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Review

Riparian vegetation recovery in Yellowstone: The first two decades after wolf reintroduction

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ABSTRACT

During the seven decades of gray wolf (*Canis lupus*) absence in Yellowstone National Park intensive browsing by Rocky Mountain elk (*Cervus elaphus*) suppressed the growth of young deciduous woody plants within the park's northern ungulate winter range. Since wolf reintroduction, 24 assessments of deciduous woody plants in riparian areas have been published, including eleven on willow (*Salix* spp.), six on aspen (*Populus tremuloides*), five on cottonwood (*Populus angustifolia* and *Populus trichocarpa*), and one each on berry-producing shrubs and thinleaf alder (*Alnus incana* spp. *tenuifolia*). All but two of these studies found increases in plant height, stem diameter, stem establishment, canopy cover, or recruitment. More than half of the studies measured ungulate browsing and, in all instances, increased growth/cover of woody plants over time occurred concurrently with a decrease in browsing. Almost half of the studies also compared observed plant community changes to climatic/hydrologic variables but the results of these analyses were often inconsistent. Although the long-term warming and drying trends underway in northern Yellowstone appear unlikely to have contributed to the occurrence of improved riparian plant communities during the last two decades, these vegetation changes were consistent with reestablishment of a tri-trophic cascade involving an intact large predator guild, elk, and woody plant species. This early stage of vegetation recovery in northern Yellowstone, although not occurring everywhere, represents a major departure from the wide-spread suppression of woody plants by elk browsing that occurred in the decades when wolves were absent.

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Contents

1. Introduction

Riparian areas, occurring transitionally between terrestrial and aquatic ecosystems, characteristically have strong biophysical gradients (National Research Council, 2002b). The resulting diversity in structure, composition, and function of native plant communities occupying these gradients provide food-web support and habitat structure for numerous faunal species and are of fundamental importance to the inherent resilience of these systems (Tabacchi et al., 1998; Kauffman et al., 2001; Naiman et al., 2005). Vegetation diversity is also crucial for helping to stabilize alluvial streambanks, maintain channel morphology, shade

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streams, protect water quality, and provide allochthonous inputs, all of which contribute to productive and sustainable aquatic ecosystems (National Research Council, 2002b; Bennett and Simon, 2004).

After seven decades of absence, gray wolves (*Canis lupus*) were reintroduced into Yellowstone National Park in 1995–1996, again completing the park's large predator guild (Smith et al., 2003). Following reintroduction of this apex predator, young deciduous woody plants that had been suppressed by ungulate browsing in previous decades began to increase in height and recover in some riparian areas (Fig. 1). Two major hypotheses often have been presented to explain the changes in vegetation that are currently underway. One hypothesis indicates that the re-establishment of a trophic cascade following the return of wolves has decreased ungulate herbivory on palatable woody plants (e.g., Fortin et al., 2005; Beyer et al., 2007) thereby allowing height increases that, at least in some areas, have again begun to exceed the upper browse level (~200 cm) of Rocky Mountain elk (*Cervus elaphus*). Such a top-down cascade requires that reintroduced wolves, in conjunction with other large predators, mediate the behavior (e.g., foraging habits, spatial use of habitat) and/or density of elk. Alternatively, bottom-up forces (e.g., climatic trends and fluctuations, hydrologic disturbances, site productivity) could represent major factors initiating and subsequently influencing any recovery of riparian plant communities (e.g., Tercek et al., 2010; Marshall et al., 2014).

To help understand the relative importance these contrasting influences (i.e., top-down vs. bottom-up) might have on plant community dynamics, we undertook a synthesis of published studies that have evaluated changes to riparian vegetation in northern Yellowstone during the two decades following wolf reintroduction. We summarized the extent to which plant community dynamics have changed since 1995–1996 and the relative importance of top-down (herbivory) versus bottom-up influences (climate, hydrology) in affecting these dynamics.

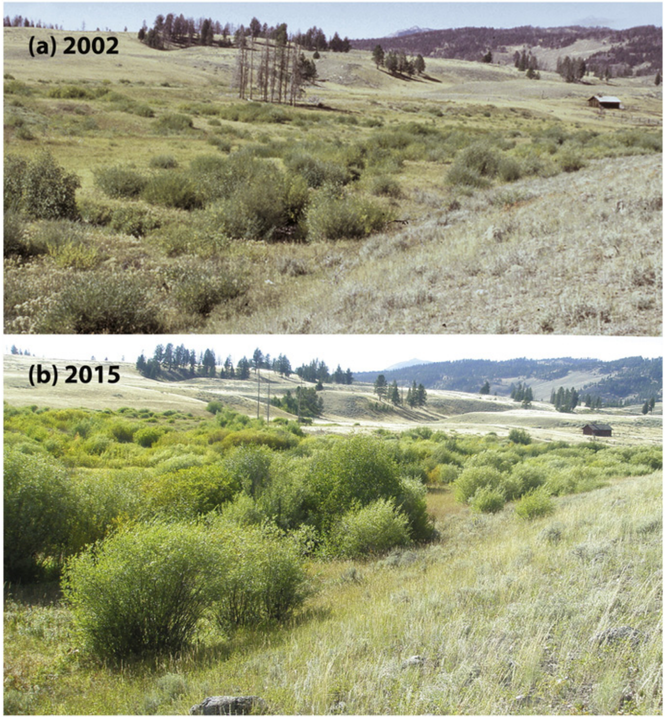

Fig. 1. Chronosequence of photos along the west fork of Blacktail Deer Creek in Yellowstone's northern range: (a) in 2002 young willows were beginning to increase in height after decades of suppression by intensive elk browsing; (b) in 2012 willow heights and cover have continued to increase and many plants now exceed 200 cm in height. Beaver have been active along the west fork of Blacktail Deer Creek in recent years and in late summer of 2015 eight beaver dams, averaging 51 cm in height (range = 20 to 100 cm), were present. Photo credits: (a) W.J. Ripple, 8/27/2002 and (b) R.L. Beschta, 8/31/2015.

Our synthesis focused on studies of deciduous woody species because they are (1) important to the biodiversity and functioning of riparian and aquatic systems (National Research Council, 2002b), (2) long-lived, and (3) generally resilient to disturbance (Kauffman et al., 1997). Furthermore, most of them had been height-suppressed by ungulate browsing during the decades when wolves were absent (Kay, 1990; Barmore, 2003).

2. Yellowstone National Park prior to wolf reintroduction

Although Native Americans resided within the area that was to eventually become Yellowstone National Park, aboriginal hunting, gathering, and burning came to an end when Indians were removed following the park's establishment in 1872 (Nabokov and Loendorf, 2004). Early park administrators attempted to protect ungulates from market hunters whereas wolves, bears (*Ursus* spp.), cougar (*Puma concolor*), and coyotes (*Canis latrans*) were persecuted. Even after the National Park Service assumed management responsibility in 1918, predators continued to be hunted, trapped, and poisoned (Schullery and Whittlesey, 1992; Wagner, 2006). Wolves were extirpated from the park by the mid-1920s, thus removing any effect this apex predator may have had on ungulate prey in the 1500 km^2 northern ungulate winter range, or “northern range”, of which approximately two-thirds lies within the park. Additional information regarding northern range terrain, plant communities, wildlife, and management history can be found in Houston (1982); Schullery and Whittlesey (1992), and Yellowstone National Park (1997), but see also Chase (1986); Chadde and Kay (1991); National Research Council (2002a); Barmore (2003), and Wagner (2006).

