



Bison limit ecosystem recovery in northern Yellowstone

Robert L. Beschta ^{a,*}, William J. Ripple ^a, J. Boone Kauffman ^b, Luke E. Painter ^b

^a Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, United States of America

^b Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, United States of America



ARTICLE INFO

Article history:

Received 15 January 2020

Received in revised form 10 February 2020

Accepted 11 February 2020

Available online xxxx

Keywords:

Yellowstone

Large carnivores

Bison

Elk

Riparian vegetation

Channel morphology

Trophic cascade

ABSTRACT

American bison (*Bison bison*) numbers in northern Yellowstone National Park increased during the last two decades, while those of elk (*Cervus canadensis*) decreased. We undertook this study to assess the potential effects of bison on woody vegetation and channel morphology in the park's northern ungulate winter range. Based on differences in the number of elk and bison, body mass, and the amount of time each utilizes the northern range, foraging pressure from bison began to exceed that of elk in 2007 and is currently ~10 times greater than that of elk. In the Lamar Valley study area, stand structure data (i.e., tree frequency by diameter class) for aspen (*Populus tremuloides*) and cottonwood (*P. spp.*) indicated that the growth of seedling/sprouts of these species into tall saplings and trees has been extensively suppressed by bison herbivory. For streams that crossed the valley floor, woody riparian vegetation was absent along their banks and channels were relatively wide and deep, conditions sustained by high levels of bison use. Overall, our findings indicated that the elevated numbers of bison, via herbivory, trampling, and tree bark effects, are limiting the structure, composition, and distribution of woody plant communities in the Lamar Valley, affecting the character of the valley's stream and river channels, and, in turn, influencing habitat and food-web support for terrestrial and aquatic wildlife species. The conservation success of bison recovery now may be adversely affecting another conservation goal, the restoration and maintenance of woody riparian vegetation and riparian ecosystems.

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1. Introduction

Bison are a highly interactive species, capable of producing significant ecosystem change. As “ecosystem engineers,” large groups of bison have the capability to influence species composition and distribution across shrub steppe and grasslands, as well as contributing to more localized effects via forage selection, hoof action, bison wallows, nitrogen availability, and others (Knapp et al., 1999; Soulé et al., 2003; Allred et al., 2011; Kowalczyk et al., 2011; Bailey, 2013; White et al., 2015; Blackburn, 2018). The distribution of bison in the United States (US) originally extended from east of the Appalachians to west of the Rocky Mountains with the vast majority of them residing on the Great Plains where their evolution largely occurred (Bailey, 2013). While bison may have historically totaled 30 million animals (Lott, 2002), their numbers sharply decreased in the 1800s and their distribution became more constricted as the cultural and land-use effects of Euro-Americans extended westward across the country (Hornaday, 1889). In the 1830s bison were extirpated from east of the Mississippi River and from the Snake River Plains. Within another half century, market

hunting on the Great Plains had decimated its vast herds of bison almost to the point of biological extinction (Lott, 2002).

Several small herds of bison were reported in the vicinity of the Yellowstone National Park (YNP) during the years immediately before the park's establishment in 1872 (Schullery and Whittlesey, 1992), perhaps driven there due to the intense market hunting that bison were experiencing on the Great Plains (Heller, 1925). Poaching of bison occurred after park establishment but they became fully protected in 1901, at which time only 22 bison were present in the park's northern ungulate winter range, or “northern range” (Meagher, 1973).

Rocky Mountain elk (*Cervus canadensis*) were historically the principal ungulate utilizing YNP's northern range and their behavior and densities have been influenced by large carnivores. In the early 1900s, after decades of Euro-American hunting, trapping, and poisoning, gray wolves (*Canis lupus*) and cougars (*Puma concolor*) were extirpated (NRC, 2002a; Ruth, 2004; Wagner, 2006). With diminished predation pressure, and prohibitions of hunting inside the park, increased elk herbivory soon began to suppress the height growth of young woody plants in the northern range (Wright and Thompson, 1935; Grimm, 1939; Barnmore, 2003). This led to decreased recruitment (i.e., the growth of seedlings and sprouts into tall saplings and trees) of quaking aspen (*Populus tremuloides*), cottonwood (*P. spp.*), willow (*Salix spp.*), thinleaf alder (*Alnus incana* spp. *tenuifolia*), and berry-producing shrubs (Kay, 1990; Ripple and Larsen, 2000; Beschta, 2005; Wolf et al., 2007;

* Corresponding author at: Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, United States of America.

E-mail address: robert.beschta@oregonstate.edu (R.L. Beschta).

Ripple et al., 2010; Beschta et al., 2016), as well as the loss of North American beaver (*Castor canadensis*) (Jonas, 1955; Ripple and Beschta, 2004).

Cougars were again back in the northern range by the 1980–90s (Ruth, 2004), a recovery that was followed by the 1995–96 reintroduction of wolves, thus restoring the park's large predator guild (Smith et al., 2003). Changes in elk behavior were soon observed following the return of wolves (Laundré et al., 2001; Fortin et al., 2005; Gower et al., 2005; Hernandez and Laundré, 2005) and predation of elk calves by bears (*Ursus* spp.) appears to have increased (Barber-Meyer et al., 2008). With predation pressure from wolves, cougars, and grizzly bears, a degraded winter range, and human hunting of elk that wintered outside the park, annual counts of the northern range elk herd began to decrease from their historical highs in the 1990s.

Within two decades of wolf reintroduction, deciduous woody species in many portions of the northern range had increased in establishment, young plant height, diameter growth, recruitment, canopy cover, and berry production, all associated with reduced herbivory from elk and indicative of an ongoing trophic cascade (Beyer et al., 2007; Baril et al., 2011; Painter et al., 2014; Beschta and Ripple, 2016). Yet for portions of the northern range, such as in the Lamar Valley where bison are common, woody vegetation has continued to decline (Painter and Ripple, 2012; Beschta and Ripple, 2015).

We hypothesized that the historical effects of intensive elk herbivory on the status and dynamics of woody plant communities in the Lamar Valley have, in recent years, been supplanted by those of bison. We focused on woody plant species in this study because they are relatively long-lived, thus capable of providing an important perspective of changing plant community and food-web dynamics over time. We additionally hypothesized that bison, via the suppression of riparian vegetation and trampling of streambanks, may be increasingly influencing channel morphology of the Lamar River and tributary streams that cross the valley floor.

2. Yellowstone's bison

In 1907, over 60 bison from a growing Mammoth herd were transferred to the Lamar Valley. There a cabin was built on the Rose Creek alluvial fan that would eventually become known as Buffalo Ranch, with an attendant barn, machine shop, and corrals. Bison management activities subsequently included constructing drift fences across the valley floor, seasonally moving bison to various foraging areas in the northern range, corralling them in the Lamar Valley for winter feeding, castrating male calves to maintain a desired sex ratio, and other practices. Ranching operations on the valley floor also involved removing willows, plowing fields, seeding non-native grass and forb species, and the irrigating, harvesting, and storing of hay (Skinner and Alcorn, 1952; Meagher, 1973; Gates and Broberg, 2011). Haying operations on the valley bottom produced 200–500 tons of hay annually from 1908 to 1952, representing a major source of winter feed for bison (Skinner and Alcorn, 1952).

By 1925 the Lamar Valley bison herd had grown to over 750 animals and it became “apparent that some action would have to be taken to limit their numbers” (Skinner and Alcorn, 1952, p. 9). Whether the need to reduce bison numbers was due to concerns about the effects of bison herbivory and trampling in the Lamar Valley, increased haying needs for winter feeding, or a desire to remove “excess bulls” is not clear. Culling of the Lamar herd began in 1925 and continued for more than four decades during which >100 bison per year, on average, were removed (Skinner and Alcorn, 1952; YNP, 1997; White et al., 2015). In the 1920s, Park Service managers also became increasingly concerned about the environmental effects of elk in the northern range and similarly began to reduce their numbers via a culling program (Grimm, 1939; Kay, 1990; YNP, 1997).

Public and congressional concerns about elk herd reductions inside YNP led park administrators to terminate the culling of both elk and

bison in 1968 (Allin, 2000), at which time there were approximately 4000 elk and 100 bison in the northern range. However, within two decades their populations had increased to nearly 20,000 elk and 1000 bison. The park service characterized the years after 1968 as a period of “natural regulation” (YNP, 1997; NRC, 2002a), yet the park's large carnivore guild remained incomplete for nearly another three decades. Following 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 increased to a historical high of approximately 4000 animals (YNP annual ungulate counts).

3. Study area

YNP's northern range comprises ~1500 km² of low- to mid-elevation mountainous terrain of which approximately two-thirds lies within the park (Fig. 1). Our study area, in the eastern portion of the northern range encompassed ~9 km² of “valley floor” within the Lamar Valley at an elevation of ~2000 m. The up-valley end of the study area occurred at the confluence of Soda Butte Creek and the Lamar River and the down-valley end at the beginning of the Lamar Canyon, a valley length of 8 km. The valley floor varied in width from 0.6 to 1.8 km and was bordered by hill toeslopes and several alluvial fans; these landforms were not included in the study area. Late Pleistocene glacial outwash deposits occurred mostly across the up-valley portion of the study area with the remainder of the area in Holocene alluvial gravels and fine-grained humic alluvium (floodplain soils), the latter capable of supporting sedges (*Carex* spp.) and tall grasses (Pierce, 1974a, 1974b).

Big sagebrush (*Artemesia tridentata*)/Idaho fescue (*Festuca idahoensis*) represents the dominant plant community in the Lamar Valley. Other common grasses include bearded wheatgrass (*Elymus caninus*), Richardson's needlegrass (*Achnatherum richardsonii*), and tufted hairgrass (*Deschampsia sspitosa*) (Houston, 1982; Despain, 1990). Exotic grasses and forbs are also common. Historically, woody plant communities in riparian areas included willow, aspen, cottonwood, thinleaf alder, and other shrubs, along with scattered stands of lodgepole pine (*Pinus contorta*) (Houston, 1982; Despain, 1990; Kay, 1990; YNP, 1997).

Several tributary streams cross the valley floor before discharging their flows into the Lamar River. Perhaps the most notable of these are the West Fork of Rose Creek (perennial stream) and Chalcedony Creek (intermittent stream). Upon leaving the Rose Creek alluvial fan the West Fork continues ~1400 m across floodplain deposits and Chalcedony Creek crosses >2000 m of valley floor, mostly associated with Pleistocene glacial outwash deposits. Two other tributaries, the East Fork of Rose Creek (intermittent stream) and Amethyst Creek (perennial stream), each have <400 m of channel length on the valley floor.

4. Methods

4.1. Historical vegetation change

We searched for historical photographs illustrating the general character of riparian vegetation in the early 1900s. We used these photographs, along with repeat photographs in 2018, to identify potential long-term changes in woody plant communities. We also determined the total area of aspen crown cover (ha) on 1954 and 2015 aerial photographs.

4.2. Ungulates

We summarized annual bison counts and removals for the northern range over the period 1902–2018. We also used annual park service counts of elk and bison since 1987 for comparing the relative foraging needs of these two large herbivores, using an elk-month (EM = 1 adult elk foraging for 1 month) as a basis for normalizing the two data sets.

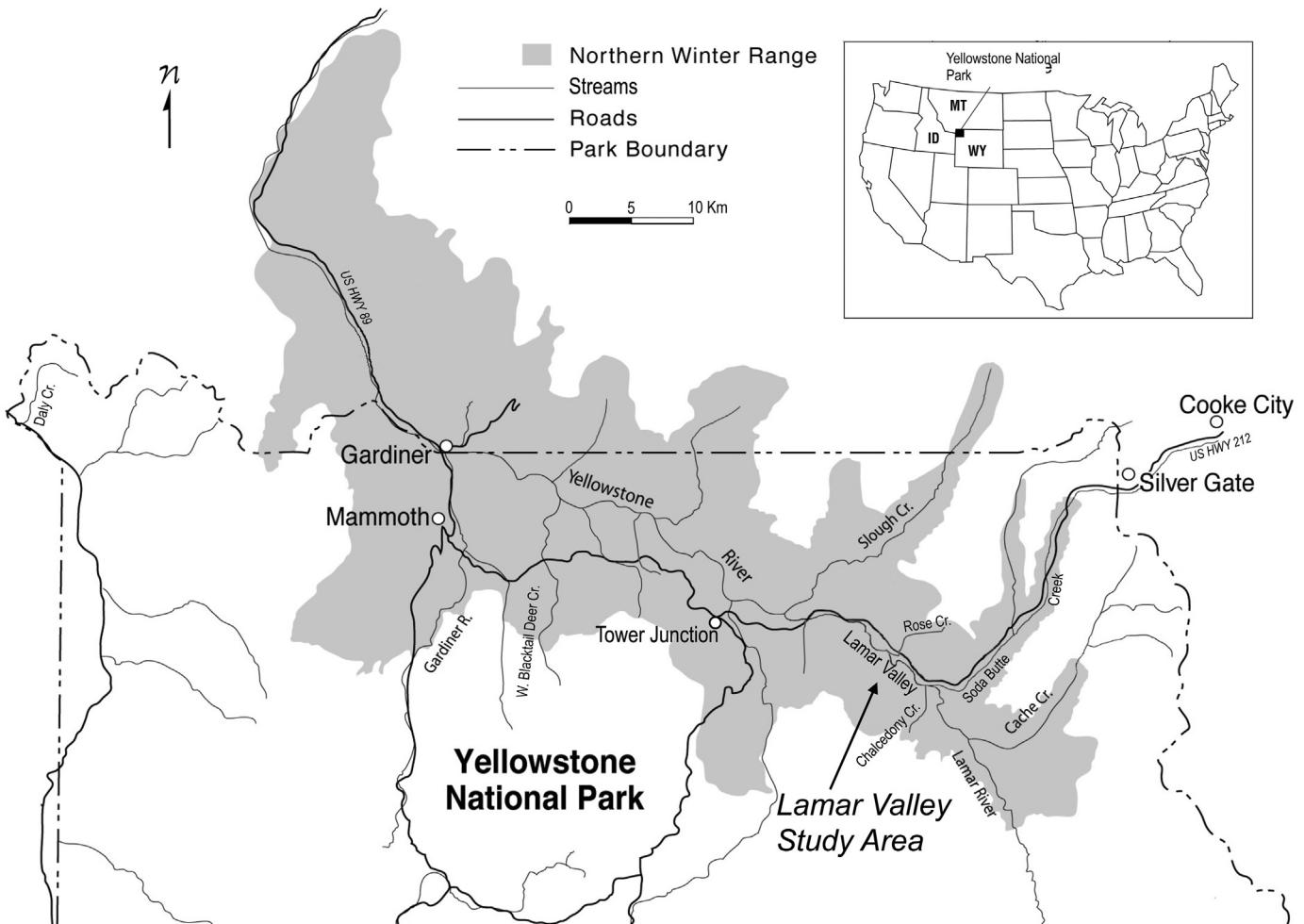


Fig. 1. Location of the Lamar Valley study area in the eastern portion of Yellowstone National Park's northern winter range.

