



Can large carnivores change streams via a trophic cascade?

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Abstract

Large carnivores were persecuted in Yellowstone National Park, WY, USA, during the late 1800s and early 1900s, leading to extirpation of grey wolves (*Canis lupus*) and cougars (*Puma concolor*). Soon thereafter increased herbivory of riparian plant communities by Rocky Mountain Elk (*Cervus elaphus*) became widespread in the park's northern ungulate winter range or "northern range." Wolves were reintroduced in 1995–1996, again completing the park's large carnivore guild. In 2004 and 2017, we sampled Geyer willow (*Salix geyeriana*), a commonly occurring tall willow, along the West and East Forks of Blacktail Deer Creek in the central portion of the northern range. Results indicated high levels of elk herbivory in the 1990s, as in previous decades, not only continued to keep willows short, generally ≤ 52 cm in height, but also resulted in stream widening and incision, leading to "oversized" channel cross-sections and a drastically reduced frequency of overbank flows. However, by 2017, willow heights ≥ 200 cm ($\bar{x} = 310$ cm) were prevalent, and canopy cover over the stream, essentially absent in 1995, had increased to 43% and 93% along the West Fork and East Fork, respectively. These recent increases in tall willow heights, greater canopy cover, well-vegetated streambanks, and the recent development of an inset floodplain all pointed towards a riparian/aquatic ecosystem beginning to recover. Overall, results were consistent with a landscape-scale trophic cascade, whereby reintroduced wolves, operating in concert with other large carnivores, appear to have sufficiently reduced elk herbivory in riparian areas to initiate the recovery of Blacktail Deer Creek's riparian plant communities and stream channels.

KEYWORDS

beaver, channel morphology, elk, riparian vegetation, trophic cascades, wolves, Yellowstone National Park

1 | INTRODUCTION

Riparian areas occur at the intersection of terrestrial and aquatic ecosystems. Riparian plant communities, because of their high biodiversity and productivity, normally support the physical habitat and food web requirements for numerous terrestrial and aquatic biota (Kauffman, Mahrt, Mahrt, & Edge, 2001; Naiman, Décamps, & McClain, 2005; National Research Council, 2002b). These plant communities can also resist the erosive forces of high flows via (a) the cohesive effects of root systems and organic matter that bind soil and alluvial particles and (b) the hydraulic roughness associated with

above-ground stems and leaves that locally decrease flow velocities, thereby helping to maintain stable streambanks (Bennett & Simon, 2004; Richardson & Danehy, 2007; Sedell & Beschta, 1991). During overbank flows, the hydraulic roughness imparted by plants is also effective at causing the incremental deposition of suspended sediment that, over time, forms floodplains. Additionally, root masses and downed boles of woody plants in riparian areas can provide local cover for aquatic organisms, influence pool-riffle morphology, and sometimes help anchor the dams of North American beaver (*Castor canadensis*; Baker & Cade, 1995; Gregory, Swanson, McKee, & Cummins, 1991; Harmon et al., 2004). Thus, the composition and

structure of riparian plant communities interact with streamflow regimes to shape the morphology of alluvial channels and their adjacent floodplains (National Research Council, 1992, 2002b).

Large mammalian carnivores can have an important influence on the behaviour and density of wild ungulates, with effects transmitted downward to plant communities (i.e., a trophic cascade; Terborgh & Estes, 2010). In the area that was to eventually become Yellowstone National Park (YNP), WY, USA, native ungulate populations were heavily impacted by market hunting and large carnivores were generally persecuted during much of the late 1800s. Native ungulates in YNP became protected from hunting after arrival of the U.S. Cavalry in 1886. However, persecution of grey wolves (*Canis lupus*) and cougars (*Puma concolor*) continued (Cahalane, 1939), and both species were extirpated in the 1920s (National Research Council, 2002a; Ruth, 2004; Yellowstone National Park, 1997). With wolves and cougars absent, grizzly (*Ursus arctos*) and black bears (*U. americanus*) fed on both animals and plants, including preying on neonate ungulates. Furthermore, many bears were at least partially diverted to feeding on garbage until all refuse dumps were closed by 1971 (Schullery, 1992). Except for humans, wolves represent perhaps the most significant ungulate predator in the northern hemisphere, primarily due to group hunting, year-round activity, and widespread geographic distribution (Peterson, Vucetich, Page, & Chouinard, 2003).

With the effective dismantling of YNP's large carnivore guild in the early 1900s, herbivory of Rocky Mountain elk (*Cervus elaphus*) in Yellowstone's northern ungulate winter range or "northern range," began increasing with resulting impacts upon plant communities (Grimm, 1939; Keigley, 2018; Wagner, 2006). One consequence of increased ungulate herbivory for young deciduous woody species was that the number of seedlings and root sprouts capable of growing into tall saplings and trees (i.e., recruitment) began to decline over time. Herbivory effects were so strong that recruitment of aspen (*Populus tremuloides*) and cottonwood (*P. spp.*) was almost completely absent during the last half of the 20th century (Beschta, 2003, 2005; Kay, 1990; Painter, Beschta, Larsen, & Ripple, 2014; Ripple & Larsen, 2000; Wagner, 2006). Elk herbivory similarly impacted other woody species such as willows (*Salix spp.*), thinlineaf alder (*Alnus incana* spp. *tenuifolia*) and berry-producing shrubs (Beschta & Ripple, 2012a; Kay, 1990; Ripple, Beschta, & Painter, 2015; Wolf, Cooper, & Hobbs, 2007). Even though willows are multistemmed shrubs, thus likely more resistant to the effects of intensive browsing than the single-stemmed growth form of young aspen and cottonwood, willow recruitment on the northern range remained exceptionally low during the last half of the 20th century (Figure 1).

Cougars returned to the park by the early 1980s (Ruth, 2004), and after approximately seven decades of absence, wolves were reintroduced into northern Yellowstone in 1995–1996, thus completing the park's large carnivore guild of wolves, cougars, and bears (Barber-Meyer, Mech, & White, 2008; Ruth, 2004; Smith, Peterson, & Houston, 2003). During the first two decades following wolf reintroduction, most published studies of woody riparian species in Yellowstone's northern range, 22 out of 24 studies, found an increase in establishment, height and diameter growth, recruitment, canopy cover, or berry production (see synthesis by Beschta & Ripple, 2016). In Figure 2, we provide an example of willow improvement

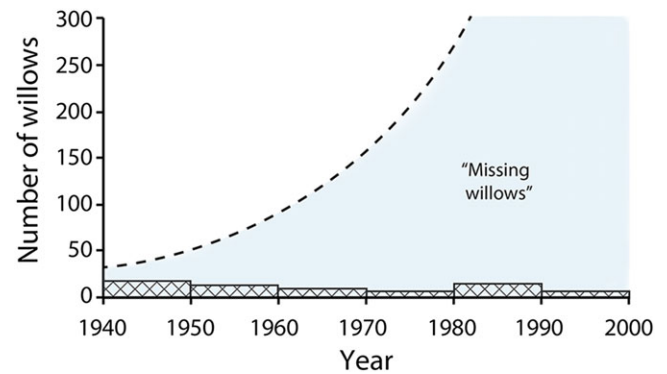


FIGURE 1 Expected (dashed line) and observed (hatched bars) willow recruitment from 1940 to 2000 for northern range riparian areas (adapted from Wolf et al., 2007). "Missing willows" represent the difference between expected and observed



FIGURE 2 Photo chronosequence for (a) 2004 and (b) 2017 illustrating increased riparian willow heights and cover on the historical floodplain of the East Fork of Blacktail Deer Creek over a 13-year period. After multiple decades of height suppression from intensive elk browsing, willows in 2004 were just beginning to increase in height due to a reduction in browsing. An ungulate enclosure with a 2.4-m tall fence, constructed in 2001, is visible in the right-center of each photo

over the last 13 years along a portion of the East Fork of Blacktail Deer Creek.

Our working hypothesis for this study was as follows: wolves, in concert with an intact large carnivore guild, mediate the

behaviour/density of elk, their primary prey, thereby indirectly influencing the composition, structure, and functioning of riparian plant communities with potentially consequent effects on channel morphology. In other words, the question “Can large carnivores change streams?” inherently involves assessing effects upon both riparian plant communities and channel morphology. Our specific objectives were to (a) characterize riparian vegetation and channel morphology that was present in the late 1990s, conditions reflective of the high levels of elk herbivory during previous decades, and (ii) determine to what extent, if any, the recovery of vegetation and channel morphology has begun to occur following 1995–1996 reintroduction of wolves.

2 | STUDY AREA

YNP contains nearly 9,000 km² of diverse terrain in the Rocky Mountains. Along the park's northern boundary occurs the 1,500 km² northern range, of which approximately two-thirds lies within the park (Yellowstone National Park, 1997). Big sagebrush (*Artemisia tridentata*)-steppe is the predominant vegetation type across the northern range, grading into mixed-species coniferous forests at higher elevations. Diverse assemblages of plant species are found along streams and rivers of the northern range, variously including conifers, cottonwoods, aspen, willows, thinleaf alder, and berry-producing shrubs. Multiple species of sedges (*Carex* spp.), grasses, and forbs are also common along streams and rivers.

The Blacktail Plateau occurs near the geographic centre of YNP's northern range, with elevations mostly between 2,000 and 2,500 m. The West and East Forks of Blacktail Deer Creek join to form the main stem of this stream, which eventually flows into the Yellowstone River ~6 km further downstream. Sagebrush-steppe prevails across most of the gentle-moderately sloping terrain of this northerly facing plateau with scattered stands of aspen in swales or along hill toeslopes, where they utilize meltwater from winter snowpack accumulations or local groundwater sources. Willow-sedge communities are common along stream channels and floodplains (Figure 2); their occurrence sometimes augmented by subsurface water sources along toeslopes.

3 | METHODS

3.1 | Predator, prey, and beaver

We summarized National Park Service counts of wolves, elk, and beaver in the northern range over approximately the last two decades (i.e., 1995–2017) to identify population trends; both wolves (Carroll Michael, Phillips, Phillips, Lopes-Gonzalez, & Schumaker, 2006) and beaver (Goldfarb, 2018; Rossell, Bozsér, Collen, & Parker, 2005) are considered keystone species. Wolf and elk counts occurred annually whereas beaver colonies were generally enumerated every other year. General trends in grizzly bear (Hamlin, Cunningham, & Alt, 2009; Schwartz et al., 2006) and cougar populations (Ruth, 2004; Stahler & Anton, 2014) were also summarized. Northern range population estimates of black bear were not available.

3.2 | Riparian willows

In late August 2004, we sampled Geyer willow (*S. geeyeriana*), a commonly occurring tall willow found along the West and East Forks of Blacktail Deer Creek, to characterize the long-term effects of intensive elk herbivory upon willow communities. Three 100-m reaches were utilized, two along the West Fork and one along the East Fork (fig. 1 in Beschta & Ripple, 2007a). The drainage area upstream of our West Fork and East Fork study reaches was 38 and 16 km², respectively. In each reach, a 4-m wide and 100-m long belt transect, parallel to the stream and consisting of 25 segments (4 × 4 m in size), was established along a side of the channel. We selected the tallest Geyer willow stem within each segment for detailed measurement. Because willows heights and recruitment had been suppressed by elk browsing over a period of many decades (Figure 1), the selected stems represented a “leading edge” indicator of any recent increases in willow heights. Along the entire length of each sampled stem, we recorded the occurrence of browsing (browsed or unbrowsed) at annual growth nodes as well as plant age and height at each node. On the basis of these plant architecture measurements, we were able to characterize browsing intensity from the late 1990s through 2004 by using only those stems <200 cm in height (i.e., accessible to elk) for calculating an average browsing rate (%) by year. We also delineated 25 sections (each 4 m in length) along our 100-m reaches where canopy cover (%) over the stream surface was visually estimated for each section (Beschta & Ripple, 2007a).

Some 13 years later, in early September of 2017, we reoccupied the vegetation transects along the three study reaches. We measured the 2017 spring height (cm) and the occurrence of browsing (browsed or unbrowsed) of the tallest Geyer willow stem within each of the 25 segments (4 × 4 m) along the three reaches. We again estimated willow canopy cover over the stream, repeating our methods from 2004.

