# Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone, USA

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## ABSTRACT

Understanding the potential effect apex predators may have on riparian plant communities, via a trophic cascade, represents an important research challenge in Rocky Mountain ecosystems. In the northern ungulate winter range of Yellowstone National Park where grey wolves (*Canis lupus*) were historically present, absent for seven decades, and recently reintroduced, our objective was to evaluate patterns of cottonwood (*Populus* spp.) recruitment for two adjacent reaches of the Lamar Valley. Results indicated that recruitment was common in both reaches when wolves were historically present and declined because of intensive herbivory from elk (*Cervus elaphus*) after wolves were extirpated in the early 1900s. By the 1970s, cottonwood recruitment along both reaches had essentially ceased. Wolves were reintroduced in the mid-1990s, and by 2012, some 4660 young cottonwoods ≥2 m in height (the general upper browse level of elk) had become established within the 2-km-long upper Lamar study reach, consistent with re-establishment of a tri-trophic cascade involving wolves, elk, and cottonwoods. However, within the 8-km-long lower Lamar study reach, only 22 young cottonwoods had attained a height of ≥2 m because of high levels of herbivory, especially from bison (*Bison bison*). Top–down trophic interactions involving wolves and elk, as well as reach characteristics and browsing by bison, appear to explain the strongly contrasting patterns of recent riparian cottonwood recruitment currently underway in the northern Yellowstone – one reach represented by a recovering riparian ecosystem and the other an alternative stable state with highly altered riparian vegetation and channel conditions. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS    riparian forests; channel erosion; cottonwoods; peakflows; herbivory; ungulates; wolves; Yellowstone National Park

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## INTRODUCTION

Across the American West, large mammalian predators such as grey wolves (*Canis lupus*), cougar (*Puma concolor*), and grizzly bears (*Ursus arctos*) experienced extensive range contraction and habitat fragmentation by Euro-Americans in the 1800s and early 1900s (Laliberte and Ripple, 2004). Even Yellowstone National Park (YNP), the nation's first national park in 1872, was not exempt from apex predator loss. The effects of large carnivores can reverberate through ecosystem food webs with potentially far-reaching effects on species, habitats, and ecosystem functions (Estes *et al*., 2011; Teichman *et al*., 2013; Ripple *et al*., 2014). Thus, maintaining or recovering ecologically relevant carnivore populations may have important ecosystem benefits (Kuijper *et al*., 2013; Ordiz *et al*., 2013; Wilmers *et al*., 2013), particularly for riparian and riverine systems (Beschta and Ripple, 2008, 2012b).

When grey wolves were historically present in YNP, the recruitment of deciduous woody species (i.e. growth of seedlings or sprouts into tall saplings and trees) in the park's northern ungulate winter range was ongoing (e.g. Ripple and Larsen, 2000; Beschta, 2005). However, with the extirpation of this apex predator in the mid-1920s and its absence during the subsequent seven decades, recruitment of browse plants declined because of intensive herbivory, particularly by elk (*Cervus elaphus*). This increased herbivory was especially effective at suppressing seedlings and sprouts of deciduous woody species (Kay, 1990; Keigley, 1997; NRC, 2002a), as well as affecting other vegetation, soils, and the habitats of terrestrial and aquatic species (NPS, 1961). By the 1970s and 1980s, recruitment of aspen (*Populus tremuloides*) (Ripple and Larsen, 2000; Kay, 2001; Halofsky and Ripple, 2008), willows (*Salix* spp.) (Chadde and Kay, 1996; Wolf *et al*., 2007), and cottonwoods (*Populus angustifolia* and *P. trichocarpa*) (Beschta, 2003, 2005) in northern Yellowstone had essentially ceased. In other areas of western North America, where apex predators have been extirpated or displaced, native ungulate herbivores (consumers) have

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also been found to have major top–down effects on plant communities (producers) and ecosystem processes (White et al., 2003; Hebblewhite et al., 2005; Beschta and Ripple, 2009, 2012b).

Wolves were reintroduced into YNP during the mid-1990s, again completing the park's large predator guild (Smith et al., 2003). Soon thereafter, elk, which represent the primary prey of this apex predator, began to alter their vigilance, foraging, movements, group size, habitat use, and other traits (e.g. Creel et al., 2005; Laundré et al., 2010; White et al., 2012), and their populations began to decrease (Vucetich et al., 2005; White et al., 2012). With the return of wolves, deciduous woody species that had previously been browsing-suppressed by elk also began to demonstrate increased height and/or diameter growth in portions of northern Yellowstone indicating a re-establishment of a trophic cascade involving wolves, elk, and vegetation (see review of northern Yellowstone studies; Ripple and Beschta, 2012). However, field observations indicated that major differences in contemporary patterns of cottonwood recruitment were underway in the Lamar Valley of Yellowstone's northern range. We thus undertook this study to evaluate potential factors affecting these divergent patterns of cottonwood recovery. This represents the first northern range study to consider the long-term age structure of riparian cottonwoods over three treatment periods: (1) when wolves were present (prior to the mid-1920s), (2) when they were absent (mid-1920s to mid-1990s), and (3) following reintroduction (mid-1990s to the present). It is also the first to identify the contrasting effects of elk and bison (Bison bison) herbivory upon the recruitment of riparian cottonwoods since the reintroduction of wolves.

## METHODS

### Study area

The 1500-km$^2$ northern ungulate winter range, or 'northern range', is located in the north-central portion of YNP and is utilized by elk and bison, as well as smaller populations of pronghorn (Antilocapra americana) and mule deer (Odocoileus hemionus) (NRC, 2002a). After the park service ceased culling of elk and bison in 1968, the northern range population of ~3000 elk increased to nearly 20 000 elk within two decades (Figure 1a), attaining densities >10 elk km$^{-2}$. Bison numbers during these two decades increased from less than 150 to nearly 1000 animals (Figure 1a).

Wolves were reintroduced into YNP in 1995–1996, and the northern range elk population has since decreased to levels not seen since the mid-1960s. In contrast, bison have increased to nearly 2000 animals, historically high. Elk normally use the northern range for foraging and habitat needs from late fall to early spring, whereas bison use is year-round (NRC, 2002a; White et al., 2012). Although elk and bison are normally considered to be grazers, depending upon the availability of herbaceous plants and seasonal conditions, they will also browse woody plants (Larter and Gates, 1991; Toweill and Thomas, 2002).

The Lamar Valley, located in the eastern portion of the park's northern range, is 1–1·5 km wide and 10 km long with scattered groves of mature cottonwoods occurring along the river's broad floodplain. These overstory cottonwoods consist of trees >20-cm diameter at breast height (DBH). A lack of intermediate diameter classes (10- to 20-cm DBH), representing a major 'recruitment gap', has been associated with intensive browsing of elk that effectively suppressed the heights of young cottonwoods during the latter half of the 20th century when wolves were absent (Beschta, 2003, 2005). Consistent with herbivory impacts to riparian plant communities, accelerated lateral migration of the Lamar River, often involving erosion of floodplain soils and alluvial terraces, has been relatively common since at least the 1950s (Rosgen, 1993; Rose, 2012) and has created large areas of unvegetated alluvial deposits along the river.

We delineated two study reaches – the upper and lower Lamar – which in total comprised the full length of the Lamar Valley. From the upstream end of the valley, the upper Lamar study reach extended downstream ~2 km to the river's confluence with Soda Butte Creek. From this confluence, the lower Lamar study reach continued downstream another ~8 km to where the Lamar River enters a canyon.

### Field measurements

In August 2012, we measured the DBH (cm) of all overstory cottonwoods along the active channel and floodplain within both study reaches. Because young cottonwoods ≥1·5 m in height (i.e. breast height) were numerous within the upper Lamar, we sampled them for determining population DBHs. Within this reach, we delineated a total of 21 discrete areas (polygons) ≥20 m in length that contained young cottonwoods ≥1·5 m in height. A 1-m-wide belt transect perpendicular to each polygon's main axis was randomly established along the first 20 m of this axis; subsequent transects occurred systematically at 20-m intervals along this same axis and resulted in a 5% sample. Within each transect, the DBH of young cottonwoods ≥1·5 m in height was measured to the nearest centimetre. For the lower Lamar, the DBH of all young cottonwoods ≥1·5 m in height was measured (a total inventory) because such plants were relatively few in number. The boundaries of eroding floodplains and unvegetated alluvial surfaces were delineated on aerial photographs (24 September 2009) and used to calculate the total area (ha) of active channel in each reach.
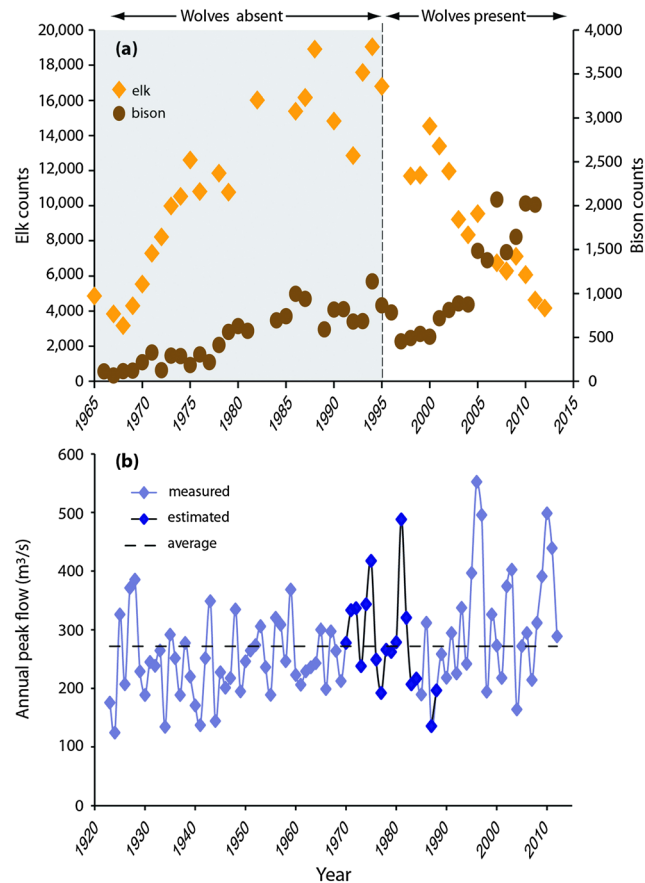
Figure 1. (a) Elk and bison counts for the northern range (1965–2012) and (b) annual peakflows of the Lamar River (1923–2012). Elk and bison counts from Yellowstone National Park (poor elk counts in 1977, 1989, 1991, and 2006 not shown). Peakflows for 1971–1985 and 1989–1989 estimated from regression between the Lamar River and the Clarks Fork of the Yellowstone (see text for methods).

The establishment year (*EY*) of cottonwoods ≥5 cm *DBH* was estimated from a regression equation previously developed for cottonwoods in the Lamar Valley on the basis of increment cores (Beschta, 2005): $EY = 2012 (0.56 \, DBH^{1.36} + 5.8, \; r^2 = 0.82, \; n = 54)$. The '5.8' in this equation approximates the average number of years needed for cottonwood seedlings to attain breast height ($\bar{x} = 5.8$ years, $SE \pm 0.2$ years; on the basis of age measurement of 50 cottonwoods 1.5 m in height). Cottonwood frequencies were 'binned' by decade from 1800 to 2009 to develop an age structure (i.e. tree frequency per decade vs decade of establishment) for each study reach. Regression analysis of tree frequency (dependent variable) versus decade of establishment utilized an exponential function (e.g. Beschta and Ripple, 2009) to characterize the general pattern of tree recruitment for those decades when wolves were historically present (i.e. 1800s to 1920s). The exponential equation obtained for each reach was then used to (1) estimate 'expected' tree recruitment in subsequent decades (i.e. 1930–2009) and (2) determine if observed recruitment in any of these later decades was significantly lower than expected (i.e. outside the regression's lower 95% confidence limit).

To further characterize young cottonwoods within each study reach and compare these results with earlier studies, we systematically sampled the number of young cottonwoods ≥0.2 m in height. Four-metre-wide belt transects perpendicular to the valley's main axis were established across the active channel at 200-m intervals along the upper Lamar and at 250 m intervals along the lower Lamar; transects were generally ≤300 m in length. Within each transect, we enumerated all young cottonwoods ≥0.2 m in height; the same procedure had been employed in 2002 (Beschta, 2005). We also measured the heights of the three tallest young cottonwoods within 50-m segments along each reach, repeating procedures used in 2002 and 2006 (Beschta and Ripple, 2010), to obtain a 'leading edge' indicator of any increase in cottonwood heights within the last decade.

As an index of bison use in each reach, we inspected all overstory cottonwoods for bark damage. If rubbing or horning by bison had injured the bark's cambium sufficiently so that the underlying wood surface was exposed, it was recorded as a 'scarred' tree. Along the valley's main axis, fecal count plots were established at

200-m intervals in the upper Lamar and at 250-m intervals in the lower Lamar. At each interval location, we established a $2 \times 50$ m plot within the active channel, approximately midway between the river and its floodplain, to enumerate fecal piles of elk, bison, pronghorn, and mule deer (Painter and Ripple, 2012). Lastly, we established five widely separated ($\geq 300$ m apart) linear transects within each reach for measuring the occurrence of browsing on young cottonwoods. These transects varied from 60 to 150 m in length and were subdivided into 30 equally spaced points along their main axis. At each point along a given transect, the nearest young cottonwood $\leq 1$ m in height (within the browse level of both elk and bison) was selected and, on the basis of plant architecture (Ripple and Beschta, 2007), we recorded whether its tallest stem (leader) had been browsed between 2011 and 2012; an average browsing rate was calculated for each transect. Comparisons of average scat densities (fecal piles 100 m$^{-2}$) and browsing rates (%) between the two reaches were compared using $t$-tests (a $p$-value of $<0.05$ was considered to be statistically significant).

Peakflows and associated channel adjustments can have an important influence on riverine/riparian systems because these disturbances often create areas of unvegetated alluvium, sites that are important for cottonwood seedling establishment (Stettler *et al.*, 1996). We compiled annual peakflows for the Lamar River gage (drainage area = 1710 km$^2$) from 1923 to 2012, inclusive. To evaluate potential changes in the magnitude of peakflows following the 1988 wildfires, we (1) established a pre-fire linear regression between annual peakflows of the Lamar River (dependent variable) with those of the Clarks Fork of the Yellowstone (drainage area = 2990 km$^2$) and then (2) compared post-1988 estimated peakflows (from regression) to observed peakflows for the Lamar River. Although wildfires in 1988 did not occur along the valley bottom of the Lamar Valley, ~70% of the catchment burned that summer (Rothermel *et al.*, 1994), mostly higher-elevation summer range. The Clarks Fork drained mountainous terrain immediately east of and adjacent to the Lamar River catchment and experienced wildfire on ~15% of its catchment in 1988.

## RESULTS

In 2012, overstory cottonwoods numbered 370 and 199 in the upper and lower Lamar study reaches, respectively (average $DBH = 61$ cm, range = 21–130 cm). In comparison to a 2001 inventory (Beschta, 2003), 22% and 10% of the overstory cottonwoods along the upper and lower Lamar, respectively, have been lost during the last decade from various causes (e.g. floodplain erosion, disease, old age mortality, and beaver cutting).

For the period when wolves were historically present in the park (i.e. 1920s and prior), we obtained statistically significant relationships between cottonwood frequency and establishment date for the upper ($r^2 = 0.79$, $p < 0.001$) and lower ($r^2 = 0.61$, $p = 0.002$) study reaches (Figure 2). These equations were used to approximate a 'j-shaped' pattern of age structure that is often associated with uneven-aged forests. Observed cottonwood frequencies in each reach, following the extirpation of wolves in the 1920s, began to significantly decrease from expected (i.e. compared to the exponential relationships) and eventually dropped to zero, or nearly zero, in both reaches during the 1960s, 1970s, 1980s, and 1990s. However, by the first decade of the 21st century, this situation fundamentally changed in the upper Lamar where cottonwood recruitment began to increase. By the end of this decade, some 380 young cottonwoods had attained a $DBH$ of $\geq 5$ cm (Figure 2a). In contrast, cottonwood recruitment along the lower Lamar remained extremely low during the first decade of the 21st century, and only seven young cottonwoods had attained a $DBH$ of $\geq 5$ cm within this reach (Figure 2b).
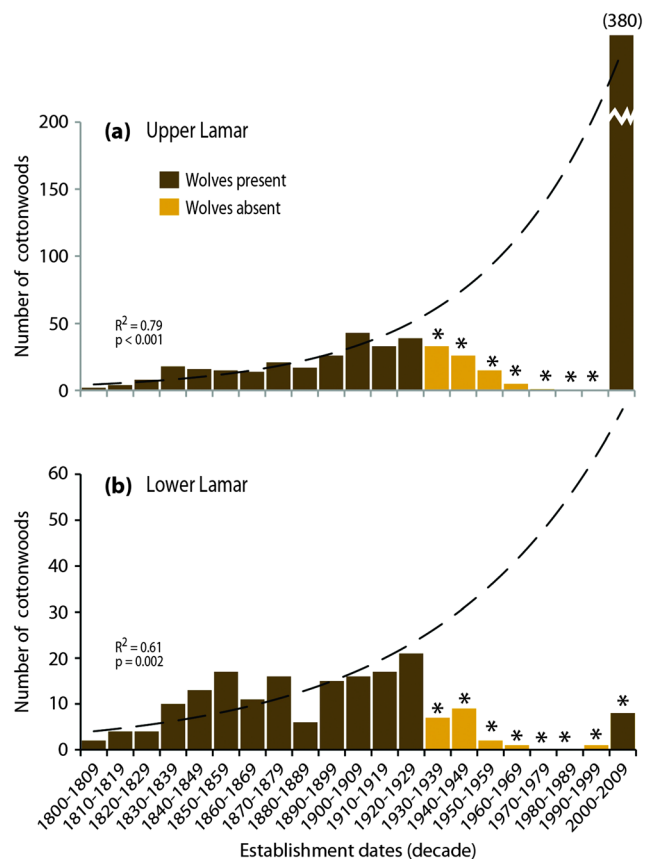


Figure 2. Frequency of cottonwoods $\geq 5$ cm in diameter at breast height, by decade, from 1800 to 2009 for the (a) upper Lamar and (b) lower Lamar study reaches. The exponential regression lines (dashed) were fitted through data for 1800s to 1920s, when wolves were present; an * indicates values outside the regression's lower 95% confidence limit.

Approximately 28 and 78 ha of active channels (on the basis of 2009 aerial photograph measurements) were present along the upper and lower Lamar, respectively. Our field sampling in 2012 indicated an estimated 41 700 ($SE \pm 4600$) and 75 700 ($SE \pm 27\,500$) young cottonwoods $\geq 0.2$ m in height along the upper and lower Lamar, respectively. Of the 16 900 ($SE \pm 2730$) young cottonwoods that had attained a height of $\geq 1.5$ m in the upper Lamar, some 4660 ($SE \pm 1100$) exceeded the upper browse level of elk (~2 m), and 1210 ($SE \pm 450$) were $\geq 5$ cm in $DBH$, a more than threefold increase since 2009. In contrast, along the lower Lamar, only 54 young cottonwoods $\geq 1.5$ m in height were found of which 22 were $\geq 2$ m in height and 11 were $\geq 5$ cm in $DBH$. With regard to the three tallest young cottonwoods measured in 2012 within 50-m-long segments along each reach, median heights (50th percentile) of 5.1 and 0.2 m were obtained for the upper and lower Lamar, respectively (Figure 3).

Scarring of overstory cottonwoods by bison occurred on 12% and 32% of these trees within the upper and lower Lamar, respectively. The average number of bison fecal piles in the upper Lamar ($\bar{x} = 5.6$ fecal piles 100 m$^{-2}$) was significantly less than in the lower Lamar ($\bar{x} = 10.0$ fecal piles 100 m$^{-2}$; $t$-test, $p = 0.028$, $n_1 = 7$, $n_2 = 22$, log-transformed variables). Although the upper Lamar had an average of 0.3 fecal piles 100 m$^{-2}$ of elk and the lower Lamar 0.2 fecal piles 100 m$^{-2}$ of pronghorn, our plots indicated an absence of scat for (1) elk in the lower Lamar, (2) pronghorn in the upper Lamar, and (3) mule deer in

both reaches. The average percentage of young cottonwoods browsed between 2011 and 2012 in the upper Lamar ($\bar{x} = 30.7\%$) was significantly less than in the lower Lamar ($\bar{x} = 59.3\%$; $t$-test, $p = 0.024$, $n_1 = n_2 = 5$, arcsine transformed variables).

During the 66 years of streamflow record prior to the 1988 fires, the Lamar River's largest annual peakflow of 490 m$^3$ s$^{-1}$ occurred in 1981(Figure 1b). However, following the 1988 fires, this peakflow has been exceeded three times, in 1996, 1997, and 2010. On the basis of the linear regression of the Lamar River ($y$) versus the Clarks Fork ($x$) peakflows prior to 1988 ($r^2 = 0.71$, $p < 0.001$), annual peakflows of the Lamar River since 1988 have increased an average of 22%.

## DISCUSSION

Our cottonwood age structures confirmed that recruitment was ongoing in both study reaches when wolves were historically present and declined precipitously after the extirpation of wolves, consistent with trophic cascade theory. Furthermore, the decline in cottonwood recruitment due to intensive elk browsing in the absence of wolves was similar in each reach. Others have documented a comparable reduction in the recruitment of aspen (Romme *et al.*, 1995; Kay 1990, 2001; Ripple and Larsen, 2000) and willow (Chadde and Kay, 1996; Wolf *et al.*, 2007) following the loss of wolves.

With the return of wolves to Yellowstone in the mid-1990s, elk numbers in the eastern portion of the Yellowstone's northern range, which contains the Lamar Valley, declined (White *et al.*, 2012) and decreased browsing and increased heights of young cottonwoods, were initially observed at several locations along the Lamar River and Soda Butte Creek (Ripple and Beschta, 2003). Annual census data indicate that elk densities in the eastern portion of the northern range have declined to $\leq 1$ elk km$^{-2}$ (White *et al.*, 2012).

Consistent with reduced elk herbivory following the return of wolves, our 2012 results for the upper Lamar indicate that some 4660 young cottonwoods within the 28 ha of active channel currently exceed the browse level of elk (~2 m). In addition, the median height (i.e. 5.1 m) of the three tallest young cottonwoods per 50-m segment has increased more than four metres from that measured a decade earlier (Beschta and Ripple, 2010). Whereas there were no young cottonwoods $\geq 5$ cm in $DBH$ in either study reach in 2002 (Beschta, 2005), our results indicate that an estimated 1210 young cottonwoods exceeded this diameter in the upper Lamar by 2012. Eventually, a portion of these young cottonwoods will functionally replace overstory trees along this reach, trees that have experienced considerable mortality (22%) within the last decade.
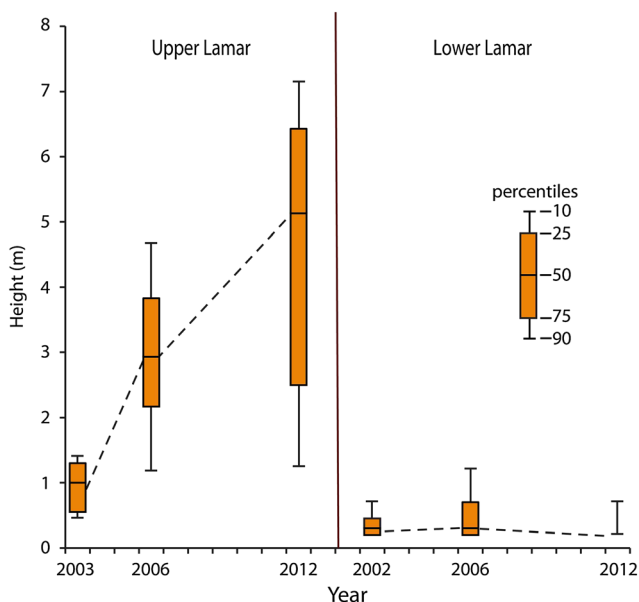


Figure 3. Box and whisker plots of the percentile of young cottonwoods exceeding the indicated height within the upper (left) and lower (right) Lamar study reaches. Results based on measuring the three tallest cottonwoods along 50-m segments of each reach; $n = 108$ for upper Lamar, $n = 525$ for lower Lamar; see text for methods.

Collectively, these results confirm a remarkable improvement in cottonwood recruitment from previous decades when young cottonwoods were unable to grow above the browse level of elk.

The ongoing increase in cottonwood recruitment occurring along the upper Lamar may be indicative of a broader recovery of riparian plant communities is underway because willows and thin-leaf alder (*Alnus incana*) also occur within this reach (Figure 4a). Other recent studies in northern Yellowstone have also observed improved height/diameter growth of willows (Beyer *et al.*, 2007; Baril *et al.*, 2011), aspen (Ripple and Beschta, 2012; Painter, 2013),

and berry-producing shrubs (Beschta and Ripple, 2012a; Ripple *et al.*, 2013). However, the nearly total lack of cottonwood recruitment along the lower Lamar (Figure 4b) presents a major counterpoint to this pattern of improved growth for deciduous woody species following the return of wolves.