Deciduous woody species commonly found within northern range riparian areas include willow (*Salix* spp.), thinleaf alder (*Alnus incana* spp. *tenuifolia*), and various species of berry-producing shrubs. Cottonwood (*Populus angustifolia* and *Populus trichocarpa*) typically occurs along major valley bottoms and aspen (*Populus tremuloides*) is often present along tributary streams as well as on moist-sites scattered across the northern range's shrub-steppe terrain (Despain, 1990).

Perhaps the first recorded observations of increased levels of elk browsing in northern Yellowstone were those of Smith et al. (1915). By the 1930s, ungulate herbivory of northern range vegetation had become of sufficient concern that park administrators initiated a program of ungulate culling (Grimm, 1939), reducing the elk population to <5000 animals by the mid-1960s. Culling of elk in the park was terminated after 1968 (Allin, 2000) and their population rapidly increased, approaching nearly 20,000 by the late 1980s. Between 1935 and 1989, studies of young willow, aspen, and other woody species consistently found these plants generally unable to grow above a height of 100 cm due to intensive elk browsing (Kay, 1990; Chadde and Kay, 1991; Singer, 1996; National Research Council, 2002a; Barmore, 2003). Relatively recent studies of cottonwood and aspen age structure (i.e., frequency of plants by date of establishment) in the northern range have confirmed a major decline in their recruitment (i.e., growth above the upper browse level of elk) between the early 1900s and the 1990s (Fig. 2). By 1990, the difference between observed and expected stem frequencies represented an estimated 51% and 89% decline in total number of cottonwood and aspen, respectively (Fig. 2). Results from Wolf et al. (2007) similarly indicate a 91% decline in willows. In other areas of the western North America, high levels of ungulate herbivory following the displacement or extirpation of large predators profoundly reduced the recruitment of woody species over time (e.g., Hess, 1993, White et al., 1998; Ripple and Beschta, 2004b; Beschta and Ripple, 2009). Additionally, Bork et al. (2013) found that summer browsing by various large herbivores, including bison, elk, and cattle (*Bos taurus*), could significantly increase mortality of aspen saplings in the northern Great Plains.

As a consequence of long-term and intensive ungulate herbivory in the northern range during the decades of wolf absence, depleted

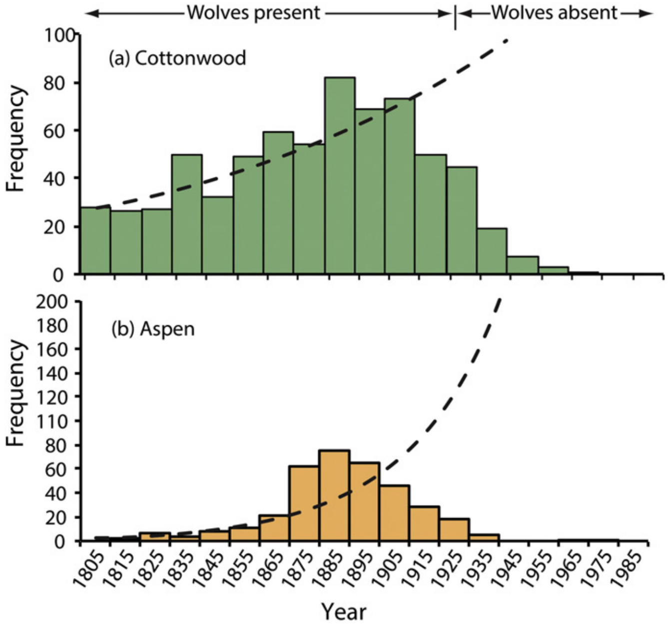

Fig. 2. Age structure (frequency of plants by decade of establishment) for (a) cottonwood ($n = 674$) and (b) aspen ($n = 330$) in Yellowstone's northern range before wolf reintroduction. Dashed lines represent expected frequencies based on an exponential fit to data from 1800 to 1920 (wolves present); "year" represents the mid-point of each bar (i.e., 1805 represents data for 1800–1809). Adapted from: (a) Beschta (2005) and (b) Ripple and Larsen (2000); Kauffman et al. (2013), and Painter et al. (2014).

riparian plant communities resulted in accelerated streambank erosion along alluvial channels (Rosgen, 1993). Altered riparian plant communities were no longer capable of supporting beaver (*Castor canadensis*) and many streams incised (Wolf et al., 2007). Thus, the mutualism normally expected between the presence of beaver dams and high levels of moisture available to riparian vegetation (Weaver, 1978) was lost. High levels of herbivory also reduced allochthonous loadings in streams and decreased the diversity of their macroinvertebrate trophic structure (Travers and Meier, 1996). By the time wolves returned to Yellowstone's northern range in the mid-1990s, riparian plant communities and their dependent aquatic ecosystems had shifted toward an alternative state — a state dominated by the long-term effects of intensive elk herbivory.

3. Methods

We searched for published northern range studies that had assessed temporal changes of woody riparian vegetation during the 1st two decades following wolf reintroduction. We compiled these studies in tabular format identifying the plant species evaluated, the period of time represented by the field data, and a synthesis comment. Where available, we also reported any trend in browsing rates and the presence/absence of correlations between vegetation change and climatic/hydrologic variables. If a study measured vegetation change in both riparian and upland sites (i.e., aspen), whenever possible we emphasized results for riparian areas. We graphically presented the results of studies that measured riparian vegetation changes over time to illustrate the timing and magnitude of such changes. If multiple field sites were used in a given study, we averaged those results to illustrate a generalized outcome.

We compiled annual wolf population estimates from 1995 to 2014 based on park service counts for the northern range. We also compiled, based on park service counts, annual estimates of northern range elk and bison populations from 1975 to 2014, a period encompassing 20 yrs before and 20 yrs after the reintroduction of wolves. Although visual ungulate counts are consistently undertaken each year, they represent a minimum estimate of these mammal populations. We calculated an annual predator/prey ratio (i.e., number of wolves/1000 elk) from 1995 to 2014 to index the potential ecological effectiveness of wolves (Mech and Boitani, 2003).

We summarized long-term climatic/hydrologic data from stations located within or adjacent to the northern range to identify trends that might influence plant community dynamics. Annual time series, on a water year basis (Oct. 1–Sept. 30), were compiled for the following sets of variables:

(a) Climate — air temperature (°C), degree-days (°C-days above a base temperature of 4.4 °C [40 °F]), precipitation (cm), and snowfall (cm) for the Mammoth climatic station (elev. = 2000 m) (Mountain States Weather Service, Western Regional Climate Center).
(b) Snowpack — snowpack water equivalent (cm) averaged from Jan. 1, Feb. 1, Mar. 1, and Apr. 1 measurements for the Lupine Creek (elev. = 2250 m) and Northeast Entrance (elev. = 2240 m) snow courses (National Resources Conservation Service Water and Climate Center).
(c) Stream discharge — peak discharge (m^3/s), mean discharge (m^3/s), and July–August discharge (m^3/s) for the Yellowstone River at Corwin Springs (elev. = 1550 m) (United States Geological Survey National Water Information System). The 6780 km^2 watershed area upstream of the Corwin Springs gage consists mostly of mountainous terrain in the north-central portion of Yellowstone National Park, including the entire northern range.

