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Changing aspen stand structure following large carnivore restoration in Yellowstone

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ABSTRACT

Restoration of large carnivores in northern Yellowstone National Park in the late 20th century resulted in a sustained reduction of Rocky Mountain elk (*Cervus canadensis*) and their herbivory, facilitating new growth of quaking aspen (*Populus tremuloides*) saplings. In 2020–21, we examined 87 randomly selected, previously sampled aspen stands across northern Yellowstone, combining random plots with stand-wide observations. Forty-three percent of stands contained a new cohort of small trees (5–10 cm dbh), the first documented recruitment of overstory aspen trees in northern Yellowstone since the 1940s. Both aspen saplings (≥2 m tall) and small trees were absent in 1998 but increased rapidly after 2007, to a mean density in 2020–21 of 1460/ha (95 % CI: 833–2087). This increase resulted in a $\log_e$ ratio effect size of 5.0, a strong effect compared to other trophic cascade studies. Stand conditions in 2020–21 varied widely: 30 % of stands had saplings throughout, 32 % had patchy sapling recruitment, and 38 % had few or no saplings. The proportion of young aspen ≥2 m tall was inversely related to browsing rates of aspen <2 m ($p<0.001$), which averaged 59 % of leaders browsed (range 0–100 %). These results suggest a restoration of ecological processes resulting in widespread but highly variable recruitment of new aspen trees. Bison (*Bison bison*) numbers and their effects have increased in recent years, limiting aspen recovery in some areas. While future conditions may not replicate the past, new aspen trees resulting from a trophic cascade increase the likelihood that aspen stands will persist in northern Yellowstone.

1. Introduction

Quaking aspen (*Populus tremuloides*) is one of the few deciduous tree species to occur in the northern Rocky Mountain ecosystem. Aspen stands provide an important element of habitat diversity, supporting a variety of plant and animal species including North American beavers (*Castor canadensis*) and cavity-nesting birds (DeByle and Winokur, 1985). Large herbivores such as Rocky Mountain elk (*Cervus canadensis*), moose (*Alces alces*), deer (*Odocoileus* spp.) and bison (*Bison bison*) browse the palatable young shoots of aspen, especially in winter when other forage may be scarce. Intensive browsing can suppress growth of young aspen and prevent recruitment of new saplings and trees; therefore, a relatively low density of herbivores is necessary to allow significant aspen recruitment (White et al., 1998, Painter et al., 2015).

Fire can stimulate aspen sprouts from roots and seed and remove competing coniferous trees, and this may result in pulses of aspen recruitment, but only if the density of herbivores is low enough to allow some aspen to escape intensive browsing (Romme et al., 1995, Smith et al., 2016). Fallen trees can further facilitate aspen recruitment by creating partial barriers that make access by large herbivores more difficult (Kota and Bartos, 2010, Painter et al., 2023b). These basic patterns and processes affecting aspen establishment and recruitment have been documented in various locations in the Rocky Mountain region (DeByle and Winokur, 1985, White et al., 1998, Hebblewhite et al., 2005, Beschta and Ripple, 2007, Smith et al., 2016, Painter et al., 2018, Rhodes et al., 2018).

The ungulate winter range of northern Yellowstone National Park (YNP), called "the northern range" (Fig. 1) has become a living laboratory for studying the interactions of aspen and other deciduous plants, large herbivores, and large carnivores (NRC, 2002, Beschta and Ripple, 2016). By 1930, gray wolves (*Canis lupus*) had been extirpated and cougars (*Puma concolor*) nearly so (Ripple et al., 2022), and elk numbers were relatively high with significant winter starvation (Houston, 1982). The resulting intensive herbivory by elk prevented young aspen in

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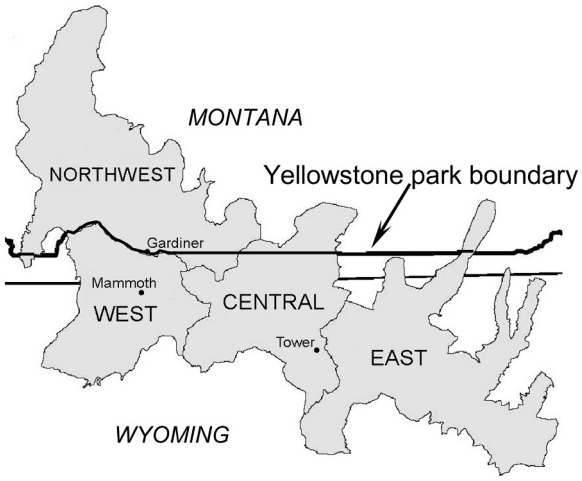

Fig. 1. Map of Yellowstone northern ungulate winter range, called "the northern range," shaded in gray, divided into four sectors: Northwest, West, Central, and East (White et al. 2012, Painter et al. 2015). The northern range consists of low elevation river valleys of the Yellowstone River and its tributaries, and extends north of the YNP boundary. The towns of Gardiner and Mammoth Hot Springs are marked, as is Tower Junction. All sampling in this aspen study was inside YNP in sectors West, Central, and East.

northern Yellowstone from growing taller to replace aging trees, despite culling of elk in the park. After the culling program ended in 1968, the northern Yellowstone elk population increased to record numbers (Fig. 2) and effects on woody browse plants such as aspen intensified (Houston, 1982, Kay, 1990, Romme et al., 1995, Wagner, 2006). Aspen age studies showed that most overstory trees originated in the late 1800s, and recruitment virtually ceased by the 1940s (Romme et al., 1995, Ripple and Larsen, 2000, Barmore, 2003, Larsen and Ripple, 2003, Beschta et al., 2016).

Wolves were reintroduced in 1995–96, adding to predation of elk by bears (*Ursus* spp.) and cougars, along with hunting outside the park (Barber-Meyer et al., 2008). With these combined pressures, elk numbers in the northern range decreased and their distribution changed (White et al., 2012, Painter et al., 2015, Smith et al., 2023). In the 21st century, much lower elk densities inside the park have been maintained by increased predation (Fig. 2). Young aspen responded to reduced browsing pressure by growing taller in many stands (Ripple and Beschta, 2007, 2012, Painter et al., 2018, Peterson et al., 2020), as did other deciduous species (Beschta and Ripple, 2016). This case of Yellowstone aspen greatly declining after the loss of large carnivores (Ripple and Larsen, 2000), and then beginning to recover following large carnivore restoration has become a textbook example of a trophic cascade and the ecological effectiveness of apex predators (Terborgh and Estes, 2010, Painter et al., 2023a). Similar patterns of aspen suppression in the absence of wolves, and new recruitment when wolves returned, have been documented in Banff and Jasper National Parks in Canada (Beschta and Ripple, 2007; Hebblewhite et al., 2005; Hebblewhite and Smith, 2010; White et al., 1998).

Various lines of evidence have demonstrated that increases in height and height variation of young aspen in northern Yellowstone have been driven by a decrease in elk browsing, not climate change or differences in site productivity (Runyon et al., 2014, Beschta et al., 2016, Painter et al., 2018). This conclusion is supported by the fact that inside