In 2012, only 22 young cottonwoods ≥2 m in height were found along the lower Lamar, more than two orders of magnitude fewer than observed in the upper Lamar. These low counts occurred even though the lower Lamar study reach is four times longer, has nearly three times as much active channel area, and has nearly two times as
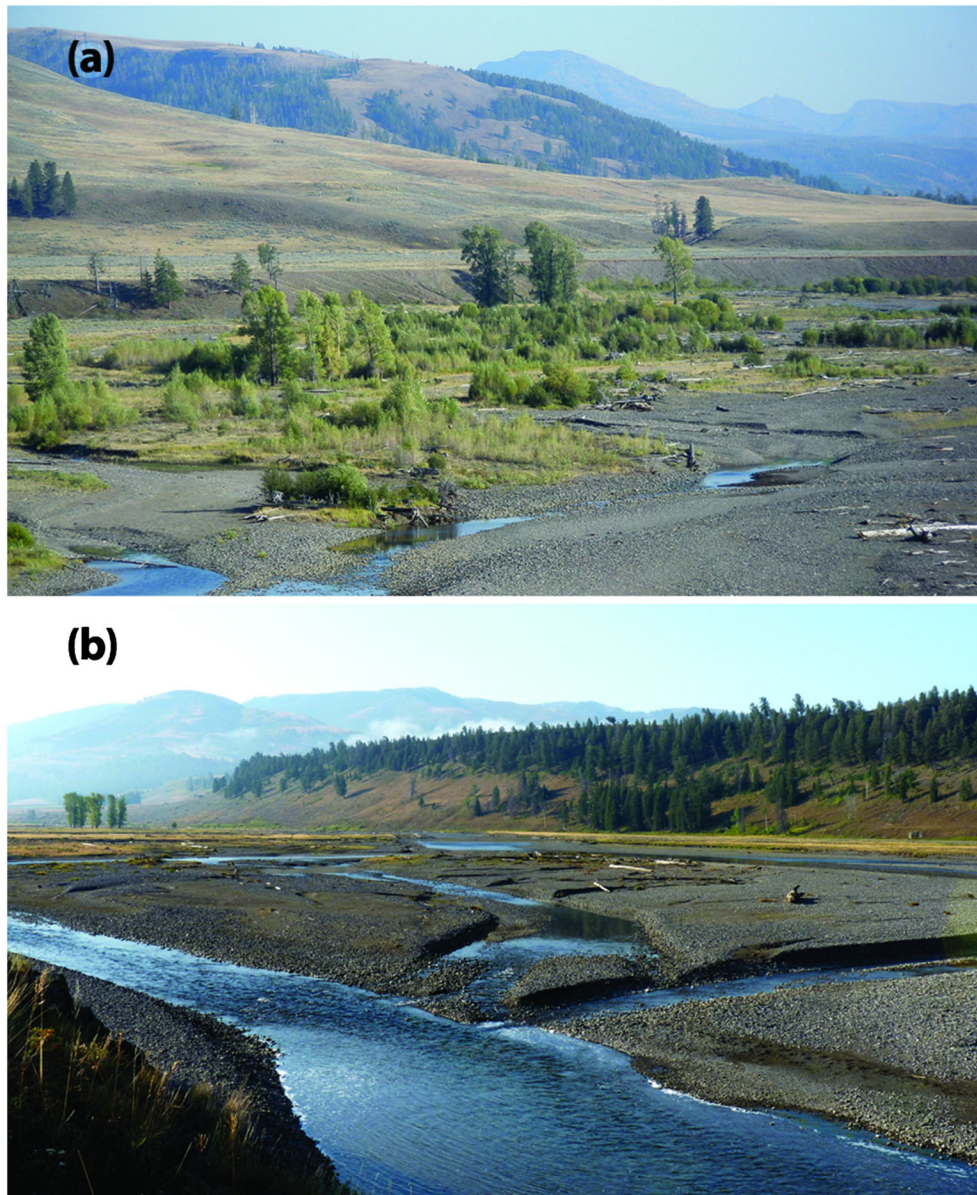


Figure 4. (a) Example of recent cottonwood recruitment, intermixed with willow and alder, in the upper Lamar study reach. Note the tall outwash terrace (photo centre) that partially limits bison access to the active channel and floodplain along this reach. (b) An area of extensive alluvium within the active channel of the lower Lamar study reach where cottonwood seedlings have been unable to grow above the browse level of large herbivores.

many young cottonwoods $\geq 0.2$ m in height relative to the upper Lamar. As potential causes for the pronounced difference in contemporary cottonwood recruitment between our two study reaches, we considered two alternative hypotheses: (1) peakflow disturbances and (2) ungulate herbivory. Because our study reaches are located in the same valley, are adjacent to each other, and did not burn during the 1988 fires, we excluded climate and any direct effects of fire as significant factors affecting cottonwood recruitment in the two reaches.

*Peakflow disturbances*

Because deciduous woody plants had experienced high levels of herbivory over several decades, greatly reducing their effectiveness to provide streambank stability, the two largest flows of record (i.e. 1996 and 1997) resulted in high levels of channel erosion (Rose, 2012) as well as widespread cottonwood seedling establishment in the Lamar Valley. However, for the upper Lamar study reach, the high flow of 2002 appears to have been more important for influencing cottonwood recruitment even though it was only ~75% as large as those occurring in 1996 and 1997. In 2002, a major channel avulsion occurred at the head of the upper Lamar that eroded the floodplain and removed 90 overstory cottonwoods. Because of their complex shapes (attached branches and root wads) and large size (average $DBH = 82$ cm; author's unpublished data), these cottonwoods eventually came to rest within the reach at various downstream locations. Also, conifer boles, resulting from the 1988 fires that had occurred higher in the catchment, were fluvially transported into the upper Lamar reach by the 2002 high flows where many of them accumulated around the downed cottonwoods and formed debris jams of varying sizes. Although some cottonwood seedlings began to grow taller within these large wood accumulations, the vast majority of the nearly 17 000 young cottonwoods $\geq 1.5$ m in height that were sampled in 2012 had established outside the physical protection of these debris jams and were readily accessible to browsing by elk or bison.