Heady (1974) indicates that comparisons of foraging needs between herbivores can be calculated from the ratio of adult weights to the $\frac{3}{4}$ power. For adult bison (445 kg) and elk (272 kg) (Heady, 1974), this relationship (i.e., $[445/272]^{0.75}$) indicates ~1.5 EMs per bison-month. Using a weighted mean body mass for Yellowstone bison (377 kg) and elk (226 kg) (Rose and Cooper, 2016) also results in ~1.5 EMs per bison-month (i.e., $[377/226]^{0.75}$). Bison use of the northern range is nearly year-round (White et al., 2015; Geremia et al., 2019) whereas elk use is seasonal, typically from late fall to early spring (Garrott et al., 2009; White et al., 2010). Although the amount of time in any given year that these large herbivores reside in the northern range can be highly variable, due to the timing and amount of seasonal snowfall amounts or other factors (Garrott et al., 2009; Gates and Broberg, 2011; White et al., 2015), for comparative purposes we assumed that elk and bison, on average, annually utilized the northern range 5 and 10 months, respectively. We calculated total EMs for elk and bison annually, based on park service counts for that portion of the northern range inside the park: (a) EMs of elk = (elk count) \times (5 months) \times (1 EM per elk-month); (b) EMs of bison = (bison count) \times (10 months) \times (1.5 EM per bison-month).

We utilized scat measurements in September 2018 to index contemporary ungulate use in the Lamar Valley study area by establishing a 3600 m baseline along the main axis of the valley for locating belt transects. At 400 m intervals along the baseline we established two perpendicular transects (each 2 \times 50 m), offset 10 m from each other, for a total of 20 belt transects. We recorded the number of bison, elk, and pronghorn (*Antilocapra americana*) scat within each transect and expressed the results as number of fecal piles per 100m².

4.3. Current vegetation status

In September 2018 we measured the diameter (cm) at breast height of any aspen, cottonwood, or lodgepole pine ≥ 1.5 m in height within the study area. We assessed whether each plant was alive or dead, based on the presence or absence of live foliage. If alive, we also determined the presence or absence of bark damage from bison horning and rubbing. A common behavior of bison involves the rubbing of tree boles by an animal's head, neck, or shoulder and the scraping and gouging of bark with their horns, or "horning," due to aggressive behavior display or as relief from insect harassment (Soper, 1941; Gates et al., 2010). Bark damage from this behavior normally occurs between 0.5 and 1.5 m above the ground and is usually associated with distinct indentations in the bark and wood from the effects of bison horns as well as tufts of bison fur that become attached to the bole during rubbing. We considered bark damage to be "present" when sufficient bark had been removed that the underlying sapwood was exposed.

We sampled reproduction associated with aspen and cottonwood trees ≥ 20 cm in diameter, trees of sufficient size that they normally produce root sprouts. Within a 7-m radius of each tree (38.5 m² of area) we selected the tallest sprouts (≤ 2 m tall), up to a maximum of five. Our selection was biased towards relatively tall sprouts because they could be easily located visually and consistently identified. Furthermore, because elk browsing in the late 1900s had suppressed height growth of aspen and cottonwood sprouts (Ripple and Larsen, 2000; Beschta, 2005), the occurrence of relatively tall sprouts could indicate plant release was underway. We measured the height (cm) of each sprout and whether the

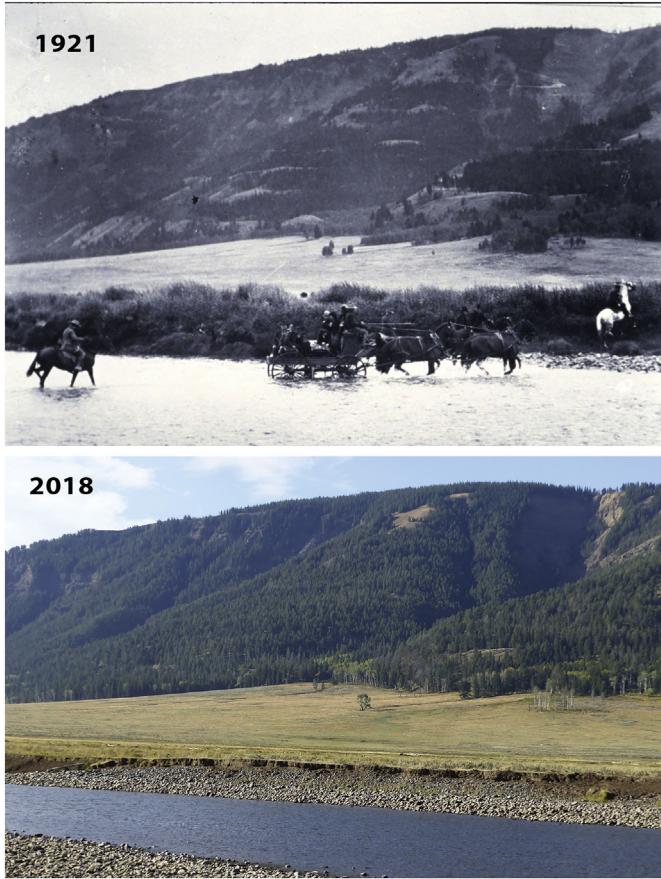


Fig. 2. Willow-shrub communities in 1921 (upper image) along the Lamar River and an absence of these communities in 2018 (lower image). Without riparian vegetation, bank erosion has become common along the Lamar River.

Photo credits: FJ Haynes (YELL 20187, upper photo); RL Beschta (lower photo).

tallest stem, or leader, had experienced browsing of the current year's growth. From these sprout measurements we calculated an average height (cm) and browsing rate (%). Within a 7-m radius of each lodgepole pine ≥ 20 cm in diameter, we similarly searched for up to five pine seedlings for measuring height and browsing.

4.4. Channels

We determined Lamar River and valley lengths between the upstream and downstream ends of the study area using 1954 aerial photographs, as well as 1994 and 2015 Google Earth images, to calculate the Lamar River's sinuosity (i.e., river length divided by valley length). Changes in sinuosity affect channel slope and stream power which, in turn, can influence a river's capability to erode banks and transport bed sediments (Richards, 1982). Aerial photographs from 1954, 1971–1972, 1988, and 1991, along with Google Earth imagery for 1994, 2009, and 2015, were used to quantify the overall length of irrigation ditches on the valley floor and any changes in tributary stream locations.

In September 2018, we measured channel dimensions and vegetation cover associated with the West Fork of Rose Creek and Chalcedony Creek to determine if channel and vegetation recovery since the reintroduction of wolves might be underway, as has been recently reported for many riparian systems in the northern range (see synthesis by Beschta and Ripple, 2016). Along the West Fork we identified three 100-m reaches: Reach A began just upstream of where this tributary discharged into a side-channel of the Lamar River, Reach B was 500 m farther upstream, and Reach C was an additional 500 m upstream, but downstream of the Rose Creek alluvial fan toe. At 4-m intervals along

each reach (25 measurements per reach), we measured (a) channel width (m) at the top of the bank, (b) bank height (m) above the water surface, (c) wetted width (m) of the stream, and (d) depth (m) of water where it was deepest (i.e., thalweg depth), following methods similar to that of Beschta and Ripple (2018).

Along Chalcedony Creek we also identified three 200-m reaches: Reach X was 0–200 m upstream of the creek's confluence with the Lamar River, Reach Y was 200–400 m upstream, and Reach Z was 400–600 m upstream. At 20-m intervals along these reaches (10 measurements per reach) we determined (a) channel width at the top of the bank as well as (b) bank height above the streambed and used these measurements to calculate average channel dimensions and cross-sectional area. Wetted width and thalweg depth could not be measured because stream discharge was not occurring in September 2018.

At 4-m intervals along the West Fork of Rose Creek and Chalcedony Creek we estimated canopy cover (%) over the streambed from woody vegetation (Beschta and Ripple, 2018). We used these estimates to calculate an average canopy cover for each reach.

5. Results

5.1. Historical vegetation change

Repeat photography indicated a complete loss of willow-dominated riparian communities for at least some portions of the Lamar River (Fig. 2) and the West Fork of Rose Creek (Fig. 3). Furthermore, the ~7.5 ha of aspen stands that were present on the valley floor in 1954 had diminished to <0.1 ha by 2015, representing a 99% loss in the cover of overstory aspen trees (Fig. 4).

