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ARTICLE

Long-term aspen dynamics, trophic cascades, and climate in northern Yellowstone National Park

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Abstract: We report long-term patterns of quaking aspen (*Populus tremuloides* Michx.) recruitment for five ungulate exclosures in the northern ungulate winter range of Yellowstone National Park. Aspen recruitment was low (<3 aspen·ha⁻¹·year⁻¹) in the mid-1900s prior to exclosure construction due to herbivory by Rocky Mountain elk (*Cervus elaphus* Linnaeus, 1758) but increased more than 60-fold within 25 years after exclosure construction despite a drying climatic trend since 1940. Results support the hypothesis that long-term aspen decline in Yellowstone's northern range during the latