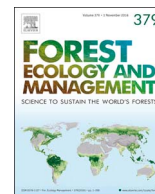Exhibit K

Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone

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ABSTRACT

Throughout much of the 20th century, the heights of young quaking aspen (*Populus tremuloides*) in Yellowstone National Park's northern ungulate winter range were suppressed due to intensive herbivory by Rocky Mountain elk (*Cervus elaphus*). However, following the 1995–96 reintroduction of gray wolves (*Canis lupus*), completing the park's large predator guild, young aspen in various portions of the northern range began to increase in height. From 1999 to 2015, a 17-yr period of declining elk densities in the northern range, browsing rates declined and young aspen heights increased once elk densities dropped below ~4 elk/km². The inverse relationship between browsing rate and young aspen height, a relationship linking elk and plants, was consistent with a re-established trophic cascade. Within the Glen Creek study area (8.3 km²), decreased browsing and increased heights of young aspen were associated, at least in part, with two hypothesized small-scale predation risk factors (i.e., *escape impediment*, *view impediment*). However, the young aspen height increases did not occur in the Mammoth study area (6.0 km²) and heights there remained short. With high levels of human activity at the Mammoth townsite, wolf activity near the townsite remained low, an example of "human shielding," thereby allowing elk browsing to continue the suppression of young aspen. Overall, results indicated that Yellowstone's contemporary large predator guild, by altering elk behavior and density at several spatial scales, has not only contributed to a relatively widespread pattern of increased young aspen heights across much of the park's northern range, but also greater spatial variation in those heights.

1. Introduction

Over a half-century ago, Hairston et al. (1960) proposed that carnivores regulate the effects of herbivores (consumers) and therefore globally maintain a high biomass of plants (producers). Such trophic cascades have since been identified in various aquatic and terrestrial ecosystems (Schmitz et al., 2000; Terborgh and Estes, 2010; Estes et al., 2011). However, assessments of top-down trophic effects of large mammalian predators in terrestrial ecosystems have been relatively uncommon (Shurin et al., 2002; Ripple et al., 2014), perhaps because both predators and prey are wide-ranging and their direct and indirect effects upon plant communities may vary across large temporal and spatial scales. Large-scale assessments of potential top-down effects upon vegetation can be further complicated because the distribution and productivity of plant communities may be influenced by various bottom-up factors, such as terrain and site conditions (e.g., elevation, slope and aspect, soil fertility and moisture), disturbance regimes (e.g., climatic patterns, fire, floods), and land uses (e.g., livestock grazing, timber harvesting).

With the exception of humans, gray wolves (*Canis lupus*) represent perhaps the most significant ungulate predator in the northern hemisphere, primarily due to group hunting, year-round activity, and widespread geographic distribution (Peterson et al., 2014). Wolves, normally in conjunction with other large carnivores, may limit a prey population *via* predation, thereby indirectly influencing herbivory on plants – a density mediated trophic cascade (DMTC). In addition, predation risk associated with this apex predator may influence prey behavior which, in turn, can also influence herbivory – a behaviorally mediated trophic cascade (BMTC) (Laundré et al., 2001; Schmitz et al., 2004; Kuijper et al., 2014). Foraging theory suggests that prey species will behaviorally adjust to predators by altering vigilance, foraging time at given location, or habitat use in a landscape, and that prey "ignore the behavioral game at one's peril" (Brown et al., 1999). DMTCs and BMTCs often occur concurrently, thus making it difficult to quantitatively separate the relative importance of each.

Predators in Yellowstone National Park (YNP) were widely persecuted during the late 1800s and early 1900s, a time when wild ungulates were increasingly protected (YNP, 1997). By the mid-1920s,

bear populations were greatly reduced, cougar (*Puma concolor*) largely gone, and wolves extirpated. Vegetation studies within the park's northern ungulate winter range, or "northern range," soon found that intensive browsing by Rocky Mountain elk (*Cervus elaphus*) was suppressing the heights of quaking aspen (*Populus tremuloides*) sprouts, as well as young plants of other deciduous woody species (Grimm, 1939; Jonas, 1955; Kay, 1990; Barmore, 2003). Aspen recruitment (i.e., growth of young aspen above the upper browse height of elk, ~ 200 cm) began to decrease in the early 1900s and the decline in recruitment became increasingly severe during the seven decades of wolf absence (Larsen and Ripple, 2003). Cottonwoods (*Populus* spp.) and willows (*Salix* spp.) also experienced declining levels of recruitment during these same decades (Beschta, 2005; Wolf et al., 2007).

By the end of the 20th century, the structure and composition of deciduous woody plant communities in the northern range were vastly different from that occurring at the beginning of the century. For example, aspen stands in the late 1900s typically consisted of relatively few overstory trees with an absence of intermediate ages and sizes. Browsing rates of young aspen were nearly 90% annually and, as a result, plant heights averaged < 50 cm (Ripple et al., 2001; Larsen and Ripple, 2003; Peterson et al., 2014). The long-term height suppression of young aspen due to intensive elk browsing raised concerns about the capability of aspen stands in northern Yellowstone to persist as older trees died without replacement (Brown et al., 2006). Declining recruitment of aspen and various deciduous woody species in other ecosystems of the western United States and Canada has been a common result of increased ungulate herbivory after large predators were displaced or extirpated (Hess, 1993; White et al., 1998; Binkley et al., 2006; Beschta and Ripple, 2007, 2009).