3.3 | Channel morphology

In 2017, we additionally measured horizontal and vertical dimensions of the channel at 25 cross-sections, spaced at 4-m intervals along each of the three study reaches (Figure 3). The presence of a “historical floodplain” was represented by elevationally paired surfaces on each side of the channel, a surface that normally extended several metres away from

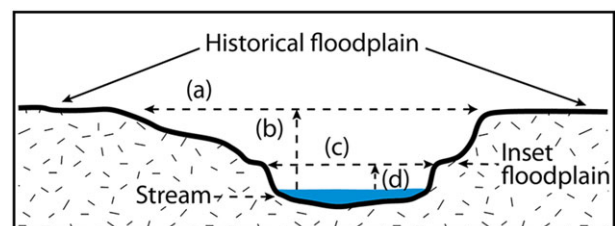


FIGURE 3 Schematic of channel dimension measurements at 4-m intervals along the West and East Forks of Blacktail Deer Creek: (a) channel width (m) at the elevation of the historical floodplain, (b) historical floodplain height (m) above the water surface, (c) channel width (m) at the elevation of the inset floodplain, (d) inset floodplain height (m) above the water surface

the channel. This floodplain consisted of a relatively dark (organic rich) soil underlain by gravel substrate (Figure 4a). We also identified the occurrence of a rather continuous and narrow band of vegetation composed mostly of sedges and grasses, which was stabilizing streambanks and maintaining or initiating the formation of an inset floodplain within the “oversized” channel cross-section (Figure 4b). Along portions of the channel, this inset floodplain was quite pronounced (Figure 5). We considered the occurrence of well-vegetated streambanks and an inset floodplain to represent indicators of a recovering channel. At each cross-section, we also measured the wetted width (m) and thalweg depth (i.e., deepest part of a wetted cross-section, m) of the stream. We used *t* tests to evaluate for significant differences in average channel and stream dimensions between the West and East Forks.

Our channel measurements were used to characterize the average cross-section geometry of the West and East Forks. On the basis of these measurements, we utilized the slope-area method to develop bankfull discharge (Q_{bf} , $m^3 s^{-1}$) estimates for the (a) historical and (b) inset floodplain cross-sections where: $Q_{bf} = n^{-1} A R^{2/3} S^{1/2}$; n = Manning's n , A = cross-sectional area of the channel (m^2), R = hydraulic radius ($m^2 m^{-1}$), and S = channel slope ($m m^{-1}$; Dingman, 1984).

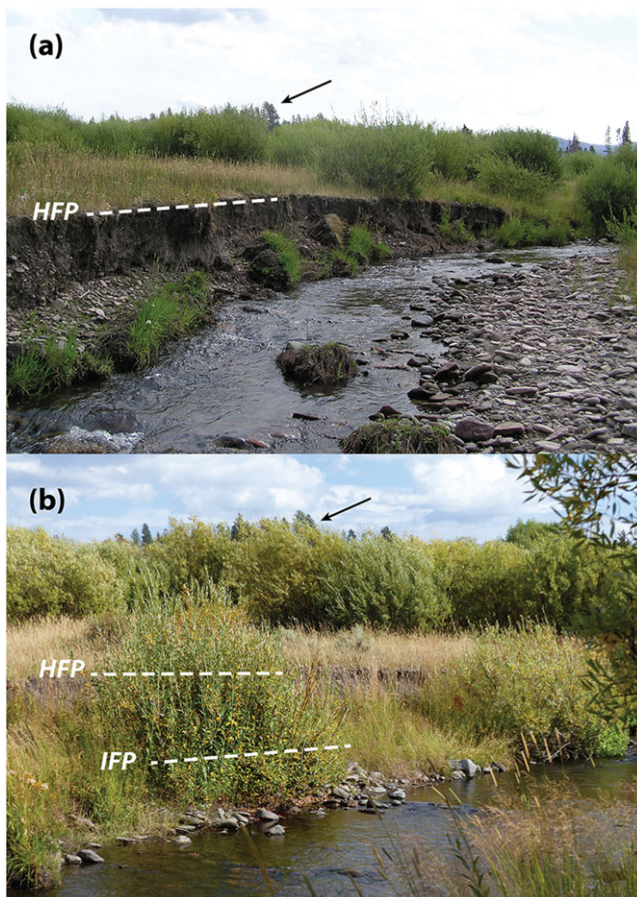


FIGURE 4 Photo chronosequence for (a) 2004 and (b) 2017 showing streambank conditions along the West Fork of Blacktail Deer Creek. In 2004, streambank erosion of the historical floodplain (HFP) was ongoing as indicated by bank collapse of the dark (organic rich) soil. In 2017, a nearly continuous cover of vegetation has developed along the edge of the channel, stabilizing the streambank and initiating an emerging inset floodplain (IFP). An arrow identifies a background conifer that is common to both photos

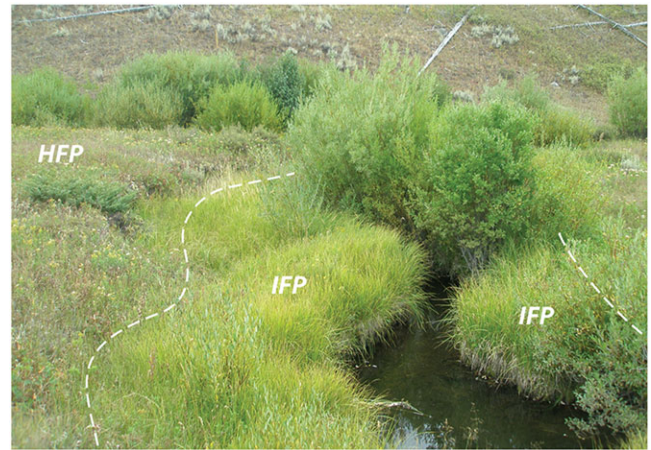


FIGURE 5 Example of a relatively well-developed inset floodplain (IFP) occurring along both sides of the East Fork of Blacktail Deer Creek (2013 photo)

Manning's n is an index of channel roughness and was estimated from $n = 0.034 R^{-0.290}$ (Beschta & Ripple, 2006), hydraulic radius is a hydraulic scaling factor for the channel and was calculated by dividing the channel's cross-sectional area (A , m^2) with its wetted perimeter (P , m), and channel slope of the study reaches was determined using Google Earth[®]. To assess the frequency of overbank flows associated with the (a) historical and (b) inset floodplains, we utilized regional equations developed by Miller (2003) to estimate stream discharges (Q_{ri}) for recurrence intervals (ri) ranging from 1.5 to 500 years. For each floodplain, bankfull discharge estimates (slope-area methodology) were compared against recurrence interval discharges (Miller, 2003) to determine the frequency, in years, of overbank flows.

3.4 | Beaver reach

Field observations indicated that beavers were absent from the West and East Forks of Blacktail Deer Creek in 2004. However, sometime prior to 2015, a beaver colony became established, and several dams were constructed approximately 700 m upstream of our West Fork study reaches. Within the 236-m long “beaver reach” on the West Fork, we ascertained dam heights (m) in September of 2015, 2017, and 2018 by measuring the difference in elevation of water surfaces immediately upstream and downstream of each structure. In 2017, we also measured the height (m) of the historical floodplain above the water surface and thalweg depth (m) of the stream at 4-m intervals along this reach.

4 | RESULTS

4.1 | Predator, prey, and beaver

A total of 31 wolves were reintroduced into YNP during the winters of 1995–1996. After reintroduction, the northern range population increased at about 10 wolves per year, peaking at nearly 100 wolves in 2004 and then declining to approximately 40 wolves by 2017 (Figure 6a). Although annual counts of female grizzly bears inside the park remained essentially unchanged during 1983 to 2002 (Schwartz

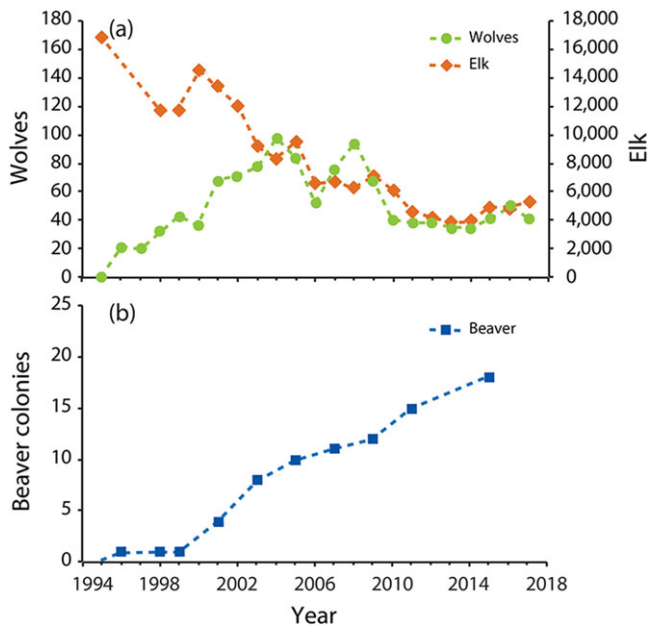


FIGURE 6 Northern range counts of (a) wolves, elk, and (b) beaver colonies from 1995 to 2017. Wolf and elk counts normally occurred annually whereas beaver colony counts were usually conducted on alternate years; elk count data for 1995 and 1996 were not available. Wolf and elk count data were provided by National Park Service; beaver colony counts were from Smith and Tyers (2012)

et al., 2006), the total number of grizzly bears in the northern range began to increase within a few years of wolf reintroduction (Hamlin et al., 2009). The minimum estimated number of adult and subadult cougars in the northern range averaged 18.2 during 1987–1991 (before wolf reintroduction) and 20.0 during 1999–2003 (after wolf reintroduction; Ruth, 2004); their numbers began to increase after 2003 (Stahler & Anton, 2014). Northern range elk populations have been in general decline since the mid-1990s but seem to have stabilized at 4,000–5,000 animals in recent years (Figure 6a). After several decades of essentially no resident beaver colonies in northern range streams, their numbers have increased during the last two decades, attaining a total of 19 colonies by 2015 (Figure 6b).

4.2 | Riparian willows

Plant architecture measurements of the selected Geyer willow stems within the three study reaches indicated browsing rates averaged 93–100% annually during 1996–1999, with plant heights averaging 28–52 cm. However, by 2004, the annual browsing rate for the three study reaches had declined to an average of 68%, and willow heights had increased to an average of 208 cm (Figure 7a). Thirteen years later, in 2017, the sampled willow stems averaged 310 cm in height, with more than 93% of them exceeding 200 cm (the general upper level of elk browse). In 2017, only one of these stems had been browsed.

Inspection of September 1995 aerial photographs indicated that vegetation canopy cover over the water surface was essentially absent along our study reaches. However, willow canopy cover over the water surface of the West and East Forks in 2004 averaged 19% and 70%, respectively, increasing to 43% and 93% by 2017 (Figure 7b).

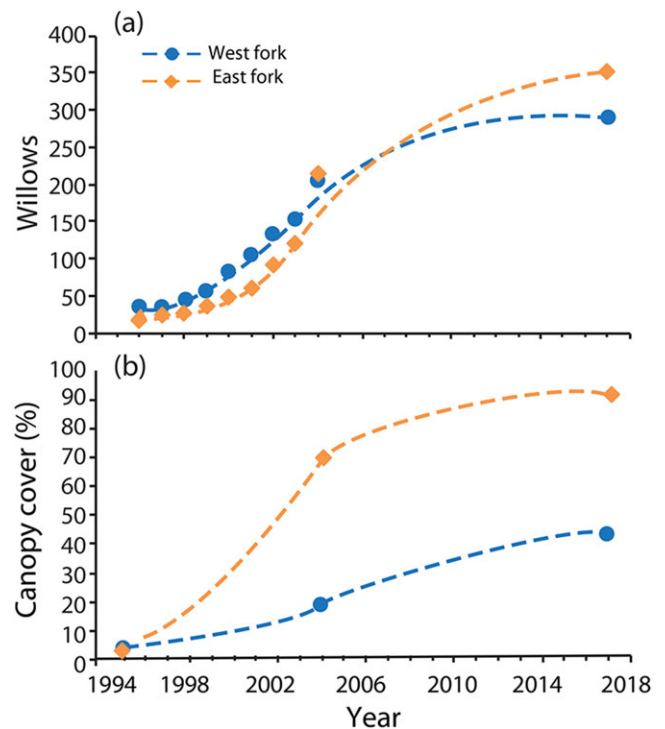


FIGURE 7 (a) Average annual willow height and (b) average canopy cover over the stream during 1995–2017 for the West and East Forks of Blacktail Deer Creek. Dashed lines represent an estimation of general trends over time

4.3 | Channel morphology

West Fork channel widths at the elevation of the historical and inset floodplains, as well as wetted widths of the stream, were significantly wider ($P < 0.01$) than those of the East Fork (Table 1), reflecting the fact that West Fork's drainage area above its study reaches was more than double that of the East Fork study reach. However, heights of the historical and inset floodplains above the water surface were not significantly different between forks ($P > 0.05$); historical floodplain heights averaged 0.86 and 0.80 m for the West and East Forks, respectively, and inset floodplain heights averaged 0.30 and 0.28 m (Table 1).

Based on the slope-area method of estimating discharge, bankfull discharge for the historical floodplain channel (i.e., the discharge that fills the channel to the elevation of the floodplain surface) was $14.7 \text{ m}^3 \text{ s}^{-1}$ for the West Fork and $4.9 \text{ m}^3 \text{ s}^{-1}$ for the East Fork. Compared with regional discharge–frequency relationships (Miller, 2003), bankfull discharges are now estimated to occur, on average, approximately once every 500 years for the West Fork and once every 75 years for the East Fork. In contrast, bankfull flows associated with the inset floodplain had recurrence intervals of < 1.5 years for both the West and East Forks (Table 1).

4.4 | Beaver reach

In 2015, seven active beaver dams were present in West Fork with heights ranging from 0.15 to 0.95 m ($\bar{x} = 0.41$ m). Field observations at the time indicated more than one of these dams had diverted streamflow across portions of the historical floodplain. Beaver abandoned this reach sometime after 2015. In September of 2017, heights of the remnant

TABLE 1 Summary of average channel and stream dimensions, hydraulic variables, and estimated discharges for the West Fork and East Fork of Blacktail Deer Creek

Variables	Streams	
	West Fork	East Fork
Channel dimensions ^a		
Horizontal measurements		
(a) Width at historical floodplain surface	6.3 m (±0.9 m)	4.0 m (±0.8 m)**
(b) Width at inset floodplain surface	3.6 m (±0.3 m)	1.8 m (±0.2 m)**
(c) Wetted width	2.7 m (±0.2 m)	1.4 m (±0.2 m)**
Vertical measurements		
(d) Height of historical floodplain surface	0.86 m (±0.05 m)	0.80 m (±0.05 m) ns
(e) Height of inset floodplain surface	0.30 m (±0.02 m)	0.28 m (±0.02 m) ns
(f) Thalweg depth	0.28 m (±0.03 m)	0.22 m (±0.04 m)*
Cross-section area (A)		
Historical floodplain channel	5.51 m ²	2.94 m ²
Inset floodplain channel	1.31 m ²	0.60 m ²
Wetted perimeter (P)		
Historical floodplain channel	8.30 m	5.62 m
Inset floodplain channel	4.60 m	2.52 m
Hydraulic radius (R)		
Historical floodplain channel	0.66 m ² m ⁻¹	0.52 m ² m ⁻¹
Inset floodplain channel	0.29 m ² m ⁻¹	0.24 m ² m ⁻¹
Roughness coefficient (n) ^b		
Historical floodplain channel	0.038	0.041
Inset floodplain channel	0.049	0.051
Channel slope (S)		
	0.018 m m ⁻¹	0.011 m m ⁻¹
Bankfull discharge (Q _{bf}) ^c		
Historical floodplain channel	14.7 m ³ s ⁻¹	4.9 m ³ s ⁻¹
Inset floodplain channel	1.6 m ³ s ⁻¹	0.47 m ³ s ⁻¹
Recurrence interval discharge (Q _{ri}) ^d		
Q _{1.5}	2.1 m ³ s ⁻¹	0.9 m ³ s ⁻¹
Q ₂	2.7 m ³ s ⁻¹	1.2 m ³ s ⁻¹
Q ₅	4.5 m ³ s ⁻¹	2.1 m ³ s ⁻¹
Q ₁₀	5.9 m ³ s ⁻¹	2.8 m ³ s ⁻¹
Q ₂₅	7.7 m ³ s ⁻¹	3.8 m ³ s ⁻¹
Q ₅₀	9.0 m ³ s ⁻¹	4.5 m ³ s ⁻¹
Q ₁₀₀	10.5 m ³ s ⁻¹	5.3 m ³ s ⁻¹
Q ₅₀₀	14.3 m ³ s ⁻¹	7.5 m ³ s ⁻¹

Note. Channel measurements are illustrated in Figure 2. All measurements occurred in September 2017; t test comparisons of channel and stream dimensions for the West Fork versus the East Fork are also shown. *Significant $0.01 \leq P \leq 0.05$. **Highly significant at $P < 0.01$. ns indicates nonsignificant at $P > 0.05$.

^aValues in parentheses represent ±95% confidence limits.

^b $n = 0.034 R^{-0.290}$, where n = roughness coefficient and R = hydraulic radius (Beschta & Ripple, 2006).

^cBankfull discharge (Q_{bf}) based on Manning equation (see Section 3.3).

^dRecurrence interval discharge (Q_{ri}) from empirical equations for Rocky Mountains Region, Wyoming (Miller, 2003, table 1, p. 20). Standard errors of estimate for recurrence interval discharges range from ±35% to ±55%.

dams ranged from 0.12 to 0.61 m (\bar{x} = 0.31 m), and they were no longer capable of diverting water onto the historical floodplain. Beaver returned in 2018, with four active dams ranging from 0.5 to 1.0 m in height (\bar{x} = 0.75 m). The average historical floodplain height of 0.61 m above the water surface along this reach was significantly lower ($P < 0.01$) and the average thalweg depth of 0.34 m significantly deeper ($P = 0.02$) in comparison with the West Fork study reaches without beaver (Table 1).

5 | DISCUSSION

The extirpation of wolves and cougar in northern Yellowstone and their eventual return represents an unplanned landscape-scale experiment over time. This natural experiment has provided new insights regarding the potential importance of a complete large carnivore guild (i.e., wolves, bears, and cougars) for maintaining biodiversity and

ecosystem integrity along stream systems. Although we have not addressed the strength of the effect of wolves on elk, this relationship has been much studied. Even if elk behaviour and density in recent years have been affected by hunting outside the park or other factors, it is clear from various studies that the restoration of large carnivores, and wolves in particular, have played an essential role indirectly affecting the status and dynamics of riparian plant communities within Yellowstone's northern range (Beschta & Ripple, 2016, 2018; Painter, Beschta, Larsen, & Ripple, 2018; Peterson et al., in press; White et al., 2010; Wilmers & Levi, 2013).

With regard to the question "Can large carnivores change streams?" our results indicate the answer appears to be "yes" via the mechanism of a trophic cascade. At the end of seven decades of wolf absence, when cougar and bears were both present, our results indicated that Geyer willows, a commonly occurring tall willow in the northern range, were heavily browsed and their heights suppressed. These conditions allowed channel widening and incision to occur, eventually resulting in oversized channel cross-sections and the loss of beaver. However, in the late 1990s, willows in our study reaches began to experience reduced herbivory leading to dramatic increases in height and canopy cover during subsequent years. Furthermore, the ongoing stabilization of streambanks by herbaceous and woody vegetation within channel cross-sections and the presence of a well-vegetated inset floodplain indicated that contemporary stream channels appeared to be in the very early stage of a long-term recovery process. Our discussion below focuses on two important eras in the recent history of the northern range: (a) when wolves were absent and (b) and following their return.