We linearly regressed each climatic/hydrologic variable (Y) against time (X, yrs) to identify the occurrence and magnitude of any temporal trend, reporting the resultant regression equation along with its coefficient of determination (r^2) and significance level (p-value). Using t-tests, we also compared climatic/hydrologic means ($\bar{x}$) for the 20-yr time period preceding (1975–1994) vs. following (1995–2014) wolf reintroduction. A $p \leq 0.05$ was used to identify a statistically significant trend (regression slope) or difference in 20-yr means (t-test).

4. Results

Twenty-four evaluations of woody riparian species have occurred within the park's northern range since the 1995–1996 return of wolves, with publication dates from 2005 to 2015 (Table 1). The vast majority found that young willow, cottonwood, aspen, thinleaf alder, and several species of berry-producing shrubs have begun to increase in height, stem diameter and establishment, crown cover, or recruitment in various northern range riparian areas. Over half of the studies (13 of 24) reported information on temporal patterns of browsing intensity and, in all cases, browsing levels were found to have decreased over time. Nearly half of the studies (11 of 24) compared observed changes in plant communities to climatic/hydrologic variables; the results of these analyses were mixed in that some indicated a significant correlation between ongoing vegetation change and a climatic/hydrologic variable, whereas others found no relationship (Table 1).

General patterns of vegetation change, over time, for northern range riparian areas are illustrated in Fig. 3. One of the earliest studies following wolf reintroduction found an increase in the basal area growth of willow stems beginning in about 1997 (Fig. 3a; Beyer et al., 2007). From aerial photography comparisons and field measurements, Baril et al. (2011) found willow cover more than doubled between 1991 and 2006 (Fig. 3b). By 2004, mean willow heights along several reaches of Blacktail Deer Creek had begun to exceed the upper browse level of elk (Fig. 3c; Beschta and Ripple, 2007a). Bilyeu et al. (2008) and Marshall et al. (2013) found that willow height increases (outside of ungulate exclosures) began in about 2000; height growth was more rapid for plants with relatively high water tables (Fig. 3d). Marshall et al. (2014) identified a major increase in northern range willow stem

Table 1
Summary of northern range studies evaluating young deciduous woody plant dynamics during the first two decades following wolf reintroduction (1995–2014).

Study period (yrs)	Vegetation change over time?[a]	Browsing change over time?[b]	Vegetation change related to climatic/hydrologic variables?[b]	Synthesis comment	Citation
Willow					
1989–2001	Growth rate {+}	[−]	Elevation [−] Precipitation [−] N. Pacific index [+] Watershed area [0] Snow depth [0]	The annual cross-sectional area (mm^2) of willow growth rings increased two-fold after 1996	Beyer et al. (2007)
1991–2006	Cover {+}	n.a.	n.a.	By 2006, the cover of "released" willows had increased from 4 to 35%, "suppressed" willows from 5 to 11%, and "tall" willows from 59 to 60%; the overall increase in cover was 170%	Baril et al. (2011)
1997–2003	Height {+}	[−]	Root collar height above stream [0]	By 2003, young willow heights, originally 25–74 cm in 1997, had increased to 149–268 cm	Beschta and Ripple (2007a)
2000–2002	Height {+}	n.a.	n.a.	Over a two-yr period, young willow heights increased from an average of 80 cm to 115 cm	Ripple and Beschta (2005)
2004	Height {+}	[−]	Root collar height above stream [0] Snowpack depth [0] Peak discharge [0] July discharge [0]	By 2004, young willow heights had increased at 53% of study sites compared to heights in 1998 and earlier; height increases began in about 2000 in conjunction with a sharp decrease in browsing rates	Ripple and Beschta (2006)
2001–2005	Height {+}	[−]	Water availability [+]	Young willow height increases were greater on sites with shallow water tables than for sites with deep water tables; height increases inside ungulate exclosures (unbrowsed) were greater than those outside of exclosures (browsed)	Bilyeu et al. (2008)
2004	Height {+}	n.a.	Ground water use [+]	Willow heights were positively correlated with ground water use	Johnston et al. (2011)
2005–2007	Height {+}	n.a.	Water table depth [−] Soil temp. [−] Snow depth [+] Snowpack water eq. [+] NO$_3$ mineral. [+]	Some young willows remained <80 cm in height (similar to pre 1995–1996 levels) while others exceeded 400 cm in height	Tercek et al. (2010)
2006–2010	Height {+}	n.a.	Water table depth [−]	Follow-up of Bilyeu et al. (2008); young willow height increases associated with shallow water tables continued to be greater than those with deeper water tables; height increases inside exclosures continued to be greater than those outside of exclosures	Marshall et al. (2013)
1980–2008	Establishment {+}	n.a.	Elk abundance [−][c] Precipitation [−][c] Annual discharge [−][c] Peak discharge [+][c]	During 2000–2008 (9 yrs), annual rate of willow stem establishment was six times greater than during 1980–1999 (previous 20 yrs)	Marshall et al. (2014)
2009–2010	Height {+}	[−]	n.a.	At two locations, summertime browsing rates of willows <200 cm in height were lower in 2010 than in 2009	Painter and Ripple (2012)
Cottonwood					
1998–2001	Height {+}	[−]	Gully depth [+]	Young cottonwoods increased in height at several locations along Lamar River and Soda Butte Creek	Ripple and Beschta (2003)
2002–2006	Height {+}	n.a	n.a.	Median heights of young cottonwoods along the Lower Lamar were 30 cm whereas those along the Upper Lamar had increased from 100 cm to 290 cm	Beschta and Ripple (2010)
2001–2010	Frequency {+}	[−]	n.a.	The total number of young cottonwoods ≥5 cm dbh in the Lamar Valley increased from zero in 2001 to 156 in 2010	Ripple and Beschta (2012)
2009–2010	Height {+}	[−]	n.a.	Young cottonwood heights were inversely correlated with summer browsing rates; browsing rates of 84% maintained young willow in a suppressed state	Painter and Ripple (2012)
2002–2012	Upper Lamar height {+} Lower Lamar height {0}	n.a.	n.a.	Median heights of young cottonwoods along the Upper Lamar increased from 100 cm to 510 cm but remained <30 cm along the Lower Lamar; in 2012 the total number of young cottonwoods >1.5 m in height was ~17,000 and 54 for the Upper and Lower Lamar study reaches, respectively	Beschta and Ripple (2014)
Aspen					
1999	Height {+}	n.a.	Site wetness [+] Burned [0]	Browsing rates of young aspen varied from 50 to 57% with no difference between low and high wolf-use areas; young aspen heights averaged 43 cm and 49 cm in low and high wolf-use areas	Ripple et al. (2001)
1998–2006	Height {+}	[−]	n.a.	Browsing levels associated with the five-tallest young aspen in a given stand began to decrease in ~2002, with heights increasing after ~2003	Ripple and Beschta (2007)
2004–2007	Height {0} Survivorship {0}	n.a.	n.a.	A mix of riparian and upland stands ($n = 16$) were sampled; browsing of young aspen generally averaged 40–90% and heights remained short (mostly 25–75 cm); none were >200 cm in height on study plots	Kauffman et al. (2010)