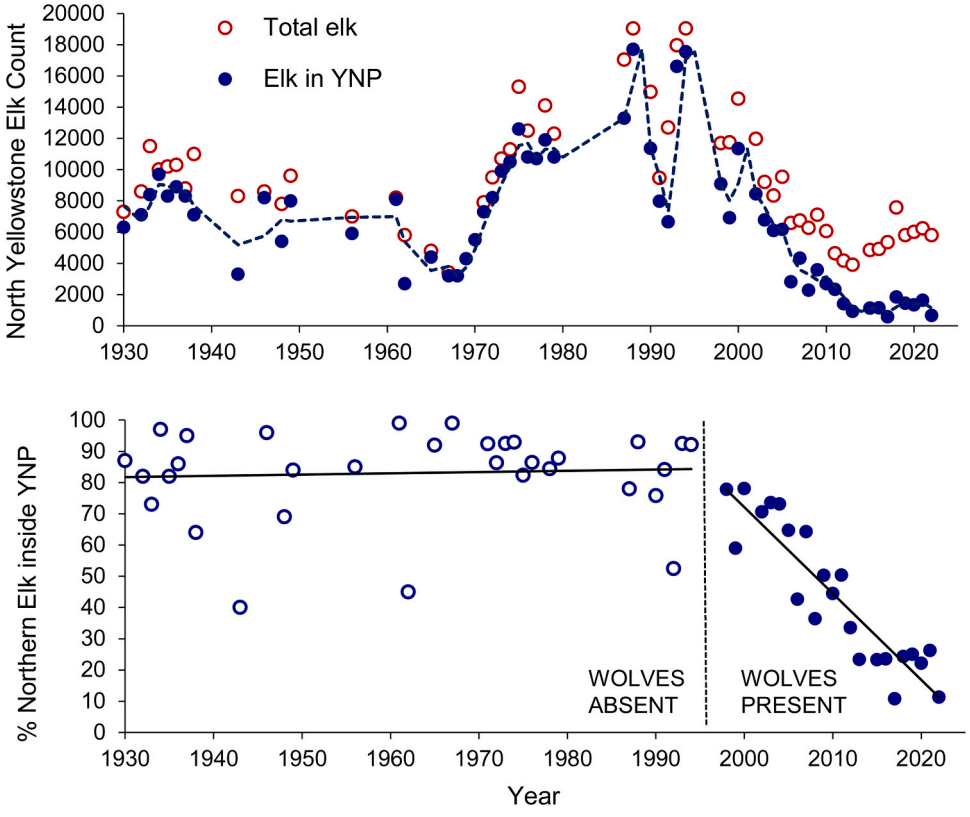

Fig. 2. Northern Yellowstone elk herd winter count trends. Top: Elk counts 1930–2022, total of northern Yellowstone elk both in YNP and north of the park (open circles), and inside YNP boundary (solid circles); dashed line displays 2-year moving average of counts inside the park. Elk counts in YNP in the last decade have been the lowest on record. Bottom: Percentage of total northern elk herd counted inside YNP boundary, regression lines show trend 1930–1994 before wolf reintroduction (r^2=0.004), and 1998–2022 after wolf reintroduction (r^2=0.83). These percentages flipped from an average of 80 % inside the park prior to 1994, to about 80 % outside during the last decade. Counts were not conducted 1995–1997. Data sources: Houston (1982), Yellowstone Center for Resources annual elk count reports 1987–2023.

exclosures, or where elk densities were lower outside the park, aspen stands continued to produce saplings and new trees in previous decades, even as stands in the park did not (Kay, 1990, St. John, 1995, Larsen and Ripple, 2003, 2005, Beschta et al., 2016, Painter et al., 2018). Inside the park, in 1998 Larsen and Ripple (2003), (2005) found young aspen growing taller only in places where they were protected from browsing, as on scree slopes or in piles of jackstraw or fenced enclosures. The presence of young aspen taller than 2 m was unrelated to the moisture conditions of the stands. Although aspen would be expected to occur in a mosaic of various ages and stages of stand development, stands in northern YNP were virtually devoid of aspen understory, even as overstory trees aged and died (Beschta et al., 2016, Peterson et al., 2020). Later, as browsing decreased and some young aspen grew taller, two different studies found that stand productivity or rate of growth of young aspen (indexed by annual leader growth) explained little of the variation in height of young aspen, while the influence of browsing was highly significant (Ripple and Beschta, 2007, Painter et al., 2014, 2015). Although many stands had similar annual growth rates, these findings showed that the reduction in browsing varied greatly among stands, resulting in a range of aspen conditions and responses unrelated to stand productivity. Certainly, site conditions can affect the rate at which a plant grows taller, and with a sustained reduction in browsing, differences in stand productivity will likely emerge as a more significant influence on young aspen height. Even so, as browsing rates have become more moderate and more spatially variable, herbivory has remained the dominant factor affecting the ability of aspen stands to grow new overstory trees in northern Yellowstone (Painter et al., 2018).

Climate variations have been suggested as a reason for aspen decline in the 20th century (Houston, 1982, Romme et al., 1995). A drought in the 1930s may have eliminated or decreased the extent of some stands (Painter et al., 2014, Beschta et al., 2016), but the stands that have persisted in northern Yellowstone were in places with sufficient moisture to survive that drought and subsequent dry periods. Recent trends of a warmer and drier climate generally have been detrimental to aspen in the mountain West (Rogers and Mittanck, 2014, Refsland and Cushman, 2021) and so would not be likely to cause observed increases in aspen height growth (Painter et al., 2014). Thus, climate can be ruled out as a primary cause of the general lack of aspen recruitment in northern Yellowstone in the late 20th century, and the recent trend toward increased aspen recruitment which began despite a significant drought during 2007–2011 (Beschta et al., 2016, Painter et al., 2018).

As the recent reduction in herbivory interacts with the stimulating effects of fire on aspen (Romme et al., 1995, Rhodes et al., 2018), aspen coverage in northern Yellowstone may expand over time toward a more aspen-dominated landscape as was present in the early 20th century (Houston, 1982, Barmore, 2003, Wagner, 2006). After the extensive fires of 1988, researchers noted new aspen seedlings and root sprouts facilitated by this event, but these new aspen were unable to grow due to the fact that “elk browsed nearly all sprouts that were accessible” (Romme et al., 1995, p. 2097). Since that time, two of the factors cited by Romme et al. (1995) as preventing aspen recruitment – absence of wolves and large numbers of elk – have changed. However, considerable time must elapse to replace the aging overstory, and the future landscape may not fully replicate past conditions due to climate change, increasing bison numbers, or other variables. For example, recent and predicted trends of a warming and drying climate may prevent aspen from growing in some places where it grew in the past, and may restrict the extent of some existing stands. Nevertheless, a process of restoration and recovery has begun where many aspen stands are no longer prevented from recruiting new trees, as a result of changes in the factors that were suppressing them.

To assess the extent and trend of aspen recovery, we randomly sampled aspen stands across northern YNP and compared results with two previous surveys of aspen in these same stands: (1) in 1997–98 (Larsen and Ripple, 2003) shortly after the 1995–96 introduction of wolves, and (2) in 2012 (Painter et al., 2014, 2015). These and other historical data collected during 1986–1989 (Kay, 1990) and 2007–2017 (Brice et al., 2021) provide context to demonstrate changes in aspen ecology and recruitment during recent decades in the Yellowstone northern range. We investigated the extent to which a new aspen cohort has been recruited into larger size classes, the relationship between browsing and aspen recruitment, and the implications for aspen stand dynamics in the northern Yellowstone ecosystem.

2. Methods

2.1. Study area

The northern range contains large valleys of the upper Yellowstone River and its tributaries that provide low-elevation winter foraging grounds for elk, deer, moose, and pronghorn (*Antilocapra americana*) in the northern portion of YNP, and north of the park boundary (Fig. 1). Sagebrush (*Artemisa* spp.) steppe is the predominant vegetation type in these valleys, transitioning to coniferous forests on the slopes above. Cottonwood (*Populus* spp.), willow (*Salix* spp.) and aspen may grow along rivers and streams, or in moist meadows fed by groundwater.

With few predators, and hunting prohibited inside YNP, by the 1930s concerns grew that elk were overgrazing the range (Wagner, 2006). Elk were removed by increasingly intensive culling in the park during 1930–1968, but elk densities remained sufficiently high to suppress aspen recruitment as about 80 % of the herd continued wintering inside the park (Houston, 1982, Painter et al., 2018). After culling ended in 1968, elk numbers greatly increased (Fig. 2). High elk population densities in the 1980s and 1990s were limited primarily by winter starvation (Houston, 1982, Singer et al., 1997, Wagner, 2006), so predation by bears and cougars was largely compensatory. This changed in the early 2000s following restoration of wolves, as predation by wolves, bears and cougars became a more important limiting factor for elk, and with lower elk densities fewer elk starved in winter (Barber-Meyer et al., 2008). Recent elk counts have been similar to previous lows resulting from culling in the 1960s, but with an important difference in elk distribution: Most of this decrease in elk density has been inside YNP (White et al., 2012, Painter et al., 2015, 2018), with about 70–80 % of the herd wintering outside of the park to the north (Fig. 2). In previous decades, elk left the park in large numbers and many died when they were driven out by severe winter starvation events, as followed the fires of 1988 (Fig. 2), but a similar mortality event in 1996–97 was not followed by the previous pattern of increasing back to high numbers. This time, elk numbers stayed lower and continued to decrease, as did the proportion of the herd wintering inside the park (Fig. 2). The result has been historically low elk densities in the park during the first two decades of the 21st century, and reduced browsing pressure on aspen. However, during this same recent period, bison numbers and the effects of bison on aspen greatly increased in the northern range (Beschta et al., 2020, Painter et al., 2023b).

A combination of factors contributed to a substantial decrease of northern Yellowstone elk in 1996–97 (Fig. 2), including thousands of elk starving that winter, and a large hunting harvest as elk were driven out of the park by starvation (Eberhardt et al., 2007). Newly introduced wolves probably played little role in this initial decrease of elk in 1996–97, but as wolf numbers increased, combined with continued high hunting harvests as elk continued to leave the park in subsequent years, concern grew that the combination of predation and hunting take was unsustainable (White and Garrott 2005b). Estimated wolf take of elk soon exceeded hunting harvest (White and Garrott 2005a), and by 2005 the Gardiner late winter hunt of these migrating elk was greatly reduced and subsequently eliminated (Hamlin and Cunningham, 2009, White et al., 2012, Painter et al., 2018). Wolf abundance on the northern range fluctuated widely as wolves became established, reaching a maximum of nearly 100 in 2003, but was relatively stable in the period 2008–2022 with an average of 46 wolves (range 33–79) reported in annual counts inside the park boundary (Cassidy et al., 2023). Cougars on the YNP

northern range were estimated at about 30–45 individuals during the period 1998–2015, with elk as their primary prey (Stahler and Anton, 2015, Marcus et al., 2022). Bears were also important predators of young elk calves, in one study accounting for the largest proportion of calf mortality of any mortality cause, followed by wolves and cougars (Barber-Meyer et al., 2008).