Wolves were reintroduced into YNP during the mid-1990s, joining recovering bear and cougar populations, thus completing the park's large predator guild. Since reintroduction of this apex predator, the northern range elk population has decreased due to predation by wolves and other large carnivores, high hunting harvests (prior to 2006) of elk that seasonally left the park, and possibly some effects of relatively dry summers (Vucetich et al., 2005; White et al., 2012; Wilmers and Levi, 2013). Changes in elk behavior also were observed in northern Yellowstone following the return of wolves, consistent with re-establishment of a landscape of fear (Laundré et al., 2001; Fortin et al., 2005b; Hernandez and Laundre, 2005; Gower et al., 2009; Laundré et al., 2014). For example, elk vigilance was significantly higher within 30 m of escape impediments than occurred farther away from these features (Halofsky and Ripple, 2008). In other studies, predation risk was found to alter habitat use by elk (Creel et al., 2005), including displacement to new areas, as a response to wolves as well as human hunters (Gower et al., 2009; Proffitt et al., 2009; Cleveland et al., 2012).

In the two decades following wolf reintroduction, young aspen in some stands began to increase in height (Fig. 1a), as browsing levels decreased across the northern range (Painter et al., 2014, 2015; Klaptosky, 2016). Although the magnitude, timing, and spatial extent of these height increases have varied, they suggest that a trophic cascade, following wolf reintroduction, is currently underway (Schmitz et al., 1997; Painter et al., 2015; Beschta and Ripple, 2016). To the extent that the decline in elk numbers over the last two decades has been associated with recovering predator populations, increased young aspen heights would appear to represent direct evidence of a DMTC, whereas the potential importance of a BMTC has remained largely speculative.

The variable height increases of young aspen currently unfolding across the northern range (Painter et al., 2014, 2015) provided an important opportunity to assess the possible effects of elk density and behavior on young aspen dynamics at several spatial scales. In this study we assessed young aspen browsing rates and heights in the northern range at three spatial scales, identified herein as large, medium, and small. For our "large scale" comparison, we examined changes in young aspen browsing rates and plant heights relative to declining elk densities for two widely separated sectors in the northern

range. Our purpose was to evaluate the potential occurrence of a DMTC whereby reduced elk densities might produce a decrease in browsing rates and an increase in young aspen heights. At a "medium scale," we evaluated browsing history and plant heights for two adjacent study areas within the same sector. In one of these study areas there was a high level of human presence that limited predator activity, providing "human shielding" of ungulate prey from predators (Hebblewhite et al., 2005; Berger, 2007), and potentially keeping young aspen heights suppressed due to high rates of herbivory. This human shielding hypothesis (BMTC) represented a reduction in predation risk at a medium scale. Lastly, we evaluated "small-scale" risk factors (e.g., viewshed limitations, impediments to escape) within aspen stands for assessing their potential to affect browsing levels and young aspen heights, relative to stands where such factors were absent. A significant decrease in browsing or increase in height associated with a risk factor would be consistent with the occurrence of a small-scale BMTC.

2. Methods

2.1. Northern range

Yellowstone's northern range comprises 1500 km^2 of mountainous terrain of which approximately two-thirds occurs within the park (Fig. 1b). Gray wolves, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and cougar comprise the northern range's large predator guild. Although wolves prey on young and adult elk throughout the year, bears prey mainly on young elk calves in spring, killing more calves than wolves, cougars, and coyotes (*C. latrans*) combined (Barber-Meyer et al., 2008). The northern range provides wintering habitat for elk as well as smaller populations of mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and moose (*Alces alces*) (NRC, 2002). Bison (*Bison bison*) populations have increased in the last two decades and these large herbivores are particularly common along major valley bottoms (e.g., Lamar Valley). Sagebrush (*Artemisia* spp.)-steppe is the predominant vegetation type, transitioning into coniferous forests at higher elevations. Although aspen stands occupy < 2% of the Greater Yellowstone Ecosystem (Brown et al., 2006), they occur on relatively moist sites in both upland and riparian settings across the northern range and normally support a diversity of understory species.

2.2. Aspen measurements

By the 1990s, a large and visually distinct gap in size between young aspen (< 200 cm in height) and overstory trees (typically > 20 cm in diameter at breast height) was characteristic of aspen stands across the northern range due to the historical suppression of young plants by elk (Larsen and Ripple, 2005; Ripple and Beschta, 2007; Painter et al., 2014). Although intensive elk browsing continued to generally suppress the heights of young aspen in the early years following wolf re-introduction, by 2013 the average height of these plants exceeded 100 cm for the first time in many decades (Peterson et al., 2014).