Table 1 (*continued*)

Study period (yrs)	Vegetation change over time?[a]	Browsing change over time?[b]	Vegetation change related to climatic/hydrologic variables?[b]	Synthesis comment	Citation
2010	Height {+}	[−]	n.a.	Follow-up of Ripple and Beschta (2007); browsing levels of young aspen in riparian stands continued to decrease and heights increase through 2010; browsing levels in upland stands began to decrease in ~2005	Ripple and Beschta (2012)
2012	Height {+} Recruitment {+}	[−]	Snowpack water equivalent [0] Palmer Z-Index [0] Fire occurrence [0]	Follow-up of Larsen (2001); average browsing rates of the five-tallest young aspen sprouts in northern range aspen stands ($n = 87$) decreased from 88% in 1998 to 44% in 2012; the proportion of young aspen taller than 100 cm increased from 1% in 1998 to 34% in 2012	Painter et al. (2014)
2012	Height {+} Recruitment {+}	[−]	n.a.	Northern range browsing rates of young aspen, which averaged 88% in 1998, had decreased to 37% and 63% in the western and eastern sectors of the northern range by 2012, respectively; 26% and 65% of stands in the western and eastern sectors, respectively, had young aspen > 200 cm in height by 2012	Painter et al. (2015)
Other deciduous species					
2003–2010	Height {+} Berry presence {+}	[−]	n.a.	Heights of five genera/species of berry-producing shrubs increased; taller shrubs had increased probability of berries being present	Beschta and Ripple (2012a)
1960–2008	Height {+}	n.a.	n.a.	Thinleaf alder recruitment was absent along study streams until ~1996 when increased stem growth began; stem frequencies have since increased at an increasing rate over time	Ripple et al. (2015)

[a] {+} = increase, {0} = no change; n.a. = not applicable/not available.

[b] [+] = direct relationship, [0] = no relationship, [−] = inverse relationship; n.a. = not applicable/not available.

[c] Only significant results from multiple binomial comparisons shown.

establishment that occurred during 2000–2004 (Fig. 3e). In the Lamar Valley (eastern sector of the northern range), increased cottonwood recruitment after 2002 occurred along the Lamar River upstream of the Soda Butte Creek confluence, whereas cottonwood recruitment downstream of the confluence remained nearly non-existent due to high levels of browsing by bison (Fig. 3f; Beschta and Ripple, 2014). Along tributaries of the Lamar Valley, young aspen in some riparian areas began to increase in height after about 2003 (Fig. 3g; Ripple and Beschta, 2012). Although thinleaf alder stem recruitment in riparian areas was absent at six study sites during the years prior to wolf

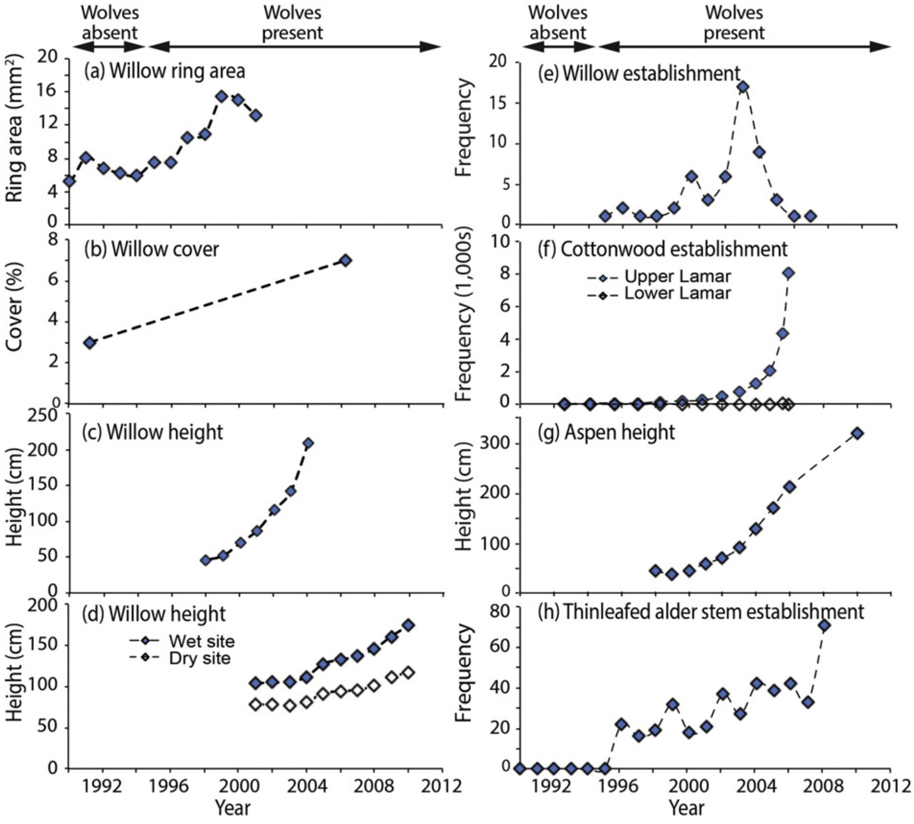

Fig. 3. Temporal changes of deciduous woody plants in Yellowstone's northern range riparian areas since 1990: (a) willow ring-area annual increment, (b) willow cover, (c, d) willow height, (e) willow stem establishment, (f) cottonwood establishment, (g) aspen height, and (h) thinleaf alder stem establishment; timing of studies vary. Adapted from: (a) Beyer et al. (2007), $n = 18$ study sites; (b) Baril et al. (2011), $n = 7$; (c) Beschta and Ripple, (2007a), $n = 3$; (d) Marshall et al. (2013), $n = 4$; (e) Marshall et al. (2014), $n = 17$; (f) Beschta and Ripple, (2014), $n = 2$; (g) Ripple and Beschta, (2012), $n = 4$; and (h) Ripple et al. (2015), $n = 6$.

reintroduction, tall alder stems have become increasingly abundant since the mid-1990s (Fig. 3h; Ripple et al., 2015).

Following the reintroduction of wolves, their northern range population increased until 2003, but has subsequently declined (Fig. 4a). The northern range elk population has been declining from the mid-1990s to the present (Fig. 4b). Although the northern range bison population remained relatively small and stable until about 2005 (Fig. 4b), their numbers have since increased. Not only are bison numbers now approaching those of elk but they also, in contrast to elk, forage in the northern range year-round. The predator/prey ratio increased from 1995 through 2003 and has since averaged ~9 wolves/1000 elk (Fig. 4c).