2.2. Aspen size categories

During most of the 20th century, elk herbivory generally kept young aspen heights to <1 m (Kay, 1990, Larsen and Ripple, 2005). However, with recent reductions in browsing the understory of young aspen in some stands began to grow taller, eventually becoming a new cohort of aspen saplings and small trees. By 2012, what remained of the older overstory consisted of trees >20 cm dbh (diameter at breast height) (Painter et al., 2014); consequently, we have defined "young aspen" as those <20 cm dbh. This new cohort was not even-aged, as the release from browsing was spatially variable resulting in a range of young aspen heights and diameters (Painter et al., 2015). As in previous studies, we defined "saplings" as aspen ≥2 m tall and <5 cm dbh, and "trees" as ≥5 cm dbh (Kay, 1990, Bartos et al., 1991, Larsen and Ripple, 2005, Kimble et al., 2011, Painter et al., 2014). Thus, the new cohort of "young trees" was defined as ≥5 cm dbh but <20 cm dbh.

Numerous studies of aspen have used 2 m in height as a general indication that aspen were escaping from elk browsing, because browsing by elk decreases rapidly with height above 2 m (Beschta et al., 2023), and this threshold has functioned well as an indicator of likely recruitment success. Moose (*Alces alces*) may routinely browse at heights above 2 m (Telfer and Cairns, 1978, Peterson and Peterson, 1992), but moose numbers remained low in northern Yellowstone (Hobbs et al., 2024) and we found little evidence of browsing of aspen above 2 m during our data collection. Of course, browsing does not abruptly cease at 2 m, but if young aspen in northern Yellowstone are consistently reaching heights above 2 m this signals an important change from previous decades when such saplings were absent due to intensive browsing. As aspen saplings grow larger their likelihood of surviving to become overstory trees increases.

2.3. Sampling and data sources

We measured young aspen in 87 randomly selected aspen stands across the northern range within the park boundary in August and September of 2020–21. These stands were previously surveyed in 1997–98 and 2012 (Larsen and Ripple, 2003, 2005, Painter et al., 2014). As in 2012, we did not include stands on scree slopes, because such conditions inhibited ungulate access (St. John, 1995, Larsen and Ripple, 2005). We used two different sampling approaches in each stand: (1) a random sampling plot, and (2) selecting five of the tallest young aspen in the entire stand (5T) (Ripple and Beschta, 2007), whether in or out of the random plot. Stands and plot locations were not physically marked but were relocated using GPS coordinates and compass bearings recorded in 2012; see Painter et al. (2023b) for a map of the northern range with sampling locations. A plot consisted of a 2×30 m belt transect that began at a live, dead, or fallen aspen tree nearest the GPS location, and extended toward the centroid of the stand. Previous sampling used standing trees as a start point, but many trees had since fallen to the ground.

Within each plot we recorded the number of aspen in several height (m) and dbh (cm) categories: <1 m tall; 1–2 m tall; ≥2 m tall but <5 cm dbh (saplings); 5–10 cm dbh (small trees); 10–20 cm dbh (intermediate trees); and ≥20 cm dbh (old overstory cohort). We recorded browsing status (browsed or not) of the top leader stem for all aspen <2 m tall, for the current growing season and the previous year, as indicated by bud scars and browsing scars (Keigley and Frisina, 1998, Ripple and Beschta, 2007). If a plot had fewer than 10 aspen <2 m, we included additional sprouts closest to the plot and at least 1 year old, for a minimum of 10 observations for browsing calculations only. We counted trees ≥20 cm dbh in a larger plot 10×30 m nested around the 2×30 m plot. These large tree counts did not include the transect starting tree.

For each of the 5T young aspen within a stand, we measured height (m) and dbh (cm). We also visually estimated: (1) the percentage of the stand covered by coniferous trees; and (2) the total number of saplings or young trees (<20 cm dbh) present in the stand (actual counts if fewer than 20, or in categories of 20–50, 50–100, >100) using the height of bark scars from elk on aspen trunks as a height reference (Beschta and Ripple, 2020).

2.4. Analysis

Aspen sampling in 1997–98 included some stands for which location data were unavailable, thus we included only the 87 stands we relocated in 2012 and 2020–21 in our analysis (Painter et al., 2014). We calculated the percentage of plots containing stems in various size classes, and the density of stems per hectare in those size classes. Browsing rate was calculated for each plot as the percentage of young aspen <2 m tall (fall height) and at least one year old on which the previous year's top leader had been browsed. Stems >2 m tall or younger than 1 year (new summer growth) were not included in browsing estimates. We used bootstrapping (100k iterations) to generate 95 % confidence intervals for percentage estimates by the percentile method (Jung et al., 2019), with function "boot.ci" (package "aod") in R Statistical Software version 4.2.3 (R) (R Core Team, 2023).

Logistic regression with binomial distribution was used to test browsing rate as an explanatory variable for the proportion of young aspen ≥2 m in sample plots, with function "glm" in R (R Core Team, 2023). Quasibinomial distribution was used if needed to account for overdispersion indicated by a dispersion parameter >1. For some comparisons, we grouped plots by the northern range sector in which they occurred: West, Central, or East (Fig. 1), as defined by White et al. (2012) and Painter et al. (2015). We calculated the strength of the trophic cascade effect on sapling density in 2020–21 compared to 1997–98, using two common methods: log ratio (Hebblewhite et al., 2005, Alston et al., 2019, Ripple et al., 2025), and Cohen's *d* (Cohen, 1988, Lakens, 2013) which is the difference in means divided by pooled standard deviation. We reported the log ratio effect strength in two ways, base 10 logarithm and natural logarithm, to facilitate comparison to other studies.

The (5T) method confirms the presence of saplings and young trees in a stand, but does not distinguish a stand with many saplings from a stand with few. Random plots, in contrast, provide an indication of overall conditions but may miss saplings outside the plot. For example, a lack of saplings in a random plot does not mean there were none in the stand. On the other hand, saplings in a random plot indicate the likely presence of more saplings in a stand, which we confirmed by comparing plots to estimates of the total number of saplings in the stand. We tested this relationship using Spearman's rho nonparametric rank correlation, with base R function "cor.test" (R Core Team, 2023). Using the strengths of the two sampling methods (random plots and 5T), we placed stands into one of three recruitment categories: (1) "Saplings likely throughout, " based on 8 or more ≥2 m tall in the random plot, an indication that saplings or young trees were likely in much of the stand; (2) Saplings or young trees "patchy," in part of the stand, indicated by 5 or more in the entire stand (from 5T sampling) but <8 in the random plot; (3) Saplings and young trees "few to none," indicated by less than 5 in the entire stand. Eight saplings per 60 m plot exceeds the minimum density threshold (1200/ha) proposed by Bartos and Campbell (1998) for young aspen (1.5–5 m in height) as an indicator of successful stand regeneration following a fire or clearcut. We compared this categorization to other indicators including: median height >2 m in random plots; saplings counted in each stand; and site photographs.

Fig. 3. A large aspen stand with few live overstory trees remaining from a distinct older cohort (>20 cm dbh), but with a dense thicket of new young trees (~6 m tall and 5–8 cm dbh). The upper height of the new cohort of aspen trees compared to the larger and older dead overstory trees demonstrates a historical lapse in recruitment. This recruitment "gap" occurred when young aspen were suppressed by intensive elk browsing for decades, then began to grow taller as herbivory decreased following the restoration of wolves and subsequent decreases in elk density. In 2020–21, 43 % of sampled stands contained small trees (≥5 cm dbh but <20 cm), the first substantial recruitment of aspen trees since the 1940s (Table 1). (View north from above Crystal Creek, photo by Luke Painter, September 2020.).

3. Results

In many of the 87 sampled stands, few to none of the older overstory trees remained, indicating these stands are likely to die if they do not gain new recruitment (Fig. 3, Table 1). Large tree density was very low, averaging only 1.2 aspen trees per 10×30 mplot (38.3 trees/ha; 95 % CI: 25.4–51.2; n=87, range 0–333), and 57 % of these plots contained no trees at all. Large coniferous tree density (>20 cm dbh) was also very low, averaging 0.82 trees per 10×30 mplot, 67 % of which contained none. Coniferous trees were absent or had <10 % estimated cover in 49 % of entire stands, while 12 % of stands were more than 50 % covered; this compares to 54 % and 18 % of stands in 2012, respectively (Table 2).