5.2. Ungulates

Bison numbers in the northern range increased from ~500 animals in the mid-1990s to ~4000 animals in recent years (Fig. 5a). These increases have occurred even though herd reductions that began in the

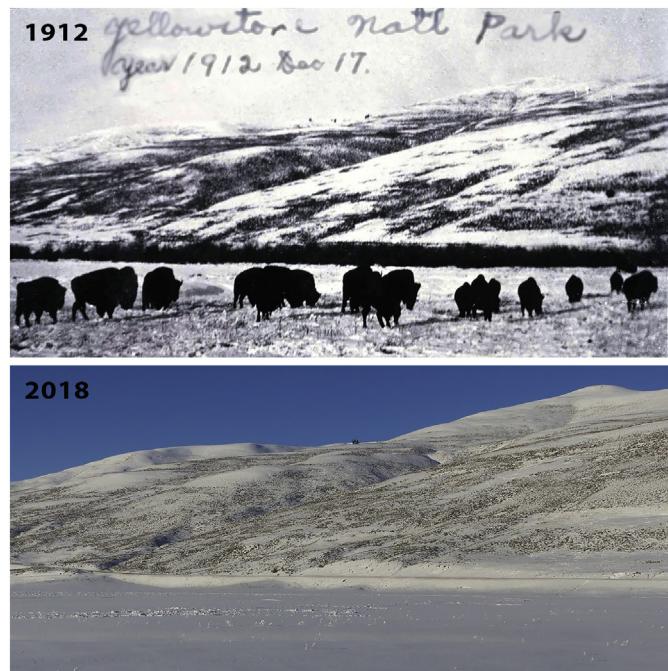


Fig. 3. Tall willow community along the West Fork of Rose creek as it flowed along the north side of the valley bottom in the winter of 1912 (upper image) and an absence of willows along this same area in 2018 (lower image). Photo credits: National Park Service (#3799-37, upper photo); RL Beschta (lower photo).

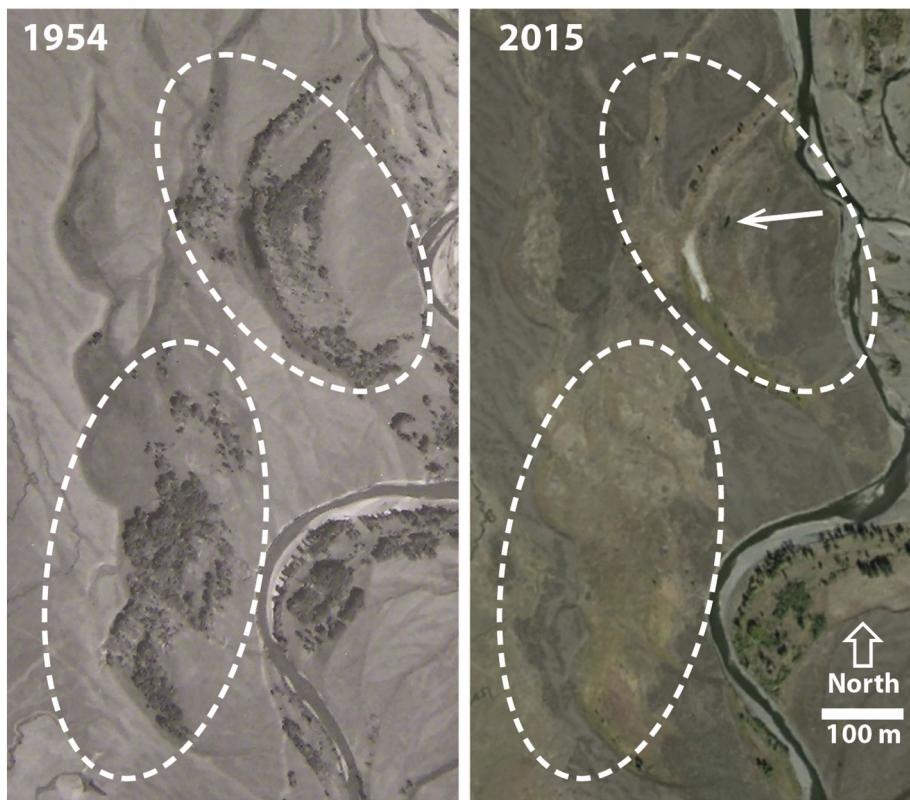


Fig. 4. 1954 aerial photograph (left image) illustrating the extent of several Lamar Valley aspen stands (within the dashed ovals) that covered a total of ~7.5 ha. By 2015 (right image) approximately 99% of aspen cover had been lost. A small aspen thicket that covered 0.016 ha is identified by an arrow on 2015 photo.

mid-1980s have, in recent years, averaged nearly 1000 bison per year (Fig. 5b). The foraging needs for elk and bison in the northern range have also drastically changed since the mid-1990s (Fig. 6). Based on a comparison of calculated *EMs*, the foraging needs of bison in the northern range now exceed those of elk by approximately a factor of 10.

Scat densities averaged 14.2, 0.05, and 0.10 fecal piles/100 m² for bison, elk, and pronghorn, respectively, indicating bison were by far the most prevalent large herbivore utilizing the study area in 2018.

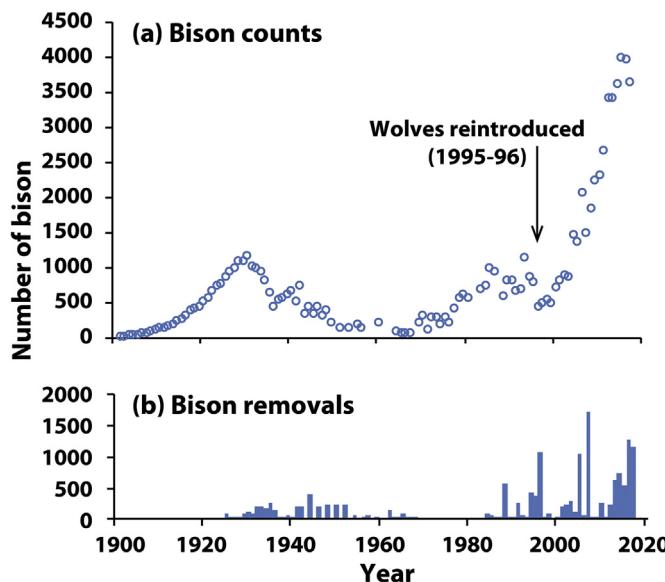


Fig. 5. Annual (a) summertime bison counts (b) bison removals (e.g., culling, hunter harvest, quarantine research). Data source: Yellowstone National Park.

5.3. Recent vegetation change

Within our 9 km² study area we found 31 live aspen trees (Fig. 7a) averaging 52.8 cm in diameter (range = 31–84 cm), of which 65% had damaged bark from the rubbing or horning of bison. Aspen sprouts ($n = 108$) averaged 51 cm in height (range = 10–130 cm) and 35% of them had experienced summertime browsing. We found 11 small diameter aspen (range = 1–8 cm in diameter) at scattered locations in the study area. These smaller aspen had varying degrees of physical protection from the branches and boles of downed aspen trees, nevertheless 45% had damaged bark that appeared to be primarily associated with bison (e.g., horn indentations that often occur vertically along a stem, snagged bison fur). Lastly, we found a single aspen thicket (Fig. 8), occupying 0.016 ha of area. This thicket was comprised of 126

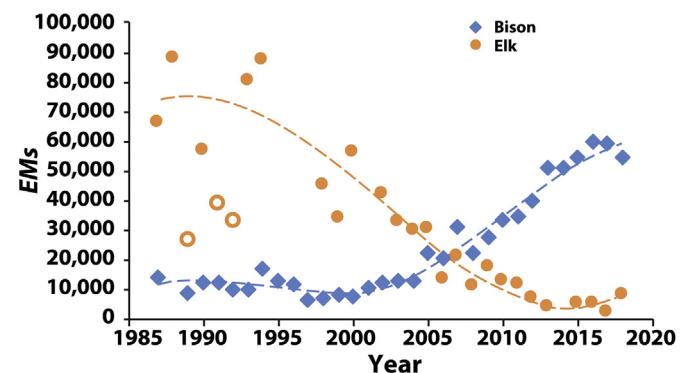


Fig. 6. Relative foraging pressure of bison and elk, in elk-months (*EMs*), within the park's portion of the northern range from 1987 to 2018. Open circles represent years of low elk counts; bison and elk counts were not available for all years.