All climatic variables had significant ($p \leq 0.05$) long-term trends over their periods of record (Table 2, Fig. 5). Based on 120 yrs of record for the Mammoth weather station, mean air temperature and total degree-days increased at a rate of +1.3 °C/100 yrs (Fig. 5a) and +267 °C-days/100 yrs (Fig. 5b), respectively, whereas precipitation and snowfall decreased at a rate of −7.0 cm/100 yrs (Fig. 5c) and −67 cm/100 yrs (Fig. 5d), respectively. Based on 69 yrs of snow course data, the snowpack water equivalent decreased at a rate of −8.3 cm/100 yrs (Fig. 5e), consistent with the observed trends of increased temperature and decreased snowfall as measured at Mammoth. From 104 yrs of record for the Yellowstone River, no significant long-term trend was found for peak discharge (Fig. 5f), mean discharge (Fig. 5g), or July–August discharge (Fig. 5h).

Air temperature, degree-days, precipitation, snowfall, and snowpack water equivalent means ($\bar{x}$) for 20 yrs preceding wolf reintroduction vs. 20 yrs following wolf reintroduction were not significantly different (Table 2). While mean peak discharge during the last 20 yrs ($\bar{x} =$ 597 m^3/s) was significantly greater than in the previous 20 yrs ($\bar{x} =$ 483 m^3/s), annual discharge and July–August discharge were not significantly different for these two time periods.

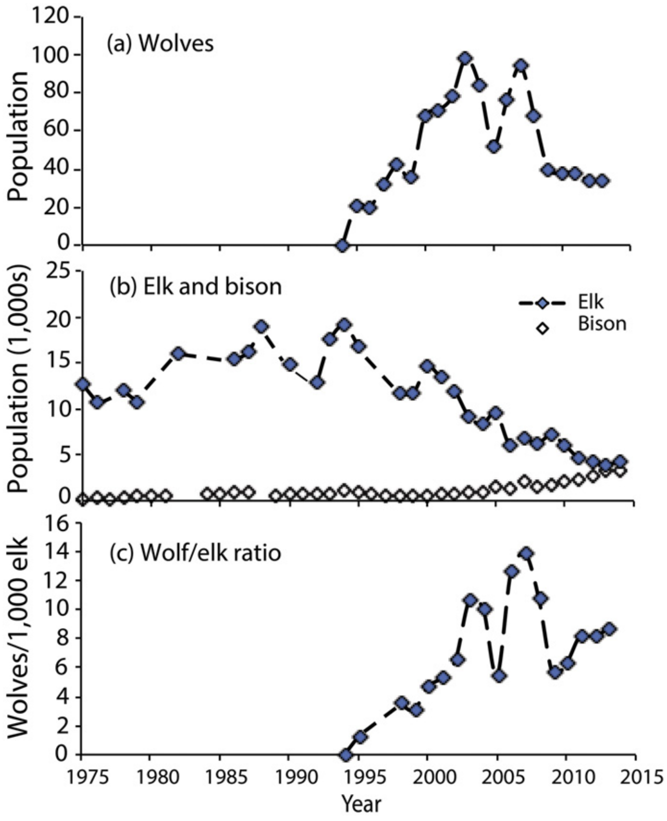

Fig. 4. Annual time series of northern range (a) wolf population, (b) elk and bison populations, and (c) wolf/elk ratio. Not shown for elk are poor count years of 1997, 1989, 1991, 2006; counts for years 1996, 1997 were not available. Data sources: annual wolf, elk and bison counts provided courtesy of the National Park Service.

5. Discussion

5.1. Trophic cascades (top–down forcing)

In the first two decades following the 1995–1996 reintroduction of wolves, all but two of the 24 northern range studies of deciduous woody species found young woody plants increasing in size or frequency (Table 1). Many of these species have different autecologies. For the 13 studies that also measured herbivory over time, all identified a decrease in browsing rates. An inverse relationship between browsing intensity and the growth of young woody plants is central to a wolves-elk-vegetation trophic cascade hypothesis because it clearly defines the mechanism connecting the lower two trophic levels (Beyer et al., 2007). Decreased browsing in recent years appears to have allowed many woody species in portions of the northern range to again grow above the browse level of elk, thus their continued height growth is no longer limited by herbivory. A relaxation of browsing pressure also suggests that bottom-up forces might now be able to influence the dynamics of recovering plant communities.

An interesting feature of the eleven northern range willow studies is that the timing of altered plant dynamics varied. For example, the increased willow growth rates found by Beyer et al. (2007) began almost immediately after wolves had returned to Yellowstone and growth rates were at their greatest by 1999 (Fig 3a). In contrast, Beschta and Ripple (2007a) found increased heights of young willow along Blacktail Deer Creek began around 2000 with mean heights attaining 200 cm by 2004 (Fig 3c). Marshall et al. (2013), with three of their four study sites along other portions of Blacktail Deer Creek, found willow height increases outside of exclosures began around 2005 and had not attained a mean height of 200 cm as of 2010, the last year of measurement (Fig 3d). In a broad sampling of northern range willow communities, Marshall et al. (2014) identified increased levels of stem establishment occurred mostly between 2000 and 2004, peaking in 2003 (Fig. 3e). An extensive assessment of northern range willows by Tercek et al. (2010) concluded that they “showed significant growth for the first time since the 1920s.” Variations in the pattern of northern range willow recovery observed by these studies may be related to differing spatial–temporal patterns of ungulate herbivory following the return of wolves as well as, at least in part, to site selection, differences in sampling protocols, plant measurements, or site productivity (e.g., water table elevations).

Five cottonwood studies have occurred since 1995, mostly along the Lamar Valley in the eastern sector of the northern range (Table 1). Three studies found an inverse relationship between young plant heights and browsing intensity, with height increases occurring as early as 2000. Height increases of young cottonwoods have also varied spatially and temporally, again emphasizing the non-uniformity of recovering riparian vegetation that is characteristic of nearly all woody plant communities in the northern range. For example, nearly 17,000 young cottonwood plants ≥1.5 m in height have become established in recent years along a 2-km reach located immediately upstream of the Lamar River-Soda Butte confluence (Upper Lamar), whereas only 54 young cottonwoods ≥1.5 m in height had established along an 8-km reach of the main Lamar Valley located immediately downstream of the confluence (Lower Lamar) (Beschta and Ripple, 2014). Elk densities have decreased dramatically in the eastern sector of the northern range following the return of wolves (White et al., 2012; Painter et al., 2015), thus greatly decreasing browsing pressure that was previously limiting the growth and recruitment of young cottonwoods. However, high levels of herbivory from an increasing northern range bison population appear to have effectively replaced elk herbivory as the dominant factor limiting young cottonwood recruitment along the Lower Lamar (Fig. 4b). Bison herbivory has also been found to be an important constraint on the growth of young willows and other

Table 2
Regression analysis of long-term trends in annual climatic/hydrologic data and comparisons of means ($\bar{x}$) for 20-yr periods before vs. after the reintroduction of wolves (bolded p-values indicate significant at $p \leq 0.05$). All data were compiled on a water year basis (e.g., Oct. 1–Sept. 30) except for degree-days which were compiled between Mar. 1 and Nov. 30. Data sources: (a), (c), and (d) Mountain States Weather Services (1895–1995) and Western Regional Climate Center (1996–2014); (b) Western Regional Climate Center; (e) National Resources Conservation Service Water and Climate Center; (f), (g), and (h) United States Geological Survey National Water Information System.