The percentage of entire stands with aspen saplings increased from 60 % in 2012 to 74 % in 2020–21, and for the first time small trees (5–10 cm dbh) were found in 43 % of stands. Two of these stands (3 %) also contained new intermediate sized trees, >10 cm dbh. In random plots, 49 % contained at least one sapling (increased from 28 % in 2012), and 22 % contained at least one young tree (Fig. 4). From a historical baseline of 0 saplings per plot in 1997–98, the density of saplings and young trees in random plots increased rapidly after 2007 (Fig. 5) to a mean density in 2020–21 of 1460/ha (95 % CI: 833–2087; n=87; range 0–20,333); mean densities and effect strengths are shown in Table 3. Because a log ratio cannot be calculated for a value of zero and no saplings were found in 1997–98, we added 0.5 sapling to each plot in the 1997–98 data for this calculation. The increase in sapling density over the 11 years of the Brice et al. (2021) study (Fig. 5) resulted in a mean density change ratio of 12.2, and a natural log effect strength of 2.5 for their 2007–2017 data. Additional information about past data sources, and the size distribution of aspen for this and previous northern Yellowstone studies, is presented in supplemental Table S2.

Some stands had few or no saplings, while others had many (Table 4, Fig. 6). The number of saplings in a plot was strongly correlated with the visually estimated total number of saplings in the stand (Spearman's rho = 0.81, p<0.001). While some stands had large numbers of saplings, 26 % of entire stands (Table 4) and 51 % of random plots had no saplings or young trees, including two stands that had died (no live trees or sprouts) since 2012. At the other end of the spectrum, 26 stands (30 %) had at least 8 saplings in a random plot, our indicator of "saplings throughout" (Fig. 6). This result was consistent with field observations and assessment of site photos, but contrasted with measures such as the mean or median height of young aspen. A median height >2 m was a much more conservative indicator of sapling recruitment, a threshold exceeded in only 13 (15 %) of plots. This threshold included a stand with only 7 saplings in the entire stand, and excluded 10 stands with more than 100 saplings, most with at least 8 saplings in the plot. The low median height in these 10 plots was due to short plants (<2 m) present

Table 1
Stand-level measurements in 2020–21 for 87 randomly selected aspen stands, in total and by sector, in the northern range study area of YNP. (1) Results of surveys of entire stands. (2) Measurements of 5 of the tallest (5T) of the new cohort of young aspen in each entire stand.

(1) Percent and number of stands	Total (%)	Total (n)	West	Central	East
Stands sampled	100	87	23	27	37
Dead stands (no live trees or sprouts)	2	2	1	1	0
Old overstory dead (none >20 cm dbh)	29	25	7	3	15
Saplings present (>2 m tall but <5 cm dbh)	74	64	14	17	33
Young trees present (>5 cm dbh but <20 cm)	43	37	5	9	23
5 or more young trees	25	22	3	4	15
(2) Height and dbh of 5 tallest (5T)		All	West	Central	East
5T Mean height (m); n=425		3.7	2.7	3.3	4.5
5T Mean dbh (cm) of all ≥2 m; n=293		4.7	4.0	4.5	5.0

Table 2
Plot-level measurements in 2020–21, from random plots (2×30 m) in 87 randomly selected aspen stands. Means were calculated for each plot, then averaged for each sector. (1) Mean percentage of young aspen ≥2 m tall, out of all young aspen (defined as <20 cm dbh) in the 87 sampling plots. (2) Browsing rates, including only stems <2 m, with 95% CI (n=85, as two stands were dead). Spring browsing indicates leaders browsed during the previous year; summer browsing indicates leaders browsed during the growing season of the sampling year. Measurements from 1997-98 and 2012 are provided for comparison (Painter et al. 2015, 2018).

(1) Mean % young aspen ≥2 m (n=87)	All	West	Central	East
1997–98	0	0	0	0
2012	5	2	3	9
2020–21	18	12	15	23

(2) Mean % browsed (n=85)	**All**	**West**	**Central**	**East**
2012 Spring (95% CI)	52 (46–58)	63 (53–74)	62 (53–71)	37 (30–45)
2020–21 Spring (95% CI)	59 (53–65)	70 (58–81)	62 (54–71)	50 (40–60)
2012 Summer (95% CI)	11 (8–14)	20 (13–28)	10 (5–16)	5 (3–8)
2020–21 Summer (95% CI)	19 (14–24)	37 (24–51)	6 (3–9)	17 (11–23)

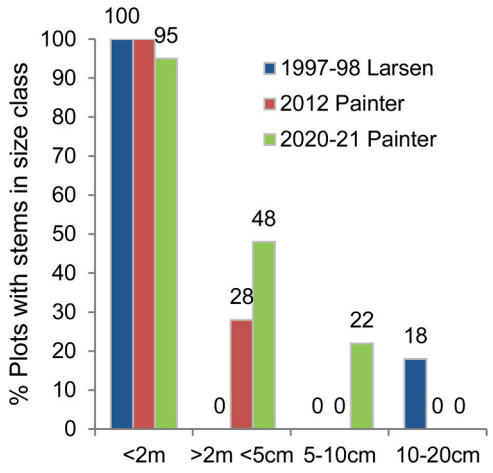

Fig. 4. Percentage of random sampling plots with stems in four size classes, from 87 randomly selected aspen stands in three sampling periods. In 1998, all young aspen in these plots were shorter than 2 m (Larsen and Ripple, 2005), demonstrating a lack of recruitment due to intensive herbivory, despite continued production of aspen sprouts, and the old cohort of overstory trees contained some of intermediate size (10–20 cm dbh). By 2012 (Painter et al. 2014), some young aspen had grown to be saplings (≥2 m tall and <5 cm dbh), and the remaining trees were all >20 cm dbh. By 2020–21, 49 % of plots contained saplings, and 22 % of plots contained at least one small aspen tree ≥5 cm dbh, representing a new cohort of aspen trees replacing the dying overstory. In 2020–21, two of the stands were dead, but all live stands contained young aspen <2 m.

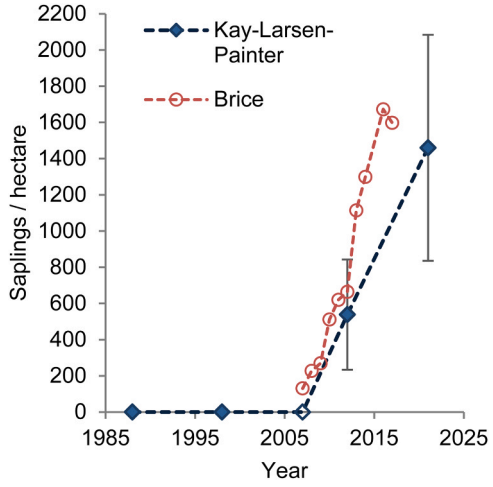

Fig. 5. Average density (stems/ha) of young aspen (≥2 m tall) from four different studies: 1986–89 (Kay, 1985), 1997–98 (Larsen and Ripple, 2005), 2012 (Painter et al. 2014), and 2020–21 (this study), with 95 % confidence intervals. Variance increased as plants were released from suppression. Open diamond marker for 2007 indicates sapling density estimated from plant architecture of the tallest plants (5T sampling) in each stand in 2012. Results from Brice et al. (2021) for 2007–2017 are included for comparison.

Table 4
Number of saplings in random plot versus number of saplings estimated in the entire stand, 2020–21 data. Plots with 8 or more saplings corresponded to stands with a large number of saplings; 26 % of stands had 0 saplings, while 31 % of stands had >50 saplings.

		Number of saplings in entire stand					
Saplings/plot	Plots	0	1–5	6–19	20–49	50–100	>100
8 or more	26	0	0	0	2	5	19
1–7	17	0	2	5	8	1	1
none	44	23	8	3	7	2	1
All plots	87	23	10	8	17	8	21
% All plots	100%	26	11	9	20	9	24

along with the tall ones. Therefore, metrics that were not affected by the number of short plants, such as sapling density (Fig. 5) or the number of saplings in a plot (Fig. 6), were better able to detect patchy sapling recruitment than were mean or median height.

The proportion of young aspen ≥2 m in random plots (*p2m*) was inversely and significantly related to browsing rate, but dispersion was >1 so quasibinomial logistic regression was used ($p<0.001$, $p2m = 0.612 - 0.035194$ **percent browsed*; n=83, df=81, dispersion=12.1). Four plots had no young aspen in the plot to calculate a proportion, resulting in a plot count of 83 instead of 87 for this analysis. Browsing decreased from >90 % of stems browsed annually in 1998 (adjusted to exclude new summer sprouts, Painter et al., 2018) to moderate levels in 2012 and 2020–21, with the greatest decrease in the East sector of the range (Table 2, Fig. 7). Annual browsing rate by plot in 2020–21 averaged 59 % (95 % CI: 53–65; n=85 plots), with a median of 62 %, and varied widely (range 0–100 %). Browsing rate was 30 % or less in 18 stands (21 %).