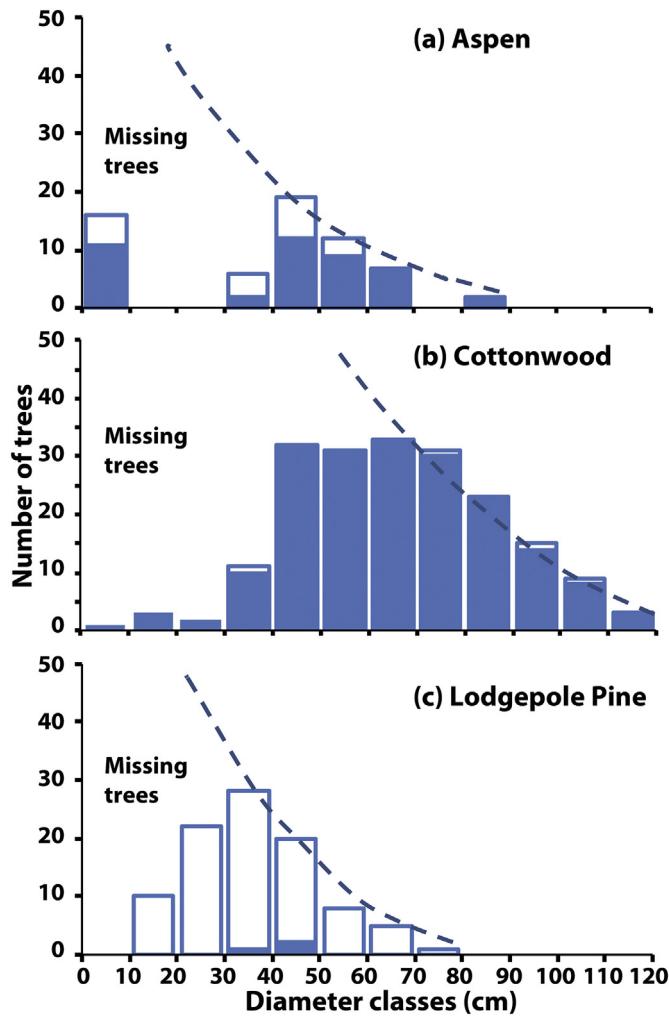


Fig. 7. Number of trees by 10-cm diameter classes, representing the stand structure of (a) aspen, (b) cottonwood, and (c) lodgepole pine within the study area. Solid bars represent live trees and open bars dead trees. Dashed lines are an exponential line fitted to the larger diameter classes, and provide an estimate of the expected number of trees for the smaller diameter classes. Differences between a dashed line (expected) and vertical bars (observed) for the smaller diameter classes represent a “missing trees” and confirm a “recruitment gap.” Sample size: (a) Aspen – 42 live and 20 dead; (b) cottonwood – 194 live and 5 dead; (c) lodgepole pine – 3 live and 88 dead.

live aspen (1–10 cm in diameter) of which 69% had bark damage, although it was not clear what proportion of the damage might be attributed to elk or to bison.

There were 188 live cottonwood trees in the study area (Fig. 7b) averaging 68.4 cm in diameter (range = 30–135 cm), of which 52% had damaged bark. Cottonwood sprouts ($n = 185$) averaged 5.1 cm in height (range = 2–24 cm), a height similar to that of grazed grasses late in summer, and 80% of them had been browsed. An additional six cottonwoods (diameter range = 9–23 cm) were growing on a mid-channel island of the Lamar River of which four had bark damage from bison.

Only 91 lodgepole pine trees occurred in the study area, of which only three were alive (Fig. 7c). The live trees averaged 42.7 cm in diameter (range = 32–49 cm) and the rubbing and horning of bison appeared to have removed bark from 60 to 80% of their circumferences. The 88 dead lodgepole pine trees averaged 36.2 cm in diameter (range = 12–73 cm) and a band of bark was typically absent from around their entire boles, signifying rubbing and horning may have contributed to their mortality. Although most of the lodgepole pines shown in Fig. 9 were alive in 1977, by 2018 the 36 trees (average diameter = 35.7 cm, range = 14–64 cm) we measured at this site were all dead.



Fig. 8. Aspen thicket where ungulate access has been partially hampered by the boles and branches of previously fallen aspen trees (September 2018). Even so, 69% of the stand's 126 live stems, 1–10 cm in diameter, had experienced bark damage. Photo credit: R Lamplugh.

We did not find any conifer seedlings within 7 m of any live or dead lodgepole pine.

5.4. Channels

The sinuosity of the Lamar River through the study area was 1.33, 1.28, and 1.23 km/km in 1954, 1994, and 2015, respectively. Over this 61-year period, the river's sinuosity had decreased ~30%.

Inspection of historical aerial photographs indicated >3000 m of irrigation channels on the valley floor, not necessarily all in use at the same time. These channels were constructed in the first half of the 20th century to support haying operations and mostly used flows from the West, Central, and East Forks of Rose Creek. In 1912, the West Fork of Rose Creek flowed along the base of hillslopes on the north side of the valley (Fig. 3). However, 1954 aerial photographs indicated the location of this stream had changed and it was now some 100–200 m farther from the hillslopes and ~400 m shorter. In addition, between 2009 and 2015 the West Fork channel acquired all flow from the Central Fork of Rose Creek. This stream capture occurred ~100 m downstream from Highway 212 and effectively removed all streamflow from 1900 m of Central Fork channel across the valley bottom. Thus, in 2018 the West Fork channel (1) was at a different location from that of 1912 and (2) contained the combined flows of the West and Central Forks of Rose Creek.

Channel measurements along the three study reaches of the West Fork of Rose Creek indicated rapidly increasing width, depth, and cross-sectional area in a downstream direction (Table 1), with the average cross-sectional area of Reach A (6.1 m^2) more than double that of Reach C (2.7 m^2). Channel measurement of Chalcedony Creek also found increasing width, depth, and cross-sectional area in a downstream direction, with the average cross-sectional area of Reach X (12.2 m^2) more than seven times greater than that of Reach Z (1.7 m^2). Channel cross-sections for both streams were relatively wide and deep, particularly immediately upstream of where each joined the Lamar River. Canopy cover (%) from woody vegetation was entirely absent over the West Fork and the Chalcedony Creek streambeds (Fig. 10).

6. Discussion

6.1. Historical vegetation change

Repeat photographs demonstrated significant willow losses along the Lamar River (Fig. 2) and West Fork of Rose Creek (Fig. 3) during the 1900s, thus dramatically simplifying the structure and function of



Fig. 9. Lodgepole pine stand along the Lamar River in 1977 (upper image) and in 2018 (lower image). Although most pines were alive in 1977, all were dead in 2018 with physical damage to the bark of these trees, from the rubbing and horning by bison, commonly observed. The arrow in the 2018 photo points to a mid-channel island in the Lamar River, one of the few places where a small number of willows, thinleaf alders, and cottonwoods have become established in recent years, possibly because ungulate access is somewhat limited by the surrounding river channel.