Within each aspen stand sampled during this study, we used browsing and height measurements of the five-tallest young aspen to index any change in plant community dynamics (Ripple and Beschta, 2012). We used the five-tallest because they (1) could be consistently identified in an aspen stand, given the history of long-term height suppression, (2) likely denoted the first young aspen in a given stand to experience a reduction in browsing pressure, which we could identify over the life of each plant *via* measurements of plant architecture, and (3) represented a "leading edge" indication of a broader shift in plant community dynamics for northern range aspen stands. For example, the heights of the five-tallest have been found to be positively correlated with the heights of *all* young aspen in northern range aspen stands (r^2 = 0.59, *p* < 0.001) (Painter et al., 2014). To be included in this study, an aspen stand had to have one or more live overstory trees that were > 30 m from those in any adjacent stand.
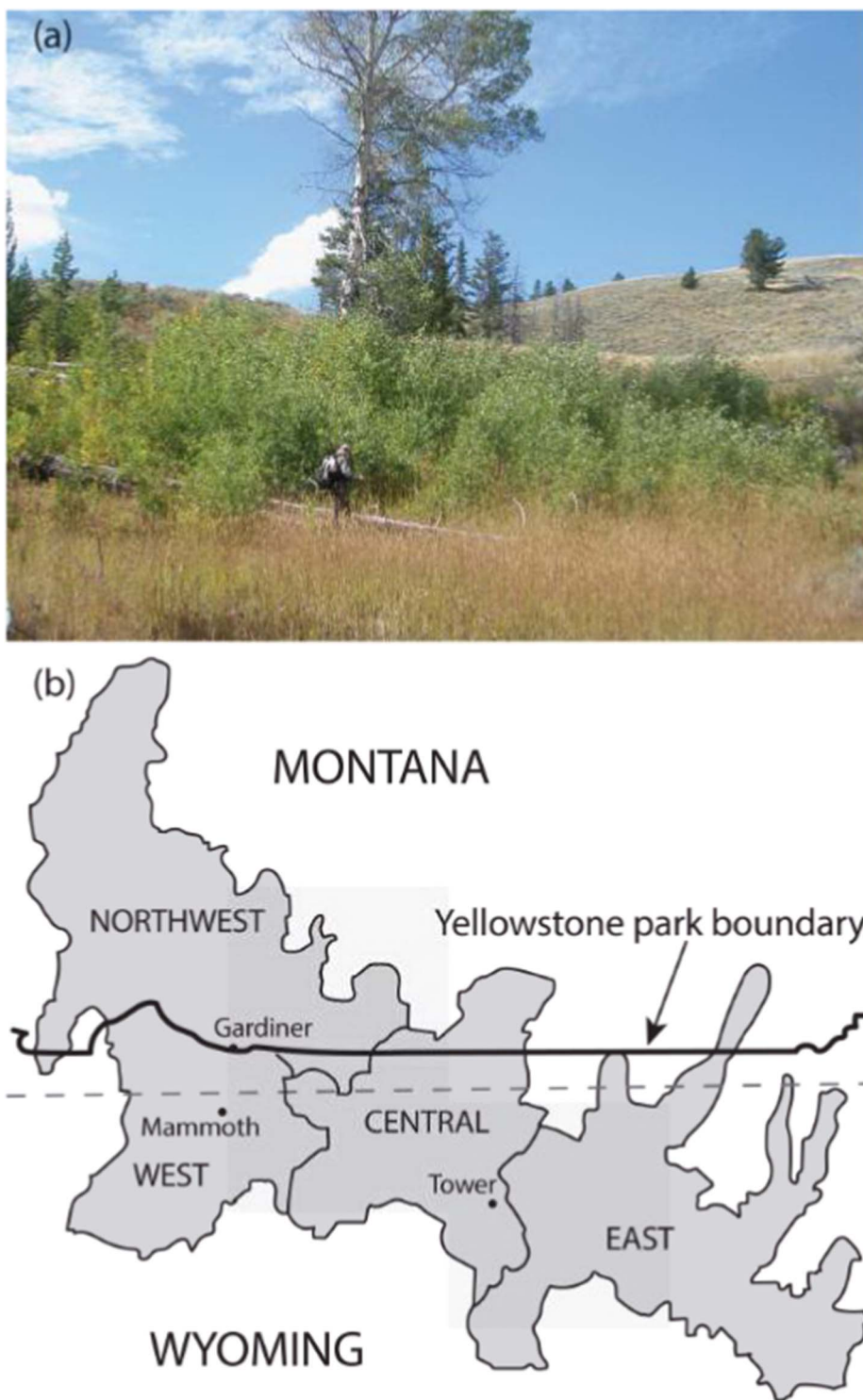
Fig. 1. (a) An example of historical decline and more recent increase in recruitment for an aspen stand in the Glen Creek study area, West Sector of the northern range. Decades of intensive elk herbivory have resulted in a single remaining overstory tree, as well as an absence of intermediate age/diameter classes. The young aspen that surround the overstory tree have developed due to a reduction in herbivory in recent years and many now surpass a height of 200 cm (thus exceeding the upper browse level of elk). (b) Map of northern range sectors along the northern boundary of Yellowstone National Park. Sources: (a): RL Beschta, September 2015, (b) adapted from Painter et al. (2015).

Young aspen normally grow vertically along a single primary stem, or leader, with a terminal bud scar marking the location where growth begins each year. If this main stem is browsed, a new leader develops the next growing season from a secondary bud along the main stem, with its location indicated by a bud scar and bend in the main stem (Keigley and Frisina, 1998). Using these indicators, we recorded plant height (cm) and browsing occurrence (browsed or unbrowsed), by year,

along the main stem of each sampled aspen. From these data we calculated two indicators of browsing intensity: (1) annual browsing rate as the percentage of young aspen browsed in a given year; and (2) browsing history (%) over the life of each plant:

$$\text{browsing history (\%)} = \left(\frac{number\ of\ years\ browsed}{total\ age\ of\ plant\ (yrs)} \right) \times 100$$

All sampled young aspen in this study were accessible to ungulates as indicated by the occurrence of browsing for one or more years along their main stems.