4. Discussion

4.1. Indications of aspen recovery

Aspen tree recruitment was rare in northern YNP during the latter half of the 20th century, primarily due to intensive herbivory by elk (Kay, 1990, Romme et al., 1995, Larsen and Ripple, 2003, Beschta et al., 2016). By 2005 this was beginning to change, following reductions in elk density influenced by the restoration of wolves, in combination with other predators. Young aspen began to grow taller in many stands (Fig. 3), while aging overstory trees increasingly died and fell to the ground (Beschta and Ripple, 2020). This beginning recovery of aspen stands was patchy, but widespread and ecologically significant (Painter et al., 2015, Peterson et al., 2020, Beschta et al., 2023).

Many stands with new young trees in the northern range have lost most or all of their older trees (Table 1). For example, the stand shown in Fig. 3 has lost almost all of the old cohort of trees, with only standing dead trees visible above the new cohort. Age measurements of existing overstory aspen trees have found that nearly all originated prior to 1940, most decades earlier (Romme et al., 1995, Ripple and Larsen, 2000, Beschta et al., 2016). Surveys of young aspen in the late 1980s and 1990s found none >2 m tall (Kay, 1990, Larsen and Ripple, 2005), with the

Table 3
Density per hectare (ha) of young aspen >2 m height (saplings and young trees), with standard deviation (*s*). Data were collected in 87 random plots in 1997–98 (y1), 2012, and 2020–21 (y3). We calculated effect sizes by two methods: log ratio ($\log_{10}$ and ln) and Cohen's *d* (pooled $s = 2068.3$). All plots in 1997–98 had 0 saplings, therefore 0.5 sapling was added to each plot for log ratio calculations. Thus, the effect ratio likely underestimates the true effect strength.

	1997–98	2012	2020–21	y3/y1	$\log_{10}$(y3/y1)	ln(y3/y1)	Cohen *d*
2 m aspen /ha (*s*)	0 [9.6*] (0)	538 (1429)	1460 (2925)	152.1	**2.18**	**5.02**	**0.71**

* 0.5 sapling added to each plot in 1997–98 for log ratio calculation.

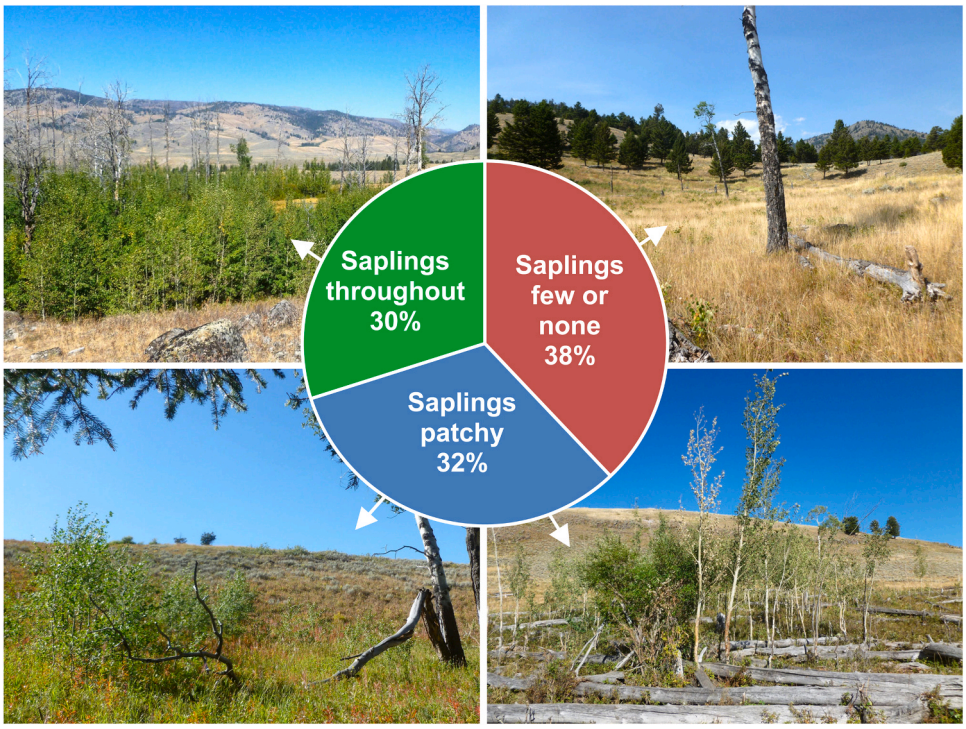

Fig. 6. Photos illustrate aspen recruitment categories, defined by combining random plots with the five tallest young aspen in each stand (5T sampling). Upper left: Saplings or young trees likely throughout much of the stand (indicated by 8 or more >2 m in the random plot). Lower: Saplings or young trees present but patchy (less than 8 in the random plot, but 5 or more in the stand). Upper right: Saplings or young trees few or none (less than 5 in the entire stand).

exception of some protected from ungulates by steep scree slopes, log piles, or fenced exclosures. Thus, aspen trees in the northern range were aging and dying without replacement until the recent growth of new trees.

New small trees were present in 43 % of stands and 22 % of random plots in 2020–21, where none were found in 2012, beginning to replace an overstory in pronounced decline (Fig. 3, Fig. 4). The five tallest young aspen in each stand (5T) averaged nearly 4 m tall and 5 cm dbh (Table 1). Small trees are vulnerable to girdling by herbivores stripping off the bark (DeByle and Winokur, 1985), but as browsing pressure from elk has lessened so has damage to aspen bark (Painter et al., 2023b). Aspen can survive some bark loss, and close proximity to other trees (Fig. 3) can protect against girdling. This new aspen cohort >5 cm dbh marks an important step in the recovery and persistence of aspen stands in northern YNP, a size class of young trees that was generally absent from the mid-1900s until now (Jonas, 1955, Kay, 1990, Barmore, 2003, Larsen and Ripple, 2005).

The dramatic recent changes in northern Yellowstone aspen dynamics are demonstrated by the rapid increase in sapling and young tree density over the last two decades (Fig. 5), resulting in a relatively large effect size indicating a 152-fold increase (Table 3). To replace zero in the ratio denominator, 0.5 saplings were added to each plot in 1997–98. It is likely that in 1997–98 these stands actually had no saplings at all, based on the complete absence of saplings in all plots in 1997–98 (Fig. 5) and the confirmed absence of saplings in 54 % of entire stands in 2012 (Painter et al., 2014). Therefore, the resulting log ratio likely underestimated the actual effect strength, but nevertheless indicated a strong effect compared with other trophic cascade studies (Borer et al., 2005, Alston et al., 2019). Cohen's *d*, which simply relates the amount of change to the standard deviation, also indicated a moderately strong effect (Cohen, 1988, Lakens, 2013). This indicator was reduced by the large increase in variance, which is consistent with a trophic cascade and would be expected as plants respond to a variable decrease in browsing pressure. Data from 1998 and 2012 indicate that the increase in sapling density began between these two times (Fig. 5), consistent with the discovery of new saplings in 2007 (Ripple and Beschta, 2007) and annual measurements of increasing sapling density beginning in 2007 by Brice et al. (2021).

Browsing rates were uniformly high in 1998 with >90 % of stems browsed annually, but decreased to moderate levels in 2012 and 2020–21 with greater variability among stands. Where young aspen were browsed less, the proportion taller than 2 m increased ($p < 0.001$). The high dispersion parameter in this relationship may reflect the fact that the growth of saplings is cumulative over years, while browsing may vary from year to year depending on winter conditions and other changes such as trees falling to the ground and blocking access. Rhodes et al. (2018) found that browsing rates above 30 % of stem leaders annually can impair aspen recruitment, with recruitment failure resulting from rates above 60 %, and this is consistent with what has occurred in Yellowstone (Painter et al., 2015, 2018). In 2020–21, some stands had low browsing rates, but half of stands sampled exceeded 60 %. This variation has resulted in a range of conditions, from stands with widespread growth of new saplings (30 % of stands), to those where young aspen continued to be suppressed (38 %), and many stands in-between with patchy sapling recruitment (32 %) often associated with large woody debris (Fig. 6). With continued high densities of elk in some areas and increasing numbers of bison in others (Painter et al., 2015, Painter et al., 2023b), it is likely that some stands will remain suppressed while others flourish.