Photo credits: J Schmidt (YELL 06951, upper photo); RL Beschta (lower photo).

these riparian communities. These changes were consistent with the general decline of willows and other woody vegetation across the northern range in the 1900s (Grimm, 1939; NPS, 1961; Chadde and Kay, 1991; Singer, 1996; Keigley, 1997; Barmore, 2003). Because elk were by far the most numerous large herbivore using the northern range during the 20th century, they generally have been identified as being responsible for the high levels of browsing that occurred during that period (Houston, 1982; NRC, 2002a; Barmore, 2003). However, the sites shown in Figs. 3 and 4 are ≤ 1.5 km from Buffalo Ranch, indicating that ranching operations and bison herbivory also may have



Fig. 10. The West Fork of Rose Creek (upper image) and Chalcedony Creek (lower image) channels in September of 2018. The absence of woody plants and sparse herbaceous vegetation due to intensive bison herbivory, as well as the trampling effects of bison accessing and crossing each channel, are major factors contributing to ongoing widening and incision of these channels. Short stubble heights of grasses and forbs on the historical floodplains adjacent to each channel represent the effects of intensive grazing pressure by bison; the stadia rod along right bank of Chalcedony Creek is approximately 1.5 m tall.

Photo Credits: RL Beschta.

contributed to the elimination of willows at these sites. Such losses effectively remove the capability of riparian plant communities to provide habitat and food-web support for terrestrial and aquatic wildlife species (NRC, 2002b).

6.2. Ungulates

The rapid increase in bison numbers in recent years, even with annual removals exceeding 1000 bison per year (Fig. 5), indicates that the park's large carnivore guild may be incapable of mediating bison populations. Similarly, Tallian et al. (2017) recently indicated that prey switching by wolves, from elk to bison, is unlikely to provide a stabilizing effect on bison populations.

The estimated foraging pressure of bison within the park has exceeded that of elk since about 2007 and is currently ~ 10 times greater (Fig. 6). In addition, in the Lamar Valley much bison foraging occurs throughout the spring and summer (Geremia et al., 2019) when growing plants are most vulnerable to high levels of herbivory. In contrast, when elk enter the Lamar Valley each fall, their herbivory normally occurs on plants that have grown all summer and have become dormant.

Bison scat densities on the valley bottom were two orders of magnitude greater than elk, a result similar to that obtained in 2010 (Painter and Ripple, 2012) and 2012 (Beschta and Ripple, 2015). For nearly a

Table 1

Average (\pm standard deviation) channel dimensions for sampled reaches of the West Fork of Rose Creek and Chalcedony Creek, Lamar Valley study area (see text for description of methods and reach selection).

Stream & reach	Bank width (m)	Bank height (m)	Wetted width (m)	Thalweg depth (m)	Cross-sectional area (m ²)	n
West Fork of Rose Creek						
Reach A	5.5 \pm 0.7	1.1 \pm 0.4	3.1 \pm 0.5	0.2 \pm 0.04	6.1 \pm 0.8	25
Reach B	4.7 \pm 1.5	0.8 \pm 0.1	2.8 \pm 0.7	0.2 \pm 0.1	4.0 \pm 1.6	25
Reach C	4.2 \pm 0.9	0.6 \pm 0.1	2.8 \pm 0.4	0.3 \pm 0.1	2.7 \pm 0.7	25
Chalcedony Creek						
Reach X	13.1 \pm 7.4	1.2 \pm 0.4	-	-	12.2 \pm 9.0	10
Reach Y	11.4 \pm 2.8	0.9 \pm 0.1	-	-	7.8 \pm 2.6	10
Reach Z	5.4 \pm 0.5	0.4 \pm 0.03	-	-	1.7 \pm 0.2	10

decade it appears that bison have been by far the dominant large herbivore in the Lamar Valley.

6.3. Current vegetation status

The partial removal of a tree's cambium, such as from horning or rubbing by bison, reduces its capability to transfer carbohydrates from leaves to root systems, thus slowing tree growth and potentially contributing to mortality (Filip et al., 2007). Full removal of cambium around a tree's circumference, or girdling, kills the tree. Bark damage can also create portals for the entry of disease organisms that may additionally contribute to tree mortality, a particular concern for aspen (DeByle and Winokur, 1985). For example, the stripping of aspen bark by elk during the 1900s appears to have accelerated aspen tree mortality in the northern range due to increased occurrence of wood-decaying fungi (Beschta and Ripple, 2019a). Even so, the rubbing and horning by bison in recent years represents an additional impact to aspen trees. Approximately two-thirds of the aspen trees in the study area, all ≥ 30 cm in diameter, appeared to have had bark damage primarily from bison. In addition, the 99% decline in aspen canopy cover between 1954 and 2015 in the study area (Fig. 6) exceeded the ~85% decline in northern range aspen stands that had been previously reported (Kay, 1990).

Aspen sprouts averaged 51 cm tall, a height well below the upper browse level of bison and 35% of them had experienced summertime browsing, thus contributing to the ongoing lack of aspen recruitment. This situation appears to be perpetuating what occurred across the northern range in the latter half of the 20th century when intensive elk herbivory limited aspen recruitment (Kay, 1990; Barmore, 2003; Ripple and Larsen, 2000). The continuation of intensive browsing pressure by bison in the Lamar Valley contrasts with other portions of the northern range, where browsing pressure has declined in recent years and woody plant communities have begun to recover (Beyer et al., 2007; Baril et al., 2011; Painter et al., 2014; Beschta and Ripple, 2016). If intensive browsing of young aspen by bison persists in the study area, overstory aspen may not be replaced when they eventually die (Komonen et al., 2020).

We observed a single aspen thicket within the study area containing 126 young aspen (all ≤ 10 cm in diameter). Although ungulate access to these aspen appeared to have been partially impeded by the branches and boles of previously downed aspen trees, as these downed trees continue to decay their capability to impede the rubbing and horning effects of bison will decrease. Because bark damage is particularly effective at increasing the mortality of small aspen trees via heart rot (DeByle and Winokur, 1985; Hart, 1986), this thicket, of which 69% currently exhibit bark damage, may not survive in the coming years.

The bark of mature cottonwoods is normally thick, furrowed, and relatively resistant to bison rubbing and horning. Even so, the proportion of overstory cottonwoods in the study area with exposed heartwood increased appreciably during the last six years, from 32% in 2012 (Beschta and Ripple, 2015) to 52% in 2018. Cottonwoods are comparatively long-lived, with some living >200 years (Beschta, 2005), however if the current rate of loss continues (i.e., 33% lost in the last 16 years), a large portion of the valley's remaining cottonwood trees may be gone within a few decades (Fig. 11).

Cottonwood sprouts in the study area had much higher summertime browsing rates than aspen (80% vs. 35%) and average heights were only one-tenth that of aspen, indicating that bison herbivory is also suppressing the growth and recruitment of young cottonwood plants, a result consistent with previous studies (Painter and Ripple, 2012; Beschta and Ripple, 2015; Rose and Cooper, 2016). This intensive herbivory from bison diverged with that found only a few kilometers up-valley along the Lamar River and Soda Butte Creek, where bison use has been lower and cottonwood recruitment has occurred (Beschta and Ripple, 2015).