2.3. Analysis

2.3.1. Large spatial scale

We indexed the potential top-down effectiveness of wolves in the northern range by calculating an annual predator/prey ratio (# wolves/1000 elk) from northern range counts of wolves and elk (Yellowstone Center for Resources, YNP, Mammoth). Annual elk counts represented minimum estimates as some are missed in the aerial counts (Eberhardt et al., 2007).

We characterized temporal trends in elk densities (elk/km^2) from the annual counts, over the period 1999–2015 for the West Sector (250 km^2) and East Sector (470 km^2) of the northern range using linear regression; these sectors are located ~45 km apart on opposite ends of the range (Fig. 1b). In the West Sector, we graphically summarized annual browsing rates (%) and young aspen heights (cm) over time for aspen stands from the Glen Creek study area (described below). We similarly summarized annual browsing rates and young aspen heights for upland stands in the East Sector, using data from a previously published study (Ripple and Beschta, 2007, 2012); aspen stands sampled in that study occurred largely in the vicinity of the Lamar Valley. In both sectors, annual browsing rates were calculated only for those young aspen whose heights were within the normal browse zone for elk (i.e., < 200 cm tall). We used these concurrent data sets of annual elk density, browsing rate, and young aspen height over time for each sector to assess temporal patterns in browsing rates and young aspen heights relative to changes in elk densities.

2.3.2. Medium spatial scale

Within the West Sector of the northern range, we utilized two study areas located ~4 km apart: Glen Creek and Mammoth. We examined a summary of mapped GPS locations (2001–12 data) of radio-collared wolves to assess their general use of habitat within the two study areas (Yellowstone Center for Resources, YNP). Comparable elk collar data for elk were not available for evaluating habitat use across study areas.

The Glen Creek study area comprised 8.3 km^2 of Glen Creek catchment largely between Highway 29 and the Glen Creek-Gardiner River pack trail. The Mammoth study area was initially defined as the area within a 1.5 km radius from the park's visitor center, but excluding those portions comprising Mammoth townsite since it included human developments (e.g., buildings, streets). Because these developments extended farther to the south from the visitor center than in other directions, we expanded our search area an additional 0.5 km to the south. This provided a study area of 6.0 km^2, exclusive of the townsite or hot springs.

The winter closure of Highway 29 each year excludes nearly all human use in the Glen Creek study area during that season; summer use is generally limited to hikers and horse packers along a few trails as well as vehicular traffic along the eastern border of the study area (Highway 29). In the Mammoth study area, the townsite and adjacent hot springs often experience several thousands of park visitors on a daily basis during the summer months. Even during the winter months, several hundred visitors per day, or more, visit Mammoth (National Park Service visitation data for 2012–16). We considered these two study areas to represent a medium spatial scale, since each was large enough to include a variety of terrain conditions, numerous aspen stands, and both wolves and elk could move easily between the two areas.

We randomly selected 60 aspen stands within the Glen Creek study area whereas we utilized all aspen stands encountered within the Mammoth study, a total of 38 stands. Plant measurements occurred during September 2015 in Glen Creek and September 2016 in Mammoth. Within each study area, we calculated an average browsing history (%), height (cm), and age (yr), based on our plant architecture

measurements of the five-tallest young aspen in each stand. We used t-tests for identifying any significant differences ($p < 0.05$) in these averages between the two study areas. All sampled aspen stands in the Glen Creek study area occurred on upland sites whereas both upland and riparian stands were present in the Mammoth study area.

2.3.3. Small spatial scale

Winnie (2012) identified four small-scale predation risk factors, based on earlier field studies by Ripple and Beschta (2004) and Halofsky and Ripple (2008), that might affect the capability of ungulate prey to detect approaching wolves or interfere with flight during an encounter, thus potentially altering browsing patterns and heights of young aspen. Following the approach of Winnie (2012), we determined the presence/absence of each factor for the selected aspen stands in the Glen Creek and Mammoth study areas. Although Winnie (2012) characterized risk factors from the centroid of each stand, we instead used the centroid of the five-tallest young aspen in a given stand. At this centroid location, or plot center, we also recorded UTM coordinates (m) and several descriptive variables, including elevation (m), slope (%), aspect (°), and the number of overstory conifers (i.e., conifers ≥ 20 cm in diameter at breast height) within 30 m of plot center.

Three of the risk factors utilized by Winnie (2012) were *escape impediment*, *view impediment*, and *conifer edge*. *Escape impediment* consisted of features such as jack-strawed conifer or aspen logs, major slope breaks, or steep embankments. *View impediment* represented a loss of view, most often due to local terrain undulations. *Escape impediments* and *view impediments* were assessed separately and each was considered present if it (a) occurred within 30 m of plot center and (b) extended across a horizontal arc of ≥ 60°, as viewed from plot center. If conifers at a given site had a relatively distinct boundary, or *conifer edge*, we considered this risk factor "present" when the boundary was within 30 m of plot center. The fourth factor, *downed logs*, was considered present if any logs at a given site occurred within 3 m of the sampled young aspen and were ≥ 0.15 m in diameter, ≥ 3 m in length, and ≥ 0.5 m above ground (Ripple and Beschta, 2007).