4.2. *Browsing measurements and the cause of reduced browsing*

Previous aspen studies varied in how they measured rates of browsing of aspen leaders. For example, Brice et al. (2021), (2024) and MacNulty et al. (2023) included aspen taller than 2 m in their browsing estimates, and because of this, suggested that reductions in browsing could simply have been a function of aspen growing taller above the preferred browsing height of elk, rather than an actual decrease in browsing pressure. As tall saplings have become more common, the potential for height to affect browsing estimates has increased. In our

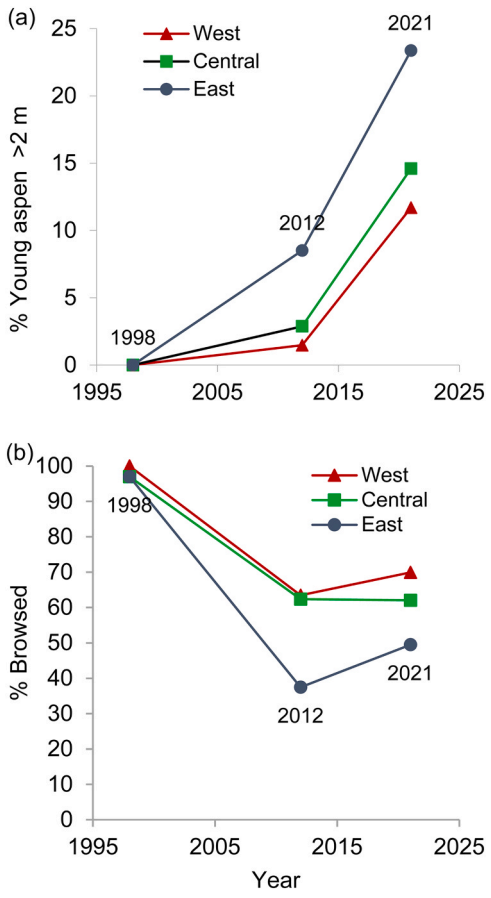

Fig. 7. Results from random sampling plots for the three sectors of the YNP northern range study area, from three sampling periods (see Table 2 for overall mean values). (a) Mean percentage of the new cohort of young aspen ≥2 m tall; and (b) mean percentage of leader stems browsed in the previous year. Increasing height with decreased browsing is consistent with intensive herbivory as the cause of historical aspen suppression. Browsing rates include only aspen shorter than 2 m, to avoid a height bias.

analysis, following Painter et al. (2014), (2015), (2018), we did not include aspen >2 m in browsing estimates and thus avoided this height bias. Browsing normally occurs at the base of current annual growth, and young aspen when measured in summer would typically have a leader 30–50 cm long or more (Painter et al., 2014). Thus, aspen shorter than 2 m would be browsed below 2 m and well within the typical browsing height of elk. In 1997–98, most young aspen on our sites were shorter than 1 m (Larsen and Ripple, 2005, Painter et al., 2014), which, according to Brice et al. (2021), (2024), would be shorter than the preferred browsing height of elk. If browsing were determined by height, these short aspen should have been browsed less than the taller ones that emerged later, but this was not the case. Rather, when elk densities were high in the 1990s they browsed everything available to them, and browsing rates were nearly 100 % (Romme et al., 1995, Painter et al., 2018).

4.3. Increased spatial variation and changes in elk distribution

The relatively large CI for sapling density in 2020–21, and the wide range of browsing intensity in sampling plots, reflect the fact that variability increased as browsing decreased. Increased spatial variation is an expected result of a trophic cascade benefitting aspen, as young aspen before this were almost uniformly suppressed and browsing rates were consistently high (Fig. 7) (Kay, 1990, Romme et al., 1995, Larsen and Ripple, 2005, Painter et al., 2018). As elk density decreased, winter starvation and browsing decreased, but the reduction in browsing was not uniform. Partial barriers such as fallen trees (Fig. 6) became an important factor influencing browsing rates, resulting in less browsing in some locations (Painter et al., 2015, Painter et al., 2023b). Elk distribution also changed, resulting in the lowest elk densities and the greatest reduction in browsing in the East sector of the northern range (Fig. 7).

Changes in elk movements, grouping, vigilance, and foraging behavior in response to wolves are well documented (Mao et al., 2005, Gude et al., 2006, Gower et al., 2009, White et al., 2009, White et al., 2012, Middleton et al., 2013) and these responses could influence the distribution of browsing, and consequently aspen recruitment. Researchers have long observed that aspen recruitment requires relatively low elk densities (e.g., DeByle and Winokur, 1985, White et al., 1998, Painter et al., 2015, 2018) but this does not negate the possible influence of predation risk in a trophic cascade (White et al., 2003, Kuijper et al., 2013, Painter et al., 2015, Beschta et al., 2018). In Yellowstone, elk density greatly decreased at the same time that elk behavior changed in response to wolf reintroduction (Fig. 2), confounding efforts to separately quantify these influences on aspen (e.g., Smith et al., 2023, Brice et al., 2024).

Responses to risk at various scales can influence elk foraging, distribution and local density (Kuijper et al., 2015, Beschta et al., 2018, Smith et al., 2023). At the scale of local terrain, Kohl et al. (2018), (2019) found that elk changed their foraging behavior in response to both wolves and cougars, accessing risky places at less risky times. This "landscape of fear" response would likely result in less time foraging in risky places, adding to the overall effect of reduced elk density. At a landscape scale, Smith et al. (2023) found that elk habitat selection in northern Yellowstone was driven more by predation risk as elk density decreased, and concluded that selection for safety can drive landscape-level shifts in population distribution. If some of the shifts in elk distribution since the reintroduction of wolves were in response to predation risk, changing the density of elk at a landscape scale, what appears to be a simple density-mediated trophic cascade could have a large-scale behavioral component. For example, elk in Banff National Park in Canada changed their movement patterns after wolf reintroduction, toward areas of less predation risk (Hebblewhite and Merrill, 2009, Hebblewhite and Smith, 2010). Similarly, the percentage of northern Yellowstone elk spending winter inside the park boundary decreased markedly after wolf reintroduction (Fig. 2). Elk were affected by greater predation and lower recruitment inside the park, but migration behavior also may have changed (White et al., 2012). On the Yellowstone northern range, 39 % of radio-collared elk cows tracked during 2000–2008 shifted their winter range (White et al., 2010), and if extrapolated to the population this suggests hundreds or even thousands of elk changed their winter range during the time of this study, many to ranges outside the park where the risk of predation was less. While these movements may have been influenced by the end of the Gardiner winter late hunt and the availability of irrigated hay fields north of the park (Haggerty and Travis, 2006, Proffitt et al., 2009, White et al., 2012, Wilmers and Levi, 2013), it is likely that behavioral responses to predation risk at various scales have played a role in the distribution and foraging of elk, resulting in more browsing in some places and less in others.

4.4. Other factors affecting aspen

In the long term, reduced herbivory may combine with fire to facilitate wider coverage of aspen as in the early days of the park (Romme et al., 1995, Wagner, 2006). However, this opportunity may be countered by increased stress on aspen associated with a warmer and drier climate and continued high rates of browsing in some stands. Successional encroachment by coniferous trees was generally low as indicated by estimates of cover and tree density, but strongly affected some stands, and this will likely increase unless changed by fire.

Aspen recovery in the west portion of the Yellowstone northern range has lagged behind other areas, particularly near Mammoth Hot Springs where elk were present year-round (Beschta et al., 2018), yet even there in the West sector saplings have become more common (Fig. 7). The East sector of the range (Fig. 7) saw the greatest reduction in elk density and greatest growth of tall saplings (Painter et al., 2015), but this sector has been strongly affected by an increasing bison herd (Painter and Ripple, 2012, Beschta et al., 2020, Kauffman et al., 2023, Painter et al., 2023b). The effects of bison on aspen demonstrate the principle that ecosystem complexity, in this case the increasing presence of another browser, can alter and weaken a trophic cascade (Terborgh and Estes, 2010). These effects have strengthened and spread as bison numbers in northern Yellowstone since 2015 have been about four times what they were before 2005 (Painter et al., 2023b), and the park plans to maintain similarly high numbers in the future (National Park Service, 2024). Where they congregate in summer, bison have prevented recruitment in some stands, and in others have broken down saplings that grew before the recent increase of these large herbivores (Painter et al., 2023b).