The bark of Lodgepole pine is relatively thin (typically ≤ 1 cm thick; Parker, 1950) and appears to be particularly susceptible to damage

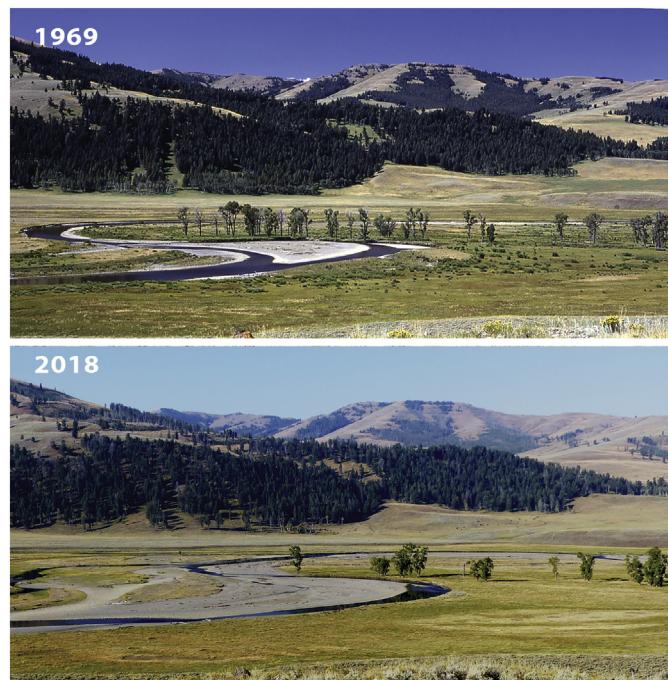


Fig. 11. A portion of the Lamar Valley <1.5 km from Buffalo Ranch in 1969 (upper image) and 2018 (lower image). During the nearly half century between photos there has been a complete lack of cottonwood and willow recruitment due to decades of intensive browsing, initially by elk but more recently by bison. Without functional riparian plant communities, accelerated riverbank erosion and lateral channel migration have removed numerous overstory cottonwoods along this reach.

Photo credits: WW Dunmire (YELL 14455, upper photo); RL Beschta (lower photo).

from rubbing and horning by bison. In an earlier study of bark damage associated with bison, Olenicki and Irby (2004) measured 1343 conifers ≥ 5 cm in diameter bordering YNP's Hayden Valley. Bark had been removed, by rubbing and horning, from $>20\%$ of the circumference for 56% of these trees. Another 28% of the trees were dead, all with visual signs of bark damage from bison, potentially representing a mechanism for bison to prevent forest margins from extending into grasslands (White et al., 2015). Approximately 97% of the lodgepole pine trees we measured in the Lamar Valley, some perhaps >150 yrs. of age (Alexander and Edminster, 1981), were dead, with considerable evidence of rubbing and horning from bison (Fig. 9).

The ongoing lack of aspen and cottonwood recruitment in the Lamar Valley, as well as the decline in aspen, cottonwood, and lodgepole pine trees, is consistent with the hypothesis that current levels of herbivory and bark damage by bison are having a strong negative influence on these plant communities. Live lodgepole pines are now effectively absent from the study area and aspen may soon follow. High rates of bark damage (this study) and river bank erosion (Rosgen, 1993; Beschta and Ripple, 2015) indicate overstory cottonwood losses could also continue at a high rate. Overall, any structural and biological diversity provided by aspen, cottonwood, and lodgepole pine communities on the valley floor may well be lost in the coming years, they only differ in the rate at which this loss is occurring. There also appears to be little likelihood of replacement if high rates of browsing continue.

Native graminoid species, such as those occurring in the Lamar Valley, likely evolved with low selection pressure by large congregating herbivores (Mack and Thompson, 1982), a situation much unlike that which is occurring today. Furthermore, herds of bison were likely uncommon in the present day park prior to the mid-1800s (Kay, 1990; Beschta and Ripple, 2019b; Keigley, 2019). These additional lines of evidence further indicate that the intensive herbivory by bison currently occurring in the Lamar Valley may be well beyond any ecological norm for this ecosystem.

6.4. Channels

Photographs from the early 1900s indicated riparian areas in the Lamar Valley contained a range of age-size classes of woody plants, and these riparian communities were present along at least some of the Lamar River's banks and tributary streams. The composition and structure of riparian plant communities can have an important role in shaping the morphology of alluvial channels, ensuring sediment deposition on floodplains during periods of over-bank flows, influencing and stabilizing channel morphology, contributing to enhanced soil moisture storage and carbon sequestration, and maintaining water quality (Asner et al., 2003; Kauffman et al., 2004; NRC, 1992, 2002b). These communities also provide resistance to the erosive forces of high flows and thus help maintain stable riverbanks via (a) the cohesive effects of roots and organic matter that help bind soil and alluvial particles and (b) the capability of plant stems and leaves to decrease flow velocities along riverbanks and on floodplains (Sedell and Beschta, 1991; Simon and Collison, 2002; Bennett and Simon, 2004; Richardson and Danehy, 2007). Furthermore, the accumulation of root masses, logs, and other woody debris in a river or stream channel often ensures adequate cover and habitat for aquatic organisms, influences pool-riffle morphology, and can help to anchor beaver dams (*Castor canadensis*) (Gregory et al., 1991; Baker and Cade, 1995; NRC, 2002b; Naiman et al., 2005; Goldfarb, 2018).

The structural and functional degradation of riparian plant communities along the banks of the Lamar River have likely contributed to the 30% decrease in sinuosity over the last six decades. This loss of sinuosity increases the capability of high flows to erode riverbanks and floodplains as well as transport bed sediments (Yang and Stall, 1974; Sedell and Beschta, 1991). The nearly complete lack of woody vegetation along the river's banks in 2018, in conjunction with a decreased sinuosity, essentially insures the continuation of accelerated bank erosion and over-widened channels (Fig. 12), a situation that has become increasingly prevalent along the Lamar River (Rosgen, 1993; Beschta and Ripple, 2015). In addition, the Chalcedony Creek streambed, where it joined the Lamar River, was ≥ 1.5 m above the elevation of the water surface of the Lamar River in September of 2018. This "hanging stream" indicates that rapid widening or down-cutting has been occurring along this portion of the Lamar River and represents an example of feedback that accelerates erosion can have following the loss of riparian plant communities.

Expansive areas of unvegetated alluvial deposits are currently found along the river where it flows through the valley (Beschta and Ripple, 2015). Normally, such deposits provide excellent sites for cottonwood regeneration since their seedlings are well adapted for establishing and growing on alluvial substrates formed by high flows (Braatne et al., 1996). Many tens of thousands of cottonwood seedlings established in the Lamar Valley during the two highest flows of record