For each study area, we utilized a multifactor ANOVA (Statgraphics Centurion 64) to determine if browsing rate (%) or height (cm) of the five-tallest young aspen was significantly associated ($p < 0.05$) with any of the four hypothesized risk factors. The multifactor ANOVA analysis decomposes the variability of a dependent variable due to various factors; the contribution of a factor is measured having removed the effects of all other factors.

3. Results

3.1. Large spatial scale (northern range sectors)

Based on annual counts of wolves and elk for the northern range, a predator/prey ratio of 0.8 wolves/1000 elk occurred in the first year of wolf reintroduction, increasing to nearly 11 wolves/1000 elk by 2003. With the general decline of both wolf and elk populations after 2003, this ratio has since averaged 8.9 wolves/1000 elk (s.d. = ± 2.6 wolves/1000 elk).

Elk densities since 1999 significantly declined in both the West ($p < 0.001$) and East ($p < 0.001$) Sectors of the northern range, with the West Sector decline lagging the East Sector by several years (Fig. 2a). Although browsing levels began to decrease (Fig. 2b) and aspen heights increase (Fig. 2c) when elk densities fell below ~4 elk/km^2 in both sectors; these height increases occurred approximately 5–6 yrs later in the West Sector. Similarly, average young aspen heights of ~200 cm for the five-tallest young aspen were attained in the West Sector ~5 yrs later than had occurred in East Sector aspen stands.

3.2. Medium spatial scale (study areas)

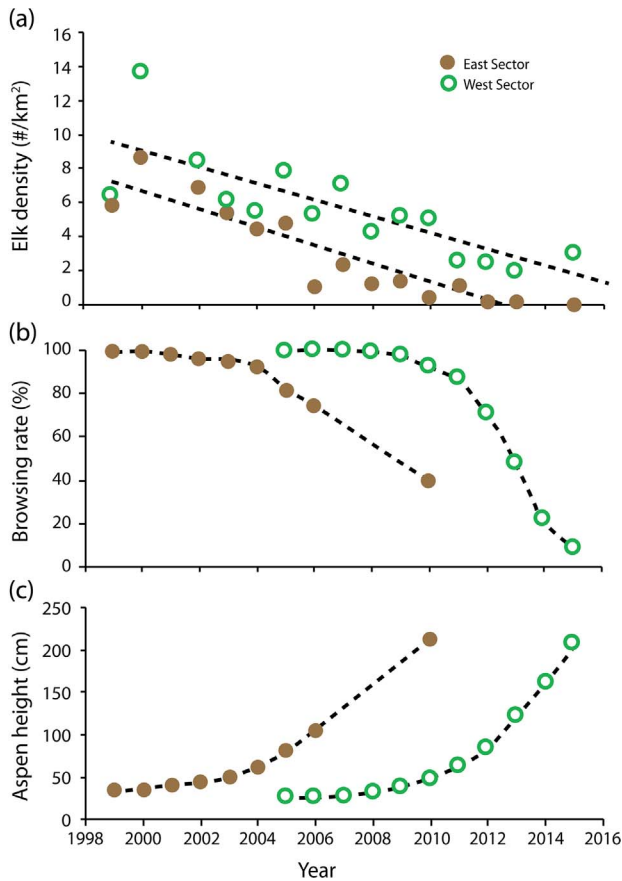Wolf collar data for 2001–12 indicated that wolves normally

Fig. 2. Annual (a) elk density over time in the West and East Sectors, as well as annual (b) browsing rate and (c) height of sampled young aspen in the same two sectors (see Methods for details). Equations for (a): *West Sector elk density* $= -0.43\,yr + 867$ ($r^2 = 0.58$, $p < 0.001$) and *East Sector elk density* $= -0.53\,yr + 1066$ ($r^2 = 0.86$, $p < 0.001$), where yr = year. Data sources: West Sector (Glen Creek study area, n = 60 aspen stands, this study); East Sector (vicinity of the Lamar Valley; n = 54 aspen stands, Ripple and Beschta, 2007, 2012).

frequented the Glen Creek study area but generally avoided coming within ~0.5 km of the Mammoth townsite (Doug Smith, NPS, personal communication). Elk primarily utilized the Glen Creek study area as winter range, with some use in summer, whereas they resided in the Mammoth study area throughout the year.

Browsing history, height, and age of sampled young aspen averaged 64%, 207 cm, and 9.4 yrs, respectively, in the Glen Creek study area and 89%, 31 cm, and 2.9 yrs, respectively, in the Mammoth study area (Table 1). Average browsing history, height, and age were each significantly different between study areas ($p < 0.001$, *t*-test, unequal variance).