5.1 | Vegetation, channels, and beaver in the absence of wolves (1926–1995)

Unbeknown at the time, extirpation of grey wolves and cougars from northern Yellowstone in the 1920s initiated an extended period of increased elk herbivory. High levels of herbivory within Yellowstone's northern range during much of the 1900s impacted plant species with differing autecologies, growth forms, and palatabilities, eventually causing major modifications to upland and riparian vegetation (Kay, 1990; Chadde & Kay, 1996; Singer, 1996; Ripple & Larsen, 2000; Barmore, 2003; Beschta, 2003, 2005; Wambolt, 2005; Wolf et al., 2007). For our study reaches, willow measurements indicated that severe ungulate browsing ($\geq 93\%$ annually) and short heights (≤ 52 cm) continued into the late 1990s.

Riparian vegetation that has been altered by ungulate herbivory can have several important knock-on effects such as (a) modification of food web support and physical habitat for terrestrial and aquatic wildlife species (Belsky, Matzke, & Uselman, 1999; Opperman & Merenlender, 2000) and (b) reduced streambank stability during periods of high discharge due to diminished root strength and reduced hydraulic roughness (Bennett & Simon, 2004; Sedell & Beschta, 1991; Simon & Collison, 2002). During the seven decades of wolf absence, plant communities along Blacktail Deer Creek deteriorated due to high levels of elk herbivory, followed by streambank erosion and channel incision. Overall, many stream and river channels in northern Yellowstone appear to have been greatly

altered due to decades of intensive elk herbivory, particularly after the mid-1900s (Beschta & Ripple, 2006, 2015; Persico & Meyer, 2009; Rosgen, 1993; Wolf et al., 2007).

The processes of channel widening and incision, either separately or in combination, ultimately results in an enlarged or oversized cross-section. By comparing bankfull discharge associated with the historical floodplain against peakflow magnitude over a range of recurrence intervals, we were able to hydrologically characterize the extent of change that has occurred. Results indicated contemporary bankfull discharges at the level of the historical floodplain now have recurrence intervals of ~ 500 and ~ 75 years for the West Fork and East Fork, respectively. In contrast, an early assessment of floodplain systems in the eastern United States found bankfull recurrence intervals of 1.1–3 years (Leopold, Wolman, & Miller, 1964). A more recent study of 76 streams across Oregon and Washington (Castro & Jackson, 2001) found bankfull flows had an average recurrence interval of 1.4 years (range = 1.0–3.1 years). Clearly, widening and incision have sufficiently enlarged channels along our study reaches such that frequent overbank flows onto the historical floodplain are now functionally absent. This dramatic shift from a frequently flooded floodplain surface to one that is rarely flooded, a surface perhaps now more accurately characterized as a "fluvial terrace" (Beechie, Pollock, & Baker, 2008), represents a major change in state for northern range channels and their riparian/aquatic systems.

Annually occurring snowmelt peakflows are a characteristic feature of Rocky Mountain stream systems, such as those in the northern range, and are an important mechanism contributing to the annual recharge of floodplain soil moisture and underlying water tables. However, oversized channel cross-sections, via channel widening or incision, diminishes the frequency of occurrence of overbank flows and saturated soil conditions for adjacent floodplains, conditions normally required for maintaining hydrophytic and wetland vegetation. Any reduction in frequency of annual flooding therefore limits the spatial extent of such vegetation or decreases the likelihood that such plants can continue to persist. In southwestern Oregon, Chapin, Beschta, and Shen (2002) found that obligate wetland herbaceous plants of sedges and rushes were linked to overbank flows having an average recurrence interval of ≤ 2 years, willow-dominated sites were linked to recurrence interval flows of 3.5 years, and other riparian plant communities were linked to recurrence interval flows of 4.6 years, indicating a relatively tight connection between the frequency of overbank flows and the composition and spatial extent of riparian vegetation on adjacent floodplains.

Channel incision has the added effect of sometimes lowering water tables under adjacent floodplains (Bilyeu, Cooper, & Hobbs, 2008; Nash, Selker, Grant, Lewis, & Noël, 2018). Unless these water tables are supplemented from other sources, such as subsurface flow or shallow groundwater from adjacent hillslopes, decreased availability of subsurface moisture for floodplain vegetation is likely to occur during late summer. Diminished frequency of overbank flows and lowered water tables represent a major loss of hydrologic connectivity between a stream and its floodplain, a loss that usually reduces the distribution of hydrophytic vegetation and shifts the composition of plant communities towards species normally associated with drier sites.

Beaver populations in the northern range, which had generally rebounded from widespread trapping in the 1800s, again underwent

decline in the early 1900s. For example, in 1921, Warren (1926) identified 25 beaver colonies in a portion of the northern range, yet none of these colonies were present during a repeat survey in 1953 (Jonas, 1955). By the mid-1900s, high levels of elk herbivory had depleted woody food sources and materials for dam construction (Ripple & Beschta, 2004; Smith & Tyers, 2012; Wolf et al., 2007). When young willow, aspen, cottonwood, and other deciduous woody species were unable to attain a sufficient size for use as food or dam construction material because of intensive elk herbivory, beaver colonies along northern range streams were no longer able to persist, and eventually, beaver pond deposits became incised (Persico & Meyer, 2009; Wolf et al., 2007). Persico and Meyer (2009) found that late Holocene beaver pond sediment deposits in northern range streams, deposits mostly <2 m in depth, were associated with nearly a third of the channels they studied, confirming that beaver historically were relatively widespread. The loss of beaver and the mutualism that normally exists between this species and diverse riparian ecosystems represents another important indirect consequence of large carnivore loss.

The severe alteration of riparian plant communities by native ungulates, following large carnivore extirpation or displacement, is an outcome that has been repeated in other portions of the western United States and Canada (Beschta & Ripple, 2007b, 2009; Hebblewhite & Smith, 2010; Hess, 1993; White, Olmsted, & Kay, 1998). Additionally, modified channels following apex predator loss have been identified in systems with vastly different peakflow regimes—snowmelt peakflows in the Rocky Mountains (Beschta & Ripple, 2006), convective storm peakflows in the arid southwest (Ripple & Beschta, 2006), and rain-on-snow peakflows in the coastal Pacific Northwest (Beschta & Ripple, 2008). Across vastly different ecosystems, the relatively consistent pattern of plant community alteration by large herbivores where large carnivores have been displaced, reduced, or extirpated and the ensuing channel adjustments in systems indicate that the indirect effects of these predators appear to have a pivotal role in sustaining the biodiversity and integrity of both riparian and aquatic habitats (Beschta & Ripple, 2012b).