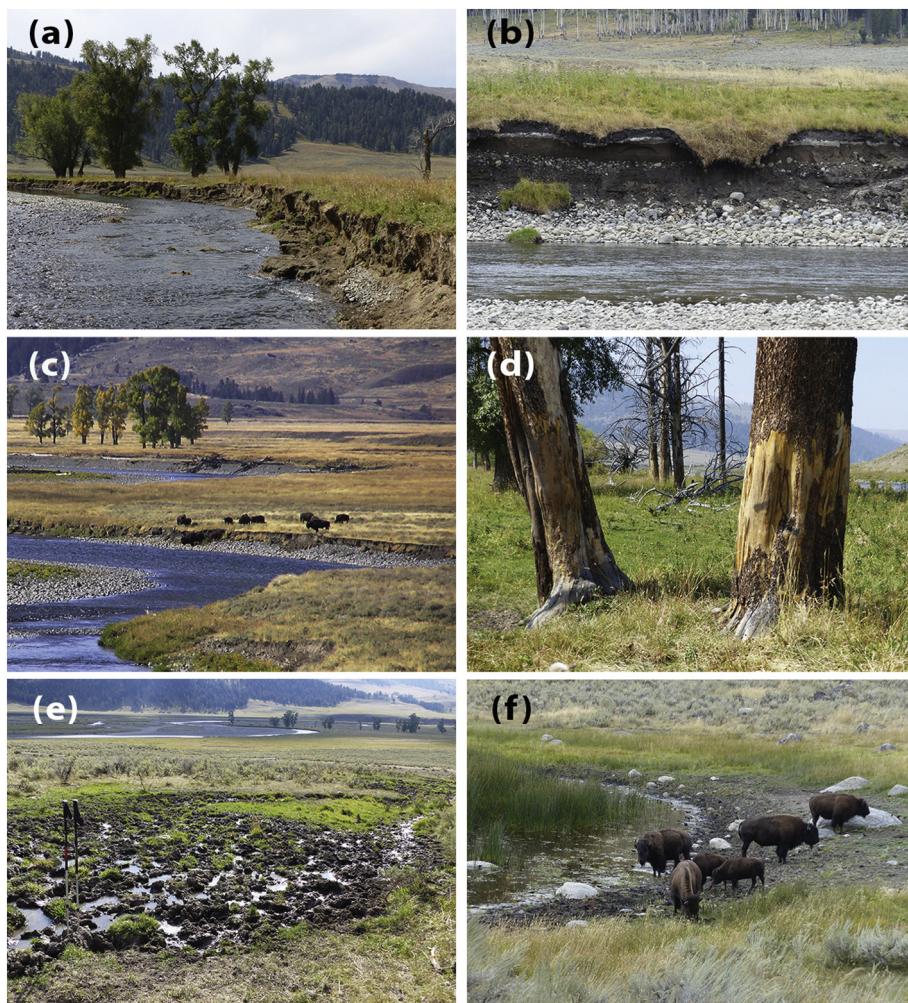


Fig. 12. Multiple ecosystem effects of high densities of bison: (a) absence of riparian plant communities allows accelerated bank erosion and lateral migration of Lamar River resulting in loss of organic rich floodplain soils and overstory cottonwoods, (b) bank collapse and a hydrologically disconnected floodplain due to channel incision of the Lamar River, (c) trampling of riverbanks contributing to accelerated erosion, (d) bark damage from the rubbing and horning of lodgepole pine trees, effectively girdling the trees, (e) trampling of seeps and springs, and (f) extensive utilization of sedges and trampling along pond edges. Photos (a)–(e) from the Lamar Valley; (f) from Little America. Photo Credits: RL Beschta.

(i.e., in 1996 and 1997) as well as during another high flow in 2002 (Beschta and Ripple, 2015; Rose and Cooper, 2016). However, by 2012 only 54 young cottonwoods within the study area had grown above 1.5 m in height (Beschta and Ripple, 2015) and by 2018 (this study) only six remained. The combined effects of intensive bison herbivory, trampling, and bark damage to young cottonwoods in recent years appear to have effectively prevented any significant recruitment of cottonwood trees on these alluvial deposits.

The channel characteristics of tributary streams crossing the valley floor also reflect the direct biological (e.g., intensive herbivory, loss of plants) and physical (e.g., trampling) effects of bison. The absence of canopy cover along the West Fork of Rose Creek indicated that woody root systems were absent, root systems that might otherwise help stabilize channel banks. Sedges can also be an important factor in stabilizing banks of northern range streams (Beschta and Ripple, 2018). They are also a primary source of forage for bison in the northern range (Meagher, 1973) and those observed along the banks of the West Fork had been heavily grazed. Such highly altered vegetation communities may have contributed to the change in location of the West Fork channel between 1912 and 1954 as well as its recent capture of all flows from the Central Fork of Rose Creek. Importantly, the loss of perennial flow from ~1900 m of the Central Fork's channel across the valley floor effectively disconnected its riparian plant communities and floodplains from their principal source of moisture.

Stream-bank collapse from bison trampling was a common feature along the West Fork of Rose Creek and Chalcedony Creek (Fig. 9), likely contributing to accelerated bank erosion during high flows. Vertical banks were normally present at the outside of meander bends, indicating that channel widening is ongoing. This enlarging of channel cross-sections indicates that overbank flows may no longer occur during periods of high stream discharge (i.e., annual snowmelt peak). Under such conditions, those riparian and wetland plants adapted to high soil moisture levels and saturated conditions from overbank flows, are unlikely to persist.

The overall condition and geomorphic trend of the West Fork of Rose Creek and Chalcedony Creek channels were remarkably different from that occurring along Blacktail Deer Creek in the central portion of the northern range, where ungulate herbivory has dramatically decreased since the reintroduction of wolves (Beschta and Ripple, 2018). Willows at Blacktail Deer Creek, which averaged <50 cm in height in 1995, have attained >300 cm in height by 2017. Similarly, canopy cover over the stream, which was <5% in 1995, had increased to 43–93% by 2017. Sedges, grasses, willows, and alders along the creek had become increasingly prevalent, thus helping to stabilize stream banks and initiate the development of an inset floodplain (i.e., Fig. 5 in Beschta and Ripple, 2018). Those results indicated there is considerable potential for woody and graminoid plants to reestablish and grow along streams in the northern range, as well as to help stabilize stream banks, but only if the overriding effects of intensive ungulate herbivory and trampling can be significantly reduced.

The consequences of high densities of bison upon plant communities and channels in the Lamar Valley are not only continuing the historical ecological effects of high elk densities in previous decades, but may well be accentuating those effects for several reasons: (a) Bison, on average, weigh considerably more than elk, thus increasing their trampling effects (e.g., soil compaction, bank collapse); (b) The frequent movement of bison herds up and down the valley insures repeated grazing and browsing pressure, soil compaction, and bank trampling during the growing season; (c) Elk have long been known to damage aspen bark by stripping and consuming it, thus increasing tree mortality due to the entry of wood-decaying fungi (DeByle and Winokur, 1985; Beschta and Ripple, 2019a). Now, the increasingly common damaging effects of bison rubbing and horning to the bark of aspen trees, as well as those of cottonwood and lodgepole pine, is likely contributing to their ongoing decline.

7. Concluding remarks

The recovery and expansion of the Yellowstone bison herd has been a major conservation success story and, as one of the few remaining herds that has not hybridized with cattle, these bison are an invaluable conservation resource. However, increased bison numbers over the last two decades appear to have come at a major ecological cost to the biological diversity and functioning of the riparian ecosystems in the Lamar Valley. Even to a casual observer there are clear indicators of highly altered ecological conditions across the Lamar Valley: short stubble heights of native grasses and forbs in late summer, a high density of bison trails, wallows, and scat, continued suppression of young woody plants by browsing, and a general absence of woody and herbaceous riparian vegetation along the banks of the river and tributary streams (Fig. 12). In addition, extensive areas of unvegetated alluvium are common, soil compaction and bank collapse along channel margins is widespread, and the physical churning of soils by bison hooves in springs and wetlands has undoubtedly altered the hydrology and biodiversity of these ecologically important areas. In short, high bison numbers in recent years have been an effective agent for accelerating the biological and physical modification of the valley's seeps, wetlands, floodplains, riparian areas, and channels, trends that had begun decades earlier by elk. Ecosystem simplification is well underway, much like that often associated with high levels of domestic livestock use in various areas of the mountain west (Belski et al., 1999; Platts, 1991; Fleischner, 1994; Donahue, 1999; Kauffman and Pyke, 2001; Batchelor et al., 2015).

An important principle for passive restoration of ecosystems is to reduce or cease those activities causing degradation or preventing recovery (Kauffman et al., 1997). In Yellowstone's iconic Lamar Valley, and elsewhere in the northern range where significant bison impacts are occurring (e.g., Yancey's Hole, Little America), the ongoing environmental effects of bison would have to be significantly reduced in order to restore biologically diverse communities dominated by willows, cottonwoods, and aspen. Restoration of these communities would result in increased soil moisture storage, nutrient availability, and carbon sequestration, improved food-web support for terrestrial wildlife species, and improved channel conditions of the Lamar River and its tributary streams, thereby improving both terrestrial and aquatic habitats, and mediating water quality. As park administrators make management decisions that affect ungulate densities and distributions in Yellowstone, as well as those in other parks and reserves with high ungulate densities, our findings indicate a need to take into account the often wide range of ecological effects that abundant large herbivores can have on terrestrial and aquatic ecosystems.

Declaration of competing interest

There are no conflicts of interest concerning our article.

Acknowledgements

We are very appreciative of elk and bison annual counts provided by Yellowstone National Park, as well as review comments by S. Fouty and figures by S. Arbogast. This work was supported, in part, by the Ecosystem Restoration Research Fund and the National Science Foundation Grant 1754221.

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