Climatic/hydrologic variable	Length of record (yrs)	Period of record (yrs)	Period of record mean	Regression equation[a]	r^2	Regress. signif. (p)	1975–1994 mean ± SE	1995–2014 mean ± SE	T-test signif. (p)
(a) Temperature (°C)	120	1895–2014	4.3 °C	$Y = 0.013X - 21.9$	0.27	**<0.01**	4.6 ± 0.2 °C	5.0 ± 0.2 °C	0.07
(b) Degree-days >4.4 °C (°C-days)	66	1949–2014	1549 °C-days	$Y = 2.67X - 3734$	0.11	**<0.01**	1560 ± 42.3 °C-days	1616 ± 35.7 °C-days	0.10
(c) Precipitation (cm)	120	1895–2014	40 cm	$Y = -0.070X + 176$	0.09	**<0.01**	37.2 ± 1.7 cm	35.6 ± 1.1 cm	0.42
(d) Snowfall (cm)	120	1895–2014	208 cm	$Y = -0.67X + 1520$	0.15	**<0.01**	173 ± 9.9 cm	179 ± 9.7 cm	0.69
(e) Snowpack water equivalent (cm)	69	1946–2014	18 cm	$Y = 0.083X + 182$	0.09	**0.01**	18.0 ± 1.2 cm	16.1 ± 1.2 cm	0.28
(f) Peak discharge (m^3/s)	104	1911–2014	521 m^3/s	$Y = 0.824X - 1098$	0.03	0.06	483 ± 26.1 m^3/s	597 ± 38.3 m^3/s	**0.02**
(g) Average discharge (m^3/s)	104	1911–2014	88 m^3/s	$Y = 0.025X + 39$	0.00	0.69	84 ± 3.7 m^3/s	92 ± 5.3 m^3/s	0.19
(h) July–August discharge (m^3/s)	104	1911–2014	140 m^3/s	$Y = -0.069X + 274$	0.00	0.70	132 ± 12.7 m^3/s	139 ± 14.0 m^3/s	0.71

Bold p-values indicate significant at $p < 0.05$.

[a] Y = Climatic/hydrologic variable in first column, X = year.

riparian shrubs in the Lamar Valley (Painter and Ripple, 2012; Beschta and Ripple, 2014).

Increased heights of young riparian aspen in the northern range, usually in association with decreases in browsing rates, were first observed within a limited number of aspen stands in 1999 (Ripple et al., 2001), with most subsequent studies finding increased heights of young aspen becoming more prevalent over time (Table 1). Because aspen sprouts accessible to ungulates were browsing-suppressed prior to the return of wolves, thus keeping their heights ≤100 cm, several studies used the five-tallest aspen in each sampled stand as a "leading edge" indicator of any change in plant community dynamics (Ripple and Beschta, 2007, 2012; Painter et al., 2014, 2015). Based on this approach, the five-tallest young aspen in riparian stands of the northern range's eastern sector began to demonstrate increased heights after about 2002, with some exceeding 200 cm by 2006 (Fig. 3g). Height increases of the five-tallest young aspen in upland stands were considerably less than those in riparian areas even though annual height growth of unbrowsed leaders, an index of site productivity, was not significantly different between upland and riparian stands (Ripple and Beschta, 2007, 2012). Regression analysis indicated that when the five-tallest

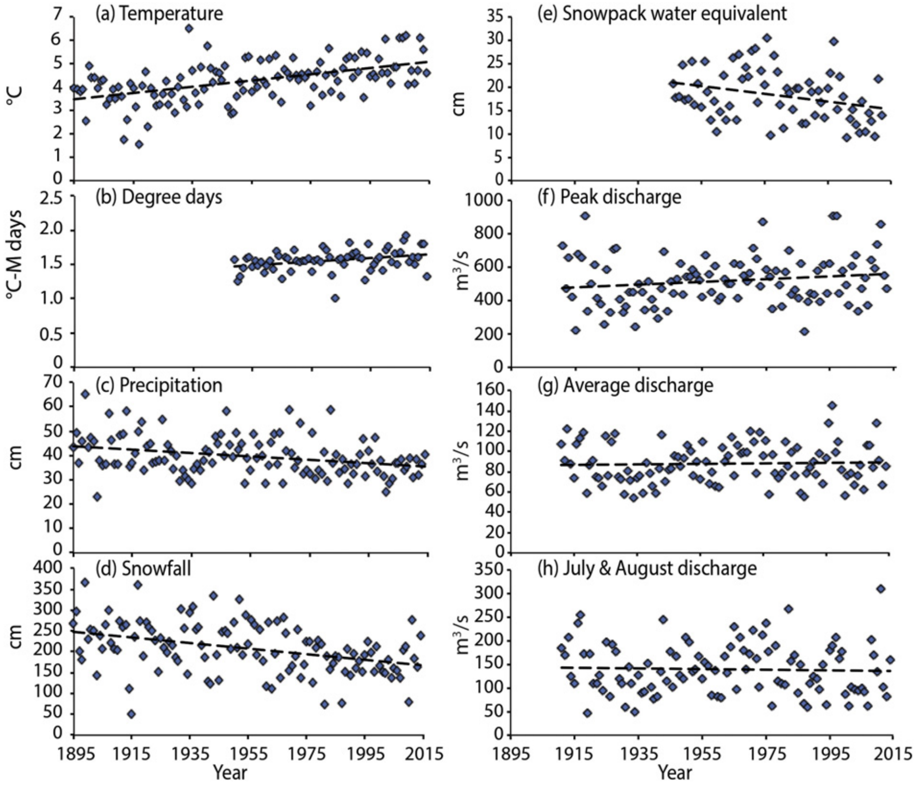

Fig. 5. Annual long-term climatic and hydrologic data: (a) air temperature (1895–2014), (b) degree days above a base temperature of 4.4 °C (1949-2014), (c) precipitation (1895–2014), and (d) snowfall (1895–2015) for the Mammoth climatic station; (e) snowpack water equivalent based on an average of Jan.1, Feb. 1, Mar. 1, and Apr. 1 measurements for Lupine and NE Entrance snow courses (1946–2014); and (f) peak discharge (1911–2014), (g) annual discharge (1911–2014) and (h) July–August discharge (1911–2014) for the Yellowstone River at Corwin Springs. All data were compiled on a water year basis (e.g., Oct. 1–Sept. 30) except for degree days which were summarized between Mar. 1–Nov. 30. Data sources: (a), (c), and (d) Mountain States Weather Services (1895–1995) and Western Regional Climate Center (1996–2014); (b) Western Regional Climate Center; (e) National Resources Conservation Service Water and Climate Center; (f), (g), and (h) United States Geological Survey National Water Information System.

young aspen attain a height of ~275 cm, the mean height of the remaining young aspen in a given stand typically begins to exceed 100 cm (Painter et al., 2014).