5.2 | Vegetation, channels, and beaver following the return of wolves (1995–present)

Wolf reintroduction in the mid-1990s completed the park's large predator guild and soon thereafter changes in elk vigilance, movement, group size, and foraging behaviour and larger scale changes in habitat selection in the northern range were documented (Fortin et al., 2005; Gower et al., 2009; Laundré, Hernandez, & Altendorf, 2001; White et al., 2009; White et al., 2012). For example, Beyer (2006) found that “elk consistently avoided being close to riparian areas at all times of the day” and detected as early as 1997 an increase in the diameter growth of Geyer and Booth (*S. boothii*) willow. For our study reaches along the West and East Forks, it was not until about 2000, when the northern range wolf population was approaching its maximum (Figure 6a), that browsing rates of Geyer willow began to decrease and their heights increase. However, the simultaneous decrease in browsing and increase in riparian plant heights we measured have also been observed in various other northern range studies (see synthesis by Beschta & Ripple, 2016). An inverse relationship

between browsing intensity and plant heights is central to a trophic cascades hypothesis as it clearly defines the mechanism via which the trophic cascade occurs (Beyer, Merrill, Varley, & Boyce, 2007).

If browsing is sufficiently reduced, willows stems can eventually escape herbivory when they become tall enough. The preponderance of the selected Geyer willow stems along the West and East Forks that were >200 cm in height in 2017 indicated these stems were sufficiently tall that they no longer were likely to experience herbivory from elk. Overall, a major shift in the dynamics of deciduous woody plant communities appears underway in various portions of Yellowstone's northern range, from a situation of where the height growth of young woody plants was continuously suppressed when wolves were absent to one of reduced browsing and increasing heights in recent years (Beschta & Ripple, 2016; Painter, Beschta, Larsen, & Ripple, 2015; Peterson et al., in press). The ongoing recovery of riparian plant communities in YNP's northern range is perhaps even more remarkable given that a long-term warming and drying trend is currently underway (Abatzoglou, Rupp, & Mote, 2014; Beschta & Ripple, 2016).

Concurrent with increased willow heights, our results indicated major increases in willow canopy cover over the stream surface, from a near absence in 1995 to 43% and 93% in 2017 for the West Fork and East Forks, respectively. The greater increase in canopy cover of the East Fork, relative to the West Fork, may be due to (a) the width of the East Fork channel at the elevation of its historical floodplain was, on average, 2.3 m narrower than that of the West Fork and (b) the wetted surface width of the East Fork stream was approximately half that of the West Fork (Table 1). Thus, even for willows of comparable size and frequencies along these two forks, those along the East Fork were able to provide a greater amount of cover directly over the stream surface.

The pronounced increase in canopy cover that occurred for both streams during the last two decades represents a crucial indicator of an improving aquatic thermal regime and improved food web support for aquatic biota, particularly cold water fish species. Canopy cover can reduce the amount of solar radiation reaching a stream, especially important during summertime periods when solar angles are high, day lengths are long, and flows are normally low, thereby mediating potential increases in water temperature (Johnson, 2004; Sun et al., 2015). Furthermore, invertebrates in the canopies of near-channel willows provide food for fish and seasonal leaf-fall represents an important carbon base for aquatic invertebrates which, in turn, provide “reciprocal flows of invertebrate prey” to adjacent terrestrial consumers (Gregory et al., 1991; Baxter et al., 2005; Saunders and Fausch, 2012).

Observations of channel banks in 2004 indicated they were generally continuing to erode. However, by 2017, a nearly continuous belt of predominantly herbaceous plants, mostly sedges and grasses, and the periodic occurrence of willows and alder had begun to stabilize streambanks and accumulate sediment, potentially contributing to channel narrowing. As part of this restoration process, we observed an inset floodplain (Beechie et al., 2008; Booth & Fischenich, 2015) within the oversized channel. If sediment deposition on this floodplain continues, over time, it will contribute to the incremental vertical accretion of its surface.

Along the West Fork's beaver reach, the tallest beaver dam was 0.95 m in height in 2015 and had diverted water onto portions of the historical floodplain, re-establishing perhaps for the first time in over half

a century the mutualistic relationship between beaver and willow-sedge communities, a relationship that normally allows both to thrive (Baker, Ducharme, Mitchell, Stanley, & Peinetti, 2005; Fairfax & Small, 2018). Beaver abandoned this reach in 2017 and the tallest remaining dam that year was 0.61 m tall, no longer of sufficient height to cause overbank flows. However, they returned in 2018, and their tallest dam was 1.0 m in height. In an eastern Oregon study, where increased willow growth occurred following the removal of livestock grazing, the annual number of beaver dams along a 25-km reach varied year-to-year during a 17-year period of study, ranging from 0.35 to 4.1 dams km⁻¹. Over time, the periodic breaching and construction of dams increased channel complexity through sediment deposition and the formation of new pools, riffles, and meanders (Demmer & Beschta, 2008). The reason for beaver abandoning the West Fork in 2017 is not known, but beaver can be prey for various carnivores, including wolves, cougar, bears, and coyotes (*Canis latrans*; Baldwin, 2017; Peterson & Ciucci, 2003).

Field observations in 2017 indicated that in-channel sediment deposition had occurred within recent years, particularly for the most upstream beaver ponds. Such accumulations can improve conditions for the germination, establishment, and growth of riparian vegetation (Bigler, Butler, & Dixon, 2001; Cooper, Dickens, Hobbs, Christensen, & Landrum, 2006). Even with this deposition, average thalweg depths along the beaver reach remained 23% deeper relative to the West Fork channel reaches without beaver, indicating a more diverse pool-riffle morphology. Streams that are deeper experience reduced daily fluctuations in water temperatures and lower maximum daily temperatures during the summer months, compared with those that are shallower (Boyd & Kasper, 2004; Brown, 1969). In addition, greater variation in pool-riffle depths in deeper channels provide improved cover and rearing habitat for fish (Roussel & Bardonnnet, 1997; Sullivan, Mažeika, Watzin, & Hession, 2006).

The height of the historical floodplain above the water surface along the beaver reach was 29% lower in comparison with the West Fork channel reaches without beaver. However, it is not known if (a) beaver select sites with relatively low amounts of channel incision or (b) the recent deposition of sediment along the streambed, due to the presence of beaver dams, had increased bed elevations relative to the historical floodplain.