Along the lower Lamar, few overstory cottonwoods were eroded into the river during the high flows of 2002. In addition, woody debris accumulations that formed from conifer boles that floated into this reach were usually relatively small, widely scattered, and ineffective for physically protecting seedlings from herbivory. Although a few young cottonwoods on a mid-channel island within this reach had grown above 2 m in height by 2012, their stems had been nearly completely girdled by bison horning/rubbing and are unlikely to survive. Thus, even after the major flow events of 1996, 1997, and 2002, resulting in large areas of unvegetated alluvium and many tens of thousands of cottonwood seedlings (Beschta, 2005;

Rose, 2012), only 54 young cottonwoods were able to attain a height $\geq 1.5$ m. The continued browsing suppression of young cottonwoods by ungulates is further indicated by a median height of the three tallest young cottonwoods measured within 50-m segments along this reach. A median height of 0.3 m in both 2002 and 2006 (Beschta and Ripple, 2009) had decreased to 0.2 m in 2012. Today, the lower Lamar remains largely devoid of any cottonwood, willow, or alder recruitment (Figure 4b). Although both reaches have experienced the same flow regime and have had tens of thousands of cottonwood seedlings established along their active channels, only the upper Lamar has experienced a major improvement in cottonwood recovery since wolves have returned.

*Ungulate use*

Concurrent with the decrease in Yellowstone's northern range elk numbers in recent years has been an increase in bison numbers (Figure 1a), many of which forage on herbaceous plants in the Lamar Valley from spring through fall months. The potential of bison to suppress woody species in the Lamar Valley was recently demonstrated by Painter and Ripple (2012) where they found that bison browsing could limit the heights of young cottonwood and willow. In another Lamar Valley study, Rose (2012) similarly indicated that cottonwood seedling heights were being 'controlled primarily by bison.' Our scat survey results showed that average fecal densities of bison (10.3 fecal piles 100 m$^{-2}$) in the lower Lamar were three orders of magnitude greater than those of elk (<0.01 fecal piles 100 m$^{-2}$). Other recent studies have similarly found relatively high densities of bison scat and low densities of elk scat in this part of the northern range (Painter and Ripple, 2012; Ripple *et al*., 2013). Although our measurements of browsing were not capable of discerning the relative level of foraging by specific ungulate species, average levels of herbivory in the lower Lamar were nearly double than that found in the upper Lamar (i.e. 59.3 vs 30.7%, respectively).

Along the upper Lamar, a tall (~20 m high) glacio-fluvial terrace occurs on the east side of the river, and its steep edge often constrains ungulate access to the river's active channel, especially for bison. On the west side of the river, an eroding and vertical streambank that is approximately 2–4 m high largely precludes bison access to the active channel from that direction. In combination, these terrain features generally limit access of bison to the active channel at relatively few locations. Even at these locations, bison trails were typically oriented perpendicular to the channel indicating that they were being used primarily for crossing to the opposite side of the valley. In contrast, low streambanks along the lower Lamar provide little obstruction to bison movements into or out of the active channel,

and we observed scat densities to be significantly higher along this reach. Because wolves currently appear to have little effect on bison behaviour or numbers, high levels of browsing along the lower Lamar by this large herbivore likely represents the major factor currently preventing young cottonwoods from growing into taller saplings and trees.

## CONCLUSIONS

The ongoing recruitment of cottonwood currently underway in the upper Lamar represents an early stage of ecological recovery, now that northern Yellowstone's large carnivore guild is again complete. This pattern reverses a multi-decadal period of recruitment decline from elk herbivory in the absence of wolves and is consistent with the re-establishment of a tri-trophic cascade involving wolves-elk-cottonwoods. However, the establishment and growth of young cottonwoods, as well as other riparian vegetation, will need to continue over a considerable period before the ecosystem services associated with a structurally diverse riparian plant community again become prevalent throughout this reach. Such vegetation will ultimately have a crucial role in stabilizing streambanks, moderating microclimates and shading streams, delivering litter and large wood to the river, providing habitat and food-web support for a wide range of terrestrial and aquatic animals, and supplying other ecosystem services (NRC, 2002b).

In contrast to the increasing numbers and improving structural diversity of cottonwoods in the upper Lamar, cottonwood recruitment along the lower Lamar remains almost entirely absent. The initial pattern of browsing suppression of young cottonwoods along this reach by elk, which began several decades earlier when wolves were absent, is being continued by bison even though wolves are again present. The inability of young cottonwood (and other deciduous woody species) to grow above the browse level of bison along the lower Lamar indicates that high levels of streambank and floodplain erosion, frequent lateral shifts in channel location, large areas of unvegetated alluvium, and an exceptionally wide active channel, collectively representing an alternative stable state, are likely to persist into the future. Such conditions represent a major loss of ecosystem services in comparison with riverine systems with biologically and structurally diverse riparian plant communities.

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