4.5. Conclusions

Results of this aspen study in northern Yellowstone support several important conclusions, when viewed within the broader historical and ecological context, including the recent role of large carnivores and their effects on the elk population:

- After decades during which aspen recruitment was suppressed by intensive elk herbivory, sapling density and the number of stands with saplings increased steadily during the first two decades of the 21st century. This aspen recovery trend began despite possible adverse effects of a warmer and drier climate (Painter et al., 2014, 2018, Beschta et al., 2016).
- In 2021, nearly half of aspen stands (43 %) had a new cohort of young trees >5 cm dbh. These new trees represent the first substantial recruitment of aspen trees in the northern range since the 1940s (Romme et al., 1995, Beschta et al., 2016).
- New aspen recruitment has been driven mainly by reductions in herbivory, with a relatively large effect size, evidence of a trophic cascade following the restoration of large carnivores. Increased predation has caused a sustained reduction of elk numbers within the park, as well as changes in elk distribution, resulting in less browsing. Restoration of these processes has allowed aspen to begin to recover.
- Herbivory from both elk and bison (Painter et al., 2015, Painter et al., 2023b) has continued to suppress young aspen in some portions of the northern range, increasing the variability of new aspen recruitment. For example, 26 % of stands had no saplings, a condition that was associated with high rates of browsing.

Many aspen stands in northern Yellowstone now have historically and ecologically significant amounts of new tall saplings as the result of trophic cascades, and these have been growing into new overstory trees. While a return to more extensive aspen stands will take time, and future conditions may not fully replicate the past, these new trees will help to ensure that aspen will persist into the future as a cornerstone of biodiversity in the northern Yellowstone landscape, and an example of widespread ecological change resulting from large carnivore restoration.

CRediT authorship contribution statement

Robert L. Beschta: Writing – review & editing, Resources, Methodology, Funding acquisition, Conceptualization. **William J. Ripple:** Writing – review & editing, Methodology, Conceptualization. **Luke E. Painter:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122941.

Data availability

Data supporting this study are provided as a supplementary file, Table S1.

References

Alston, J.M., Maitland, B.M., Brito, B.T., Esmaeili, S., Ford, A.T., Hays, B., Jesmer, B.R., Molina, F.J., Goheen, J.R., 2019. Reciprocity in restoration ecology: when might large carnivore reintroduction restore ecosystems? Biol. Conserv. 234, 82–89.

Barber-Meyer, S.M., Mech, L.D., White, P.J., 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildl. Monogr. 169, 1–30.

Barmore, W.J. 2003. Ecology of Ungulates and their Winter Range in Northern Yellowstone National Park; Research and Synthesis 1962-1970. Yellowstone Center for Resources, Yellowstone National Park.

Bartos, D.L., Campbell Jr., R.B., 1998. Decline of quaking aspen in the Interior West - examples from Utah. Rangelands 20, 17–24.

Bartos, D.L., W.F. Mueggler, and R.B. Campbell, Jr. 1991. Regeneration of Aspen by Suckering on Burned Sites in Western Wyoming, Research Paper INT-448. USDA Forest Service, Intermountain Research Station, Ogden. ⟨https://www.fs.usda.gov/research/treesearch/36690⟩.

Beschta, R.L., Painter, L.E., Ripple, W.J., 2018. Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone. For. Ecol. Manag. 413, 62–69.

Beschta, R.L., Painter, L.E., Ripple, W.J., 2023. Revisiting trophic cascades and aspen recovery in northern Yellowstone. Food Webs 36, e00276.

Beschta, R.L., Painter, L.E., Levi, T., Ripple, W.J., 2016. Long-term aspen dynamics, trophic cascades, and climate in northern Yellowstone. Can. J. For. Res. 46, 548–556.

Beschta, R.L., Ripple, W.J., Kauffman, J.B., Painter, L.E., 2020. Bison limit ecosystem recovery in northern Yellowstone. Food Webs 23, e00142.

Beschta, R.L., Ripple, W.J., 2007. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. Can. J. For. Res. 37, 1873–1885.

Beschta, R.L., Ripple, W.J., 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. Biol. Conserv. 198, 93–103.

Beschta, R.L., Ripple, W.J., 2020. Large carnivore extirpation linked to loss of overstory aspen in Yellowstone. Food Webs 22, e00140.

Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D., 2005. What determines the strength of a trophic cascade? Ecology 86, 528–537. https://doi.org/10.1890/03-0816.

Brice, E.M., E.J. Larsen, and D.R. MacNulty. 2021. Sampling bias exaggerates a textbook example of a trophic cascade. Ecology Letters dx.doi.org/10.1111/ele.13915.

Brice, E.M., Larsen, E.J., Stahler, D.R., MacNulty, D.R., 2024. The primacy of density-mediated indirect effects in a community of wolves, elk, and aspen. Ecol. Monogr. 2024, e1627.

Cassidy, K.A., D.W. Smith, D.R. Stahler, E. Stahler, M. Metz, J. SunderRaj, T. Rabe, W. Binder, M. Jackson, M. Packila, B. Cassidy, J. Rabe, N. Tatton, C. Meyer, A. Bott, C. Ho, C. Lacey, and D. Sanborn. 2023. Yellowstone National Park Wolf Project Annual Report 2022. YCR-2023-04. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Cohen, J. 1988. Statistical Power Analysis for the Behavioral Sciences. Routledge Academic, New York.

DeByle, N.V., and R.P. Winokur, editors. 1985. Aspen: Ecology and Management in the Western United States. General Technical Report RM-119. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins.