3.3. Small spatial scale (aspen stands)

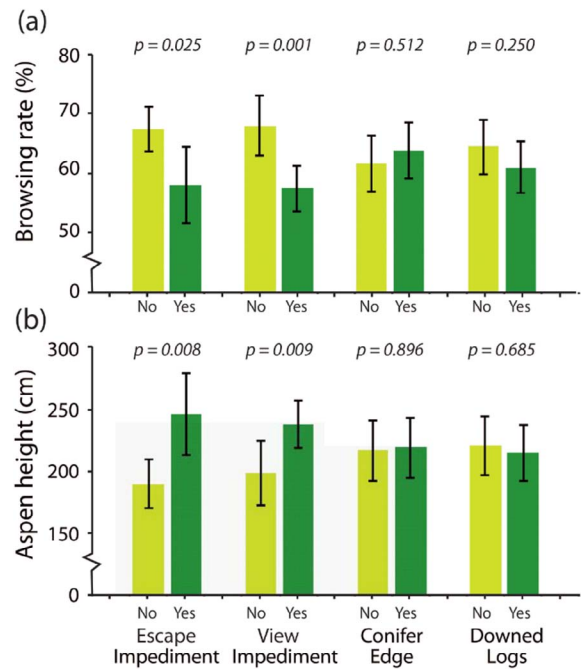A total of 0, 1, 2, 3, or 4 small-scale risk factors were found in 10,

Fig. 3. Means (vertical bars) and 95% confidence levels (capped vertical lines) for (a) browsing history and (b) aspen height *vs.* absence (no) or presence (yes) of indicated risk factors within the Glen Creek study area. *P*-values above each set of bars indicate relative significance of means comparisons.

21, 16, 7, and 6 aspen stands, respectively, in the Glen Creek study area. Both the browsing history and height of young aspen were significantly associated with two of the four hypothesized predation risk factors (Fig. 3), namely *escape impediment* ($p = 0.025$) and *view impediment* ($p = 0.001$), but were not significantly associated with *conifer edge* ($p = 0.512$) or *downed logs* ($p = 0.250$). Browsing averaged of 14 and 15% lower and heights averaged 56 and 40 cm taller in the presence of escape impediments and view impediments, respectively.

A total of 0, 1, 2, 3, or 4 risk factors were found in 1, 11, 16, 9, and 1 aspen stands, respectively, in the Mammoth study area. Browsing history was significantly associated with *downed logs* ($p = 0.049$), but not *escape impediment* ($p = 0.465$), *view impediment* ($p = 0.795$), or *conifer edge* ($p = 0.982$). Young aspen heights were not significantly associated with any of the predation risk factors: *escape impediment* ($p = 0.895$), *view impediment* ($p = 0.998$), *conifer edge* ($p = 0.916$), or *downed logs* ($p = 0.089$).

4. Discussion

4.1. Large spatial scale (northern range sectors)

An inverse relationship between browsing intensity and the growth of young woody plants is central to a trophic cascade hypothesis because it clearly identifies the mechanism connecting the two lower-most trophic levels (Beyer et al., 2007). Consistent with that hypothesis, the temporal patterns of decreasing annual browsing rates (Fig. 2b) and

Table 1

Average site conditions and young aspen characteristics for the Glen Creek and Mammoth study areas in the West Sector of Yellowstone's northern range. Standard deviations are shown in parentheses.

Study area	No. of aspen stands	Site conditions			Aspen characteristics[a]		
		Elevation (m)	Slope (°)	Conifers (no.)	Browsing history (%)	Height (cm)	Age (yrs)
Glen creek	60	2300 (± 32)	26 (± 15)	6.7 (± 8)	64 (± 12)	207 (± 60)	9.4 (± 1.8)
Mammoth	38	1917 (± 73)	23 (± 12)	15.5 (± 12)	89 (± 14)	31 (± 23)	2.9 (± 1.9)

[a] Based on plant architecture measurements of the five-tallest young aspen in each sampled aspen stand (see text for methods).

increasing young aspen heights (Fig. 2c) had an inverse relationship for stands in the West (Glen Creek study area) and East (Lamar Valley vicinity) Sectors of the northern range. Furthermore, the differential timing of elk density declines appears to have strongly influenced the timing of browsing reductions and height increases in each sector (Painter et al., 2015). While the five-tallest young aspen within upland stands in the West Sector reached an average height of 200 cm or taller in 2015, this was approximately 5 yrs after this height had been attained in the East Sector.

Most of the decrease in aspen herbivory in both sectors occurred only within the last decade (Fig. 2b), a time of slowly declining elk and wolf densities overall in the northern range and a period where the ratio of wolves-to-elk has remained relatively high. Results also indicated that elk densities needed to fall below ∼ 4 elk/km² within a given sector before browsing was sufficiently reduced for height increases to begin. Although a number of factors may have affected the elk density decline, to the benefit of young aspen, wolves have played a substantial role in these changes (White and Garrott, 2013; Painter et al., 2015).

During the early years of Yellowstone's wolf recovery, in 1999 and 2000, elk counts indicated that 58–78% of the northern range herd remained within the park (i.e., within the East, Central, and West Sectors). This situation changed dramatically in recent years whereby elk counts from 2013 and 2015 (no data for 2014) indicated the proportion of elk inside the park had dropped to only 23%. Also, 39% of elk monitored for 2–3 years during 2000–08 shifted their use of the winter range by 8–55 km, demonstrating the potential for changes in range selection by this large herbivore (White et al., 2010). If these shifts in the proportion of elk using the park in winter were, at least partially, in response to predation risk from wolves, they represent a BMTC at a large-scale. In the Madison-Firehole area of Yellowstone some elk have also altered winter range locations following the return of wolves, changes that researchers attributed to increased predation risk (Gower et al., 2009; Hamlin and Cunningham, 2009). Although the indirect effects of predation may be difficult to quantify as elk populations in Yellowstone have adjusted to wolves and other large carnivores, these effects are likely to be underestimated (Creel et al., 2013).