In an experiment designed to assess the potential for beaver dams to augment floodplain water tables, Bilyeu et al. (2008) selected four sites in the northern range (one on the West Fork of Blacktail Deer Creek, two on the East Fork of Blacktail Deer Creek, and an additional site on Elk Creek) where channel incision was >1 m in depth and floodplain water table depths in late summer averaged ~1.2 m below the surface. Even along some of these deeply incised channels, willows accessible to elk and other large herbivores have been able to slowly increase in height over time; the tallest 25% of them increasing from a height of ~100 cm in 2001–2004 to nearly 200 cm in 2016 (Peterson et al., in press). When artificial dams to the height of the historical floodplain were constructed within the incised channel, replicating the hydraulic effect of a channel-spanning beaver dam, water table depths were ~0.8 m below the floodplain surface and willow heights increased. Even larger willow height increases ensued when all herbivory was curtailed by the construction of ungulate exclosures (Marshall, Hobbs, & Cooper, 2013). In Rocky Mountain National Park, Zeigenfuss, Singer, Williams, and Johnson (2002) found that water

tables <1 m in depth did not reduce the productivity of willows and other shrubs. Similarly, Beschta and Ripple (2007a) found no significant effect on willow heights for plants with root collars <0.9 m in elevation above the surface of a stream. Even though channel incision is a common feature for many streams across the northern range (Persico & Meyer, 2009; Wolf et al., 2007), it appears that recovery of tall willow communities is likely to occur if the depth of channel incision is ≤1 m, as long as high levels of ungulate herbivory are not occurring.

Channel widening and incision since the mid-1950s may affect the capability of beaver to return to previously used reaches in the northern range. For example, if channel incision >1 m in depth inhibits the recovery of tall willow communities, this may, in turn, reduce the likelihood of colonization by beaver. And where beaver colonies and their dams are temporary (e.g., only last for a few years), any potential infilling of stream beds from sediment deposition is likely to occur sporadically over time and space. Nevertheless, if beaver populations continue to increase over time, the ecological effects of these “ecosystem engineers” (Goldfarb, 2018) may well have a significant role in restoring riparian vegetation, floodplains, and channel dimensions for at least portions of northern range streams.

There appear to be many positive ecological effects occurring now that northern Yellowstone has a complete large carnivore guild; however, several factors may limit the strength of these effects:

1. Stabilization of channel streambanks with vegetation and the occurrence of an inset floodplain are important components of channel recovery. However, the magnitude of channel widening and incision that occurred in the mid-late 1900s along some northern range streams (e.g., Blacktail Deer Creek) may have been sufficiently great that frequent flooding of the historical floodplain at some time in the future is no longer achievable. In other words, historical floodplains along some reaches may remain hydrologically disconnected from their streams (Beschta & Ripple, 2006; Bilyeu et al., 2008; Rosgen, 1993; Wolf et al., 2007), thus representing an alternative state and legacy effect of large carnivore removal.
2. For stream reaches with deeply incised channels (i.e., >1 m), recovery of willow communities on the historical floodplain may be problematic unless local water tables are naturally augmented by subsurface flow from adjacent hillslopes (Beschta & Ripple, 2007a; Marshall et al., 2013; Zeigenfuss et al., 2002).
3. Where tall willow recovery is occurring along northern range streams, this situation provides improved opportunities for beaver to recolonize whereby their dams can elevate water tables and cause sediment deposition. Beaver dams, by increasing the extent and frequency of overbank flows onto the historical floodplain, can contribute to an expanded willow-sedge community (Baker et al., 2005), thus assisting in the long-term recovery of northern range riparian and aquatic ecosystems.
4. A warming and drier climate is currently occurring in the northern range (Abatzoglou et al., 2014; Beschta & Ripple, 2016), conditions that may not be conducive to improved riparian plant communities. If ongoing trends in annual temperature (increase), annual precipitation (decrease), and annual snowfall (decrease) continue into the future, they may have a growing influence on

the composition and structure of riparian and upland plant communities. However, as Wilmers, Dairmont, and Hebblewhite (2012) indicate, restoring large carnivores may provide a hedge against the effects of climate change.

- Perhaps some of the most important factors currently limiting the recovery of riparian plant communities in portions of Yellowstone's northern range are the intensive herbivory (grazing and browsing) and trampling effects of bison (Beschta & Ripple, 2015, 2016; Keigley, 2018; Painter & Ripple, 2012). Northern range bison numbers have increased greatly over the last two decades, and the collective biomass of bison is now greater than that of elk. Bison tend to remain within the northern range throughout the year thus potentially grazing or browsing plant communities multiple times during a growing season, whereas elk use is mostly seasonal (i.e., winter range) and occurs primarily at the end of a growing season. Mature bison are considerably larger than elk and thus much more likely to cause soil compaction and streambank collapse due to trampling. Wetlands, springs, streams, and riparian areas, particularly along major valley bottoms (e.g., Lamar Valley and Little America), are currently experiencing high levels of herbivory and trampling from bison, thus generally preventing recovery of these biologically and hydrologically important systems.

The widening and incision of channels that was prevalent in our study reaches are consistent with other stream and river studies in the northern range (Beschta & Ripple, 2006, 2008, 2012b; Persico & Meyer, 2009; Ripple & Beschta, 2006; Rosgen, 1993; Wolf et al., 2007) and tend to confirm that the indirect effects of predator removal do indeed extend to streams and their channels. These results further suggest that the removal of wolves across the western United States a century ago, along with the persecution and possible extirpation of other large carnivores, may have had unintended consequences to the biodiversity of riparian communities and the dimensions of alluvial channels, consequences impacting the physical habitat needs and food webs of a wide range of terrestrial and aquatic wildlife species, including beaver.

Except where riparian areas are being heavily impacted by bison in the Yellowstone's northern range or where stream incision has been particularly severe, the increasing robustness of willow-sedge communities in the presence of an ecologically effective large carnivore guild offers considerable promise for stabilizing streambanks, narrowing channels, hydrologically reconnecting floodplains, and improving the overall ecological integrity of riparian and aquatic ecosystems. In retrospect, Yellowstone's unplanned experiment in time has provided an enriched perspective of the potential importance of large carnivores, via a trophic cascade, in mediating the structure and function of these important ecosystems. These results also have implications for the conservation of streams in other areas of the world where large carnivore species have been extirpated or reintroduced.

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