Based on measurements from 16 northern range aspen stands during 2004–2007, comprised of both upland and riparian stands, Kauffman et al. (2010) found that the typical young aspen had exceptionally high browsing rates (in excess of 90%) and were low in stature (i.e., <75 cm in height), thus indicating essentially no release from browsing pressure in these stands. However, a more recent assessment of northern range aspen stands ($n = 87$), again a mixture of upland and riparian stands, found that the proportion of young aspen >100 cm in height had increased from 1% in 1997–1998 to 35% in 2012. Furthermore, the proportion of stands with five or more young aspen ≥200 cm in height had increased from <1% in 2007 to 25% by 2012 (Painter et al., 2014). Although a broadening release of aspen in both riparian and upland aspen stands currently appears to be underway (Painter et al., 2014, 2015), there is considerable variability as to where and when aspen recovery has begun occur.

Thinleaf alder, a species of low ungulate palatability, began to grow taller within six northern range riparian areas soon after the reintroduction of wolves and since then the number of stems has continued to increase over time (Ripple et al., 2015). During 2003–2010, shrub richness as well as heights of several species of berry-producing shrubs in the eastern portion of the northern range was positively correlated with increased heights of recovering young aspen; the proportion of shrubs with berries was also positively correlated with shrub height (Beschta and Ripple, 2012a). In a study of serviceberry (*Amelanchier alnifolia*) on upland sites, thus not included in Table 1, Ripple et al. (2014a) found these shrubs unable to successfully grow outside of enclosures prior to return of wolves but began to do so after wolves returned. As a possible cascading effect, the amount of berries found in grizzly bear (*Ursus arctos*) scat has also increased in recent years (Ripple et al., 2014a).

Riparian songbird and beaver populations have begun to increase in recent years, likely associated with the ongoing improvements in riparian plant communities (Baril et al., 2011; Smith and Tyers, 2012). Beaver are often characterized as “ecosystem engineers” because their dams can dramatically alter riparian and aquatic systems, thus contributing to greater species richness of plant communities as well as increased habitat heterogeneity (Wright et al., 2002). Their dams can influence the frequency and duration of overbank flows, water table elevations, channel morphology, and vegetation diversity, thus helping to support habitat needs of numerous terrestrial, amphibious, and aquatic organisms (Wright et al., 2002). Although beaver were relatively abundant in the northern range during the early 1900s, they essentially disappeared by the mid-1900s as riparian plant communities became increasingly altered by intensive elk browsing (Jonas, 1955; Ripple and Beschta, 2004a). Only one beaver colony in the northern range was inventoried in 1996, 1998, and 1999 surveys, but with improving riparian plant communities following the return of wolves a total of 18 colonies were inventoried in 2015 (Fig. 6). If beaver colonies continue to increase in number and distribution, their dams may again have an important influence on the functioning and structuring of riparian and aquatic ecosystems, particularly for those alluvial channel reaches that have not deeply incised.

Wolves have likely had an important role in the declining numbers and changing spatial distribution of elk within the park during the last two decades (Mao et al., 2005; Hamlin et al., 2009; Painter et al., 2015), particularly in recent years when the number of wolves/1000 elk has remained relatively high (Fig. 4c). However, other factors may have contributed to reduced elk numbers and altered use of elk habitat in northern Yellowstone during the last two decades, potentially contributing to the initiation of recovery for riparian woody species, including increased bear predation (Barber-Meyer et al., 2008), large pre-2005 hunting harvests of elk that left the park (Eberhardt et al., 2007), and a period of dry years between 2000 and 2007 (White and Garrott, 2013).

In general, the results of various northern range vegetation studies (Table 1) are consistent with the establishment of a large predator-elk-woody species trophic cascade in riparian areas following the reintroduction of wolves. Recovery of plant communities previously suppressed by intensive elk browsing has also begun to occur in Banff (Hebblewhite et al., 2005) and Jasper (Beschta and Ripple, 2007b) National Parks of western Alberta following the return of wolves or an increase in their numbers.

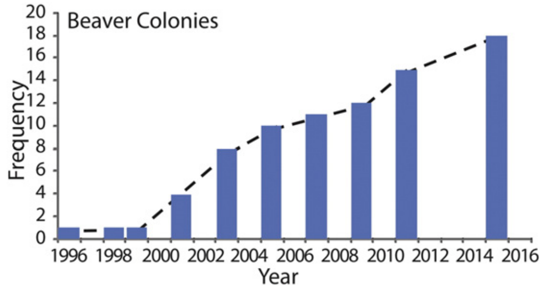

Fig. 6. Number of inventoried beaver colonies in Yellowstone's northern range for 1996–2015. Data sources: colony counts for 1996–2009 from Smith and Tyers (2012); counts for 2011 and 2015 from National Park Service surveys.

5.2. Climate/hydrologic effects (bottom-up forcing)

Changes in weather patterns (e.g., seasonal precipitation, snowfall, and temperature) or climate (longer-term fluctuations or trends) have sometimes been suggested as a mechanism for explaining the reduced growth and recruitment of young woody plants that occurred during the multiple decades of wolf absence in the northern range of Yellowstone National Park (Houston, 1982; Singer et al., 1994; Romme et al., 1995; Yellowstone National Park, 1997; Singer et al., 1998). However, others (e.g., Chadde and Kay, 1991; Wagner et al., 1995; Kay, 1997), as well as the results of more tree recent age-structure studies (Ripple and Larsen, 2000; Beschta, 2005; Wolf et al., 2007; Kauffman et al., 2013; Painter et al., 2014), were unable to demonstrate a weather/climate effect and concluded that the high levels of elk herbivory during those decades were primarily responsible for preventing plant growth and recruitment.

Our assessment of long-term climatic data indicated a +1.3 °C/100 yrs temperature trend at the Mammoth weather station. This rate of increase was nearly double that found in a 1901–2012 regional assessment (Abatzoglou et al., 2014), but consistent with an increasing annual air temperature trend that has been underway globally (IPCC, Intergovernmental Panel on Climate Change, 2014). The long-term increase in degree-days (+267 °C-days above a 4.4° C base temperature) at Mammoth was also consistent with the Abatzoglou et al. (2014) regional assessment that found the length of the frost-free period has increased by nearly two weeks since 1950. The combined effects of increasing temperature (+1.3 °C/100 yrs) and decreasing precipitation (−7 cm/100 yrs) at Mammoth are likely contributing to ongoing declines in snowfall (−67 cm/100 yrs) and snowpack water equivalent (−8 cm/100 yrs). Late 20th century snowpack reductions in this portion of the Rocky Mountains have been unprecedented (Pederson et al., 2011).

Although climate assessments normally emphasize meteorological variables, patterns of stream discharge can also be influenced by climate change since they integrate the difference between precipitation inputs and evapotranspiration losses from an area. Variations in stream discharge represent a key disturbance regime in riparian systems because the magnitude and duration of overbank flows affects the availability of moisture for many hydrophytic plant species (Chapin et al., 2002; National Research Council, 2002b). Water table depths during summertime conditions may also affect the establishment and growth of deep-rooted deciduous woody plants such as willow (Marshall et al., 2013).