Recent climate fluctuations or trends are unlikely to be a cause of the contrasting patterns of young aspen heights in the West and East Sectors, because these areas experience essentially the same climate. It is also important to note that increased young aspen heights occurred even though the northern range has been experiencing a slow warming and drying trend during the last century (Beschta et al., 2016), conditions normally considered increasingly unfavorable for aspen stands (Rehfeldt et al., 2009; Hanna and Kulakowski, 2012; Worrall et al., 2013).

Overall, our results strongly indicate that reduced browsing represents the major cause of recent increases in young aspen heights across the northern range, as well other woody browse species (Beschta and Ripple, 2016). Furthermore, a relaxation of browsing pressure allows bottom-up forces to influence the dynamics of recovering plant communities (Tercek, 2010; Marshall et al., 2014). Once herbivory has been sufficiently reduced to allow young aspen and other woody plants to grow taller, site productivity differences and natural disturbance regimes can contribute to additional variation in heights. If young aspen heights continue to increase over time, these plants may eventually grow into overstory trees and replace those that are currently dying, thus helping to sustain northern range aspen stands.

4.2. Medium spatial scale (study areas)

The strongly contrasting differences in browsing histories for the Glen Creek and Mammoth study areas, only a few kilometers apart, appear to explain the difference in young aspen plant heights observed between these study areas. While the average height of the five-tallest young aspen within the Glen Creek study area in 2015 had exceeded 200 cm (Fig. 2c), a height above the normal browse level of elk, heights of young aspen in the Mammoth study area remained short and characteristic of the intensive browsing regime commonly observed throughout the northern range before wolf reintroduction.

A spatial plot of wolf collar locations from 2001 to 2012 indicated wolves were active across the northern range but generally avoided the area immediately around Mammoth, as well as the corridor between Mammoth and Gardiner. While the food subsidy provided by irrigated grass lawns in Mammoth may help to attract elk in summer, the human developments and large numbers of visitors throughout the year have likely contributed to low wolf abundance around the townsite, thus creating an area of low predation risk, consistent with a BMTC mediated by humans. In other words, a strong human presence indirectly reduces predation risk for elk, thus allowing intensive browsing to continue within the Mammoth study area and keeping young aspen short (i.e., an average height for the five tallest of only 31 cm in 2015, Table 1). These high levels of browsing occurred even though elk densities in the West Sector have declined during recent years. Similarly, human developments and high levels of human activity in Yosemite Valley and Zion National Parks displaced cougars thereby allowing mule deer, *via* human shielding, to heavily browse California black oak (*Quercus kelloggii*) and Fremont cottonwood (*P. fremontii*) (Ripple and Beschta, 2006, 2008), contributing to the long-term decline in the recruitment of these and other deciduous woody species. In Canada, wolf activity has been relatively low around the town of Banff and elk densities relatively high, again contributing to the suppression of aspen by browsing and representing another example of a trophic cascade from human shielding (Hebblewhite et al., 2005; Berger, 2007).

4.3. Small spatial scale (aspen stands)

Results for Glen Creek were mixed with regard to the effects of hypothesized small-scale risk factors. While annual browsing rates decreased and heights increased in the presence of *escape impediments* and *view impediments* (Fig. 3), changes consistent with a BMTC, no significant effects were associated with *conifer edge* or *downed logs*. In Glacier and Waterton Lakes National Parks, Eisenberg et al. (2014) similarly found elk pellet densities were significantly lower when detection or escape impediments were present, indicating an altered predation risk from wolves at a small spatial scale. White et al. (2003) evaluated predation risk and the functional response of elk-aspen herbivory for Canadian national parks in the northern Rocky Mountains. In areas of high predation risk, such as near routes frequented by wolves, young aspen were found to have relatively low browsing rates and higher rates of recruitment.

Relatively soon after wolf reintroduction in northern Yellowstone, Beyer (2006) found that collared elk began to avoid riparian areas along small streams. Young aspen in riparian areas of the East Sector of the northern range experienced a greater decrease in browsing after 2002 than occurred in adjacent upland aspen stands and by 2010 had significantly taller plants, consistent with a BMTC (Ripple and Beschta, 2007, 2012). A more recent evaluation of aspen across the northern range also indicated that young aspen were taller in riparian stands, due to a greater reduction in browsing rates, than in upland stands (Painter et al., 2015).

Recent studies in other regions have specifically tested for the effects of altered prey behavior, in the presence of wolves, on plant communities. For example, Callan et al. (2013) evaluated the effects of white-tailed deer (*O. virginianus*) foraging on understory plant communities in Wisconsin following wolf recovery and found, consistent with a trophic cascade, increased forb and shrub richness associated with high wolf use areas. Along the Wisconsin-Michigan border, Flagel et al. (2015) evaluated the potential for wolves to reduce deer herbivory on understory vegetation. Deer densities, duration of visits, and time spent foraging were all reduced in areas of high wolf use, resulting in a sevenfold decrease in the proportion of browsed maple (*Acer* spp.)

saplings. Ungulate exclosure experiments also indicated that the effects of deer on sapling growth and forb species richness became negligible in areas of high wolf use. Flagel et al. (2015) concluded that the trophic effects of wolves benefiting plants were likely generated through trait-mediated effects on ungulate herbivory (BMTC) and not through direct mortality effects (DMTC). In the Białowieża Primeval Forest of Poland, Kuijper et al. (2014) evaluated anti-predator responses of red deer (*Cervus elaphus*) to wolf scat. The percentage of time red deer were vigilant in the presence of wolf scat was more than double that of controls; the time spent foraging in the presence of wolf scat was one-third that of the control. Such experimental approaches help to clarify the behavioral responses of ungulates to predation risk from wolves, as well as how these responses contribute to the increased growth of woody species.