Eberhardt, L.L., White, P.J., Garrott, R.A., Houston, D.B., 2007. A seventy-year history of trends in Yellowstone's northern elk herd. J. Wildl. Manag. 71, 594–602.
Gower, C.N., Garrott, R.A., White, P.J., Watson, F.G.R., Cornish, S.S., Becker, M.S., 2009. Spatial responses of elk to wolf predation risk: using the landscape to balance multiple demands. In: Garrott, R.A., White, P.J., Watson, F.G.R. (Eds.), The Ecology of Large Mammals in Central Yellowstone. Elsevier, Boston, pp. 373–399.
Gude, J.A., Garrott, R.A., Borkowski, J.J., King, F., 2006. Prey risk allocation in a grazing ecosystem. Ecol. Appl. 16, 285–298.
Haggerty, J.H., Travis, W.R., 2006. Out of administrative control: absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. Geoforum 37, 816–830.
Hamlin, K.L., and J.A. Cunningham. 2009. Monitoring and assessment of wolf-ungulate interactions and population trends within the Greater Yellowstone Area, southwestern Montana, and Montana statewide: Final Report. Montana Dept. of Fish, Wildlife, and Parks, Wildlife Division, Helena. ⟨http://fwpiis.mt.gov/content/getItem.aspx?id=36743⟩.
Hebblewhite, M., Merrill, E.H., 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90, 3445–3454.
Hebblewhite, M., Smith, D.W., 2010. Wolf community ecology: ecosystem effects of recovering wolves in Banff and Yellowstone National Parks. In: Boitani, L., Musiani, M. (Eds.), The World of Wolves: New Perspectives on Ecology, Behaviour and Management. University of Calgary Press, pp. 69–120.
Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005b. Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135–2144.
Hobbs, N.T., Johnston, D.B., Marshall, K.N., Wolf, E.C., Cooper, D.J., 2024. Does restoring apex predators to food webs restore ecosystems? Large carnivores in Yellowstone as a model system. Ecol. Monogr. 2024, e1598.
Houston, D.B. 1982. The Northern Yellowstone Elk: Ecology and Management. Macmillan, New York, New York.
Jonas, R.J. 1955. A population and ecological study of the beaver (Castor canadensis) of Yellowstone National Park. M.S. thesis. University of Idaho.
Jung, K., Lee, J., Gupta, V., Cho, G., 2019. Comparison of bootstrap confidence interval methods for GSCA Using a Monte Carlo Simulation. Front. Psychol. 10, 2215.
Kauffman, J.B., Cummings, D.L., Kauffman, C., Beschta, R.L., Brooks, J., MacNeill, K., Ripple, W.J., 2023. Bison influences on composition and diversity of riparian plant communities in Yellowstone National Park. Ecosphere 14, e4406.
Kay, C.E., 1985. Aspen reproduction in the Yellowstone Park-Jackson Hole area and its relationship to the natural regulation of ungulates. In: Workman, G.W. (Ed.), Western Elk Management: A Symposium. Utah State University, Logan, pp. 131–160.
Kay, C.E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. PhD dissertation. Utah State University, Logan.
Keigley, R.B., and M.R. Frisina. 1998. Browse evaluation by analysis of growth form. Montana Fish, Wildlife and Parks, Helena.
Kimble, D.S., Tyers, D.B., Robison-Cox, J., Sowell, B.F., 2011. Aspen recovery since wolf reintroduction on the northern Yellowstone winter range. Rangel. Ecol. Manag. 64, 119–130.
Kohl, M.T., Ruth, T.K., Metz, M.C., Stahler, D.R., Smith, D.W., White, P.J., MacNulty, D. R., 2019. Do prey select for vacant hunting domains to minimize a multi-predator threat? Ecol. Lett. 22, 1724–1733.
Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White, P. J., Smith, D.W., MacNulty, D.R., 2018. Diel predator activity drives a dynamic landscape of fear. Ecol. Monogr. 88, 638–652.
Kota, A.M., Bartos, D.L., 2010. Evaluation of techniques to protect aspen suckers from ungulate browsing in the Black Hills. West. J. Appl. For. 25, 161–168.
Kuijper, D.P.J., J.W. Bubnicki, M. Churski, B. Mols, and P. van Hooft. 2015. Context dependence of risk effects: wolves and tree logs create patches of fear in an old-growth forest. Behavioral Ecology dx.doi.org/10.1093/beheco/arv107.
Kuijper, D.P.J., C. de Kleine, M. Churski, P. van Hooft, J. Bubnicki, and B. Jędrzejewska. 2013. Landscape of fear in Europe: wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. Ecography dx.doi.org/10.1111/j.1600-0587.2013.00266.x.
Lakens, D., 2013. Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for t-tests and ANOVAs. Front. Psychol. 4, 863.
Larsen, E.J., Ripple, W.J., 2003. Aspen age structure in the northern Yellowstone ecosystem: USA. For. Ecol. Manag. 179, 469–482.
Larsen, E.J., Ripple, W.J., 2005. Aspen stand conditions on elk winter ranges in the northern Yellowstone ecosystem, USA. Nat. Areas J. 25, 326–338.
MacNulty, D.R., E.M. Brice, and E.J. Larsen. 2023. Non-random sampling measures the occurrence but not the strength of a textbook trophic cascade. Ecology Letters dx.doi.org/10.1111/ele.14344.
Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M., Merrill, E.H., 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. J. Wildl. Manag. 69, 1691–1707.
Marcus, W.A., J.E. Meacham, A.W. Rodman, A.Y. Steingisser, and J.T. Menke 2022. Atlas of Yellowstone: Second Edition. University of California Press, Oakland, California.
Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Jimenez, M.D., Cook, R.C., Cook, J. G., Albeke, S.E., Sawyer, H., White, P.J., 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. Ecol. Lett. 16, 1023–1030.
National Park Service. 2024. Record of Decision: Bison Management Plan. US Department of the Interior, Yellowstone National Park.
NRC (National Research Council). 2002. Ecological Dynamics on Yellowstone's Northern Range. National Academies Press, Washington, DC.
Painter, L.E., Beschta, R.L., Ripple, W.J., 2023a. Aspen recovery in northern Yellowstone: a comment on Brice et al. (2021). Ecol. Lett. 36, e00276.
Painter, L.E., Beschta, R.L., Ripple, W.J., 2023b. Bison alter the northern Yellowstone ecosystem by breaking aspen saplings. Ecol. Evol. 13, e10369.
Painter, L.E., Beschta, R.L., Larsen, E.J., Ripple, W.J., 2014. After long-term decline, are aspen recovering in northern Yellowstone? For. Ecol. Manag. 329, 108–117.
Painter, L.E., Beschta, R.L., Larsen, E.J., Ripple, W.J., 2015. Recovering aspen follow changing elk dynamics in Yellowstone: evidence of a trophic cascade? Ecology 96, 252–263.
Painter, L.E., Beschta, R.L., Larsen, E.J., Ripple, W.J., 2018. Aspen recruitment in the Yellowstone region linked to reduced herbivory after large carnivore restoration. Ecosphere 9, e02376.
Painter, L.E., Ripple, W.J., 2012. Effects of bison on willow and cottonwood in northern Yellowstone National Park. For. Ecol. Manag. 264, 150–158.
Peterson, R.O., Beschta, R.L., Cooper, D.J., Hobbs, N.T., Johnston, D.B., Larsen, E.J., Marshall, K.N., Painter, L.E., Ripple, W.J., Rose, J.R., Smith, D.W., Wolf, E.C., 2020. Indirect effects of carnivore restoration on vegetation. In: Smith, D.W., Stahler, D., MacNulty, D.R. (Eds.), Yellowstone Wolves. University of Chicago Press, Chicago, pp. 205–222.
Peterson, E.B., and N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie provinces, Canada. Special Report No. 1. Natural Resources Canada, Forestry Canada, Edmonton. ⟨https://publications.gc.ca/site/eng/9.808235/publication.html⟩.
Proffitt, K.M., Grigg, J.L., Hamlin, K.L., Garrott, R.A., 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. J. Wildl. Manag. 73, 345–356.
R Core Team . 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨http://www.R-project.org⟩.
Refsland, T.K., and J.H. Cushman. 2021. Continent-wide synthesis of the long-term population dynamics of quaking aspen in the face of accelerating human impacts. Oecologia dx.doi.org/10.1007/s00442-021-05013-7.
Rhodes, A.C., Larsen, R.T., St. Clair, S.B., 2018. Differential effects of cattle, mule deer, and elk herbivory on aspen forest regeneration and recruitment. For. Ecol. Manag. 422, 273–280.
Ripple, W.J., Beschta, R.L., Painter, L.E., 2022. The history of cougars in Yellowstone National Park. West. North Am. Nat. 82, 752–759.
Ripple, W.J., Beschta, R.L., 2007. Restoring Yellowstone's aspen with wolves. Biol. Conserv. 138, 514–519.
Ripple, W.J., Beschta, R.L., 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biol. Conserv. 145, 205–213.
Ripple, W.J., R.L. Beschta, C. Wolf, L.E. Painter, and A.J. Wirsing. 2025. The strength of the Yellowstone trophic cascade after wolf reintroduction. Global Ecology and Conservation dx.doi.org/10.1016/j.gecco.2025.e03428.
Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biol. Conserv. 95, 361–370.
Rogers, P.C., Mittanck, C.M., 2014. Herbivory strains resilience in drought-prone aspen landscapes of the western United States. J. Veg. Sci. 25, 457–469.
Romme, W.H., Turner, M.G., Wallace, L.L., Walker, J.S., 1995. Aspen, elk, and fire in northern Yellowstone Park. Ecology 76, 2097–2106.
Runyon, M.J., Tyers, D.B., Sowell, B.F., Gower, C.N., 2014. Aspen restoration using beaver on the northern Yellowstone winter range under reduced ungulate herbivory. Restor. Ecol. 22, 555–561.
Singer, F.J., Harting, A., Symonds, K.K., Coughenour, M.B., 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. J. Wildl. Manag. 61, 12–25.
Smith, D.S., Fettig, S.M., Bowker, M.A., 2016. Elevated Rocky Mountain elk numbers prevent positive effects of fire on quaking aspen (*Populus tremuloides*) recruitment. For. Ecol. Manag. 362, 46–54.
Smith, B.J., MacNulty, D.R., Stahler, D.R., Smith, D.W., Avgar, T., 2023. Density-dependent habitat selection alters drivers of population distribution in northern Yellowstone elk. Ecol. Lett. 26, 245–256.
St. John, R.A. 1995. Aspen stand recruitment and ungulate impacts: Gardiner Ranger District, Gardiner, Montana. M.S. Thesis. University of Montana, Missoula.
Stahler, D.R., and C.B. Anton. 2015. Yellowstone Cougar Project Annual Report 2015. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.
Telfer, E.S., Cairns, A., 1978. Stem breakage by moose. J. Wildl. Manag. 42, 639–642.
Terborgh, J., and J.A. Estes, editors. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press.
Wagner, F.H. 2006. Yellowstone's Destabilized Ecosystem: Elk Effects, Science, and Policy Conflict. Oxford University Press, New York.
White, C.A., Feller, M.C., Bayley, S., 2003. Predation risk and the functional response of elk-aspen herbivory. For. Ecol. Manag. 181, 77–97.
White, P.J., Garrott, R.A., Cherry, S., Watson, F.G.R., Gower, C.N., Becker, M.S., Meredith, E., 2009. Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. In: Garrott, R.A., White, P.J., Watson, F.G.R.

(Eds.), The Ecology of Large Mammals in Central Yellowstone. Elsevier, Boston, pp. 451–476.
White, P.J., Garrott, R.A., 2005a. Northern Yellowstone elk after wolf restoration. Wildl. Soc. Bull. 33, 942–955.
White, P.J., Garrott, R.A., 2005b. Yellowstone's ungulates after wolves – expectations, realizations, and predictions. Biol. Conserv. 125, 141–152.
White, C.A., Olmsted, C.E., Kay, C.E., 1998. Aspen, elk, and fire in the Rocky Mountain national parks of North America. Wildl. Soc. Bull. 26, 449–462.
White, P.J., Proffitt, K.M., Lemke, T.O., 2012. Changes in elk distribution and group sizes after wolf restoration. Am. Midl. Nat. 167, 174–187.
White, P.J., Proffitt, K.M., Mech, L.D., Evans, S.B., Cunningham, J.A., Hamlin, K.L., 2010. Migration of northern Yellowstone elk: implications of spatial structuring. J. Mammal. 91, 827–837.
Wilmers, C.C., Levi, T., 2013. Do irrigation and predator control reduce the productivity of migratory ungulate herds? Ecology 94, 1264–1270.