Over the period 1911–2014, there has been no significant trend in annual peak discharge for the Yellowstone River at Corwin Springs

(Table 2). However, the mean peak discharge for the last 20 yrs ($\bar{x} = 597\ \text{m}^3/\text{s}$) was significantly greater ($p = 0.02$) than for the previous 20 yrs ($\bar{x} = 483\ \text{m}^3/\text{s}$), perhaps due to increased snowpack exposure to solar radiation following the 1988 Yellowstone fires. Increased establishment and recruitment of cottonwoods are often intrinsically linked to the occurrence of large flow events because this is when extensive seedbeds are typically created (Braatne et al., 1996), however intensive herbivory of young plants can effectively uncouple the expected outcomes (i.e., increased establishment and recruitment of cottonwoods) normally associated with such disturbances. Although high flows and cottonwood seedlings have been relatively common in the Lamar Valley (Beschta, 2003, 2005), increased height growth and recruitment of these seedlings appears to have only been successful where herbivory by both elk and bison has been low (Beschta and Ripple, 2014).

No significant trend was found in annual discharge or July–August discharge for the Yellowstone River over the period 1911–2014, nor was there a significant difference in these flow categories comparing the 20 yrs before and after wolf reintroduction (Table 2). The lack of trends and differences indicates these variables are unlikely to have contributed to the riparian plant community improvements that have occurred within the last two decades (Table 1).

Eleven of the 24 riparian vegetation studies (Table 1) in the northern range undertook one or more statistical analyses to discern the potential effects of site, climate, or hydrologic variables relative to ongoing changes in plant communities. When the potential effects of these variables were compared across studies, results were varied. For example snowpack depth/water equivalent was positively correlated with plant responses in two studies but not in two other studies. Similarly, three willow studies indicated an inverse relationship between water table depth and willow height, whereas two other studies found no relationship between heights of willows close to the channel and the elevation of their root collars above the stream surface, a surrogate for water table depth.

Marshall et al. (2014) used multiple binomial regressions of single parameter models to evaluate willow stem establishment relative to annual flow, precipitation, and elk population. Results indicated willow establishment was negatively correlated with elk abundance and positively correlated with peak flow the prior year. Surprisingly, however, willow establishment was also found to be inversely correlated with annual precipitation and with annual flow, indicating relatively dry years were associated with increased willow establishment. These inverse correlations appear to be in direct contrast with Tercek et al. (2010) and Marshall et al. (2013) where increased willow heights were associated with high levels of moisture availability (i.e., relatively shallow water tables). These contrasting results suggest that regression analysis using climatic/hydrologic time series, noted for large year-to-year variability (Fig. 5), and temporal vegetation measurements may have limited utility for identifying potential cause-and-effect relationships.

The increased warming, reduced precipitation, and shallower snowpack trends in the northern range over the last century (Table 2) would seem to be unlikely to have caused the improved establishment, growth, and recruitment of young deciduous woody plants in riparian areas that have been observed in recent years. Furthermore, none of the *t*-test comparisons of means ($\bar{x}$) for climatic variables during the 20 yrs before vs. 20 yrs after wolf reintroduction were significant, again indicating these variables are unlikely to represent an important mechanism for explaining any improvements in riparian plant communities that have occurred (Table 1). Such conclusions are reinforced by studies of northern range ungulate exclosures where, regardless of ongoing climatic conditions, young woody plants of various woody species began to increase in height and recruitment once an exclosure was constructed (Kay, 1990; Marshall et al., 2013; Beschta et al., 2016), as well as eventually produce seeds and fruit (Kay and Chadde, 1991; Ripple et al., 2014a). Thus, fluctuations in climate in the decades before and after wolf reintroduction do not appear to have been a limiting factor nor have they significantly influenced patterns of deciduous woody vegetation establishment and growth in Yellowstone's northern range riparian areas.

A modeling study by Creel and Creel (2009) suggested that the limiting effects mountain snow accumulations normally have on Montana elk populations would be considerably reduced in the coming decades based on global and regional climate model predictions of reduced snowpacks. Decreased snowpacks in the Rocky Mountains are also likely to intensify large herbivore impacts upon tree recruitment (Brodie et al., 2012). Yet, in Yellowstone where local data suggest a long-term decline in snowfall and snowpack amounts is underway (Fig. 5d, e), elk numbers within the park's northern range have continued to decline since wolves were reintroduced (Fig. 4b) and the recruitment of woody species has increased (Table 1).

5.3. Ecosystem restoration

Some of the riparian plant communities in Yellowstone's northern range are in an early phase of recovery relative to the previous decades of intensive elk herbivory and “full recovery” of these highly altered riparian ecosystems, which currently represent a range of alternative states, will require time. For example, it will likely require many years of relatively unhindered growth before various shrub species exceed the browse level of elk and produce significant numbers of seeds and berries. It will require many decades of continued willow, aspen, and cottonwood recruitment to replace missing age classes as well as occupy available habitat. Less known is the extent to which channel widening and incision over the seven decades prior to wolf reintroduction reduced the hydrologic connectivity of floodplains and lowered subsurface water levels such that recovering riparian plant communities will be less able to occupy former sites (Rosgen, 1993; Wolf et al., 2007; Beschta and Ripple, 2012b). Because recovery of beaver colonies has only begun in the last decade, it is not known how rapidly and to what extent they will reoccupy former habitats, potentially reversing the effects of channel incision with their dams. However, if the northern range bison population remains at current levels or continues to increase, these large herbivores may continue to limit recovery of woody plant growth and recruitment within riparian areas for portions of the Lamar Valley and perhaps in other parts of the northern range.

6. Conservation implications

Probably nowhere in the western United States has there been a concentration of woody plant studies at the level of what has occurred in Yellowstone National Park's northern range. This interest has been largely driven by a need to understand the importance of various factors affecting vegetation responses during the decades when wolves were absent and, more recently, following their return. The multi-decade absence of wolves allowed native ungulates, principally elk, to assume a dominant role in altering the composition, structure, and function of riparian plant communities, essentially pushing these systems toward alternative states in which native species biodiversity and ecosystem services declined (e.g., Kay, 1990; Wagner, 2006; Wolf et al., 2007). In contrast, research results following wolf reintroduction are generally supportive of the concept that the contemporary large carnivore guild is increasingly, via a trophic cascade, mediating the effects of elk herbivory on riparian plant communities. The reduction in elk herbivory has thus been helping to recover and sustain riparian plant communities in northern Yellowstone, thereby improving important food-web and habitat support for numerous terrestrial and aquatic organisms.

The historical management of large carnivores in the western United States has largely been one of persecution, often leading to extirpation. However, results from Yellowstone, other areas in western North America, and around the world increasingly point to a need for recovering ecologically effective populations of large predators to help recover or maintain biodiversity in ungulate populated landscapes (Ripple et al., 2014b). In the western United States, the challenge of returning or maintaining large carnivores across public lands is made more difficult due to the widespread occurrence of domestic livestock (Beschta et al., 2013; Donahue, 2015), which compete with native ungulates for resources and sometimes become alternative prey. However, given the high level of importance public lands have for maintaining diverse plant communities during a changing climate, federal land managers and state wildlife agencies may increasingly want to consider the potential role of large carnivores for meeting biodiversity goals.

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