No significant effect of small-scale risk factors upon young aspen heights was found in the Mammoth study area. The relatively high browsing histories ($\bar{x} = 89\%$) and short heights ($\bar{x} = 31$ cm) for the five-tallest young aspen across stands in this study area essentially precluded the occurrence of a predator-driven BMTC. Such results were similar to those of earlier northern Yellowstone field studies by Kauffman et al. (2010) and Winnie (2012), studies that also attempted to detect a BMTC with young aspen. The 2004-07 field measurements ($n = 16$ stands) of Kauffman et al. (2010) occurred during a period when browsing rates across the northern range were still relatively high (Painter et al., 2014, 2015; Peterson et al., 2014). Consistent with high rates of browsing, Kauffman et al. (2010) found that young aspen averaged < 75 cm in height and showed no significant predation risk effect (i.e., no BMTC). In 2010 Winnie (2012) measured young aspen ($n = 65$ stands) within the Daly Creek drainage of the Gallatin River winter range, an area of the park where wolf activity has been relatively low since about 2006 (1995–2014 annual wolf reports, YNP). Winnie found exceptionally high rates of browsing (nearly 100%) for young aspen accessible to elk and that aspen recruitment did not respond to fine-scale risk factors in a manner consistent with a BMTC hypothesis (Winnie, 2012). Collectively, results from Kauffman et al. (2010), Winnie (2012), and the Mammoth study area (this study) have shown that when browsing rates remain high, plant heights are unlikely to be improved by the presence of small-scale risk factors.

Although an average 10% decrease in browsing rate was found for aspen stands with *downed logs* ($p = 0.049$) in the Mammoth study area, a significant increase in young aspen heights due to this factor did not occur. Field observations in the Mammoth study area indicated that once a young aspen stem grew beyond the local physical protection sometimes provided by *downed logs*, browsing rates increased. Thus, any small reduction of browsing history due to the physical protection of *downed logs*, which normally would occur for relatively young and short aspen plants, appears to be a transient phenomenon and did not result in significantly taller plants in either the Mammoth or Glen Creek study areas. In contrast, an earlier study of aspen stands in the East sector (Ripple and Beschta, 2007) as well as a study of aspen stands across the northern range (Painter et al., 2015), found increased young aspen heights were, at least to some degree, associated with the presence of *downed logs*. Similarly, studies in European forest ecosystems have found that downed logs in a wolf-cervid system can result in increased predation risk and reduced browsing intensity (Kuijper et al., 2014).

The selection of small-scale risk factors for assessment inherently involves inferences about elk behavior, yet our understanding of those risk factors may not be well understood. For example, we assumed any *conifer edge* within 30 m of plot center represented a potential risk factor in our small-scale assessment. Yet collar studies have suggested elk may use conifer edges more and aspen less when wolves are present, perhaps to avoid detection by wolves (Creel et al., 2005; Fortin et al., 2005a). An increased preference for conifer forest and a corresponding decrease in use of aspen stands suggests an alternative mechanism by which predation risk could result in less browsing of aspen. Ultimately, a

coordinated program of research using GPS collars on wolves and elk in conjunction with plant and habitat information may be needed to more fully explain the temporal and spatial effects of wolfs on plant communities at various scales.

5. Conclusions

In northern Yellowstone, the extirpation of wolves and depleted populations of other large predators in the early 1900s subsequently resulted in the suppression of young aspen and other deciduous woody plants due to intensive browsing by native ungulates, a situation that has been repeated in various national parks in western United States and Canada, and perhaps elsewhere in North America. However, the reintroduction of wolves into Yellowstone, coincident with other factors (e.g., predation pressure from bears and cougars, hunting harvest outside the park), appears to have reversed this trend as indicated by the relatively widespread reductions in ungulate browsing and increased young aspen heights in the northern range during recent years. The fact that young aspen are increasingly exceeding the upper browse level of elk indicates that plant community dynamics are undergoing a major transition from that which occurred in previous decades. Furthermore, with fewer elk in recent years and the occurrence of BMTCs, variable reductions in browsing at large, medium, and small spatial scales appear to represent a major factor contributing to the increasing variation in young aspen heights that have become prevalent across the northern range.

There appears to be little doubt that a strong wolf presence in the northern range has had a major role in setting northern Yellowstone's aspen stands on a trajectory that may ultimately allow for their recovery in both upland and riparian settings, as well as recovery of other deciduous woody species. During this important period of ecosystem change and adjustment, identifying the relative importance of behavioral and density mediated effects at various spatial scales within the complexity of a mountainous landscape represents a major scientific challenge. Tracking the dynamics of Yellowstone's plant communities into the future, as well as in other places where wolves have returned, will be needed if we are to eventually understand the important ecological effects of this apex predator.

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