomalous sites to evaluate the relative roles of sensitivity to climate change and ungulate disturbance. We observed three out of eight streams had intermittent flows partway through the summer, indicating they have different subbasin characteristics than the perennial streams. Strikingly, these intermittent streams included riparian communities dominated by both herbaceous (Chalcedony and Jasper Creeks) and willow (Crystal Creek) vegetation. In this instance, subbasin characteristics that result in differences as extreme as intermittent versus perennial did not predict riparian plant community characteristics. While this study does not directly account for variation in subbasin characteristics nor stream-riparian areas sensitivity to climate change, our findings suggest that disturbance and grazing by ungulates is a strong driver of riparian plant community state. In the face of climate change, many willow communities recovered following the reintroduction of wolves (Beschta & Ripple, 2007; Painter & Tercek, 2020), whereas willow abundance and structure along streams and rivers with high levels of bison use continued to remain suppressed (Beschta et al., 2020).

In areas of high bison use, the loss of vegetation structure due to declines in riparian willow cover appears to result in warmer microclimates and lower soil water holding capacities, thus exacerbating the warming and drying effects of climate change (Kauffman, Coleman, et al., 2022). At the levels of utilization observed for the grass-dominated riparian zones of this study (Figure 1), Northern Range bison may well be contributing to desertification, a lowered resistance to the stresses associated with a changing climate, a shift from net carbon sinks to sources of greenhouse gases, biotic impoverishment, and the loss of ecosystem services that could otherwise be provided for by native plant communities. In addition, the loss of deep-rooted shrub species due to high levels of ungulate herbivory and trampling may reduce biotic access to deep soil water, additionally exacerbating climate change effects (Franklin & Dyrness, 1973; Rau et al., 2011).

Although climate change may well be having an impact on ecosystem structure and function in Yellowstone's Northern Range, this study suggests a third hypothesis involving interactions between climate change, ungulates, and biological diversity. This hypothesis is that large ungulates, at the current levels of utilization and disturbance, are exacerbating the effects of climate change. Our results strongly suggest that large numbers of bison shift the composition of riparian species toward those adapted to warmer and drier conditions. Wetland species indicator scores (prevalence) in the sampled riparian areas were inversely correlated with grazing intensity ($r^2 = 0.89$; Figure 4), suggesting that plants more adapted to drier upland condition replace riparian-obligate species under heavy bison use. These results are similar to the influences of domestic livestock grazing that have also been found to lower the prevalence of facultative and wetland-obligate species in riparian zones (Kauffman, Coleman, et al., 2022). They found that wetland species indicator scores were significantly lower in reaches ungrazed by domestic cattle compared with the grazed reaches. The shifts in species composition between heavily and lightly impacted stream reaches clearly suggest that current densities of bison in northern Yellowstone are not only having a greater influence on composition than climate change but that they are also exacerbating the effects of climate change.

Frank et al. (2016) reported a decline in ANPP in the Northern Range of YNP associated with the recent increase in bison densities and cautioned that increases in bison numbers could result in further declines in ANPP. Preceding declines in ANPP are the degradation of riparian zones and concomitant declines in diversity through excessive defoliation and trampling by bison. Continued bison use at current population levels will likely result in the continuation of the ongoing loss of diversity and ecosystem services provided by intact riparian plant communities. Reduction in bison numbers to densities below disturbance thresholds that are causing degradation or preventing vegetation recovery in riparian zones would therefore facilitate sustainability of the diversity and structure of these ecologically valuable landscapes in northern YNP for future generations.

AUTHOR CONTRIBUTIONS

All authors contributed experimental design and the drafting of the manuscript. Jeremy Brooks and Keeley MacNeill located the study riparia/stream reaches. J. Boone Kauffman, Cimarron Kauffman, and Dian Lyn Cummings collected all plant and animal field data. They also led in the analysis and interpretation of these data. Jeremy Brooks and Keeley MacNeill collected stream/site characteristics information.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kauffman, 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.20081324.v1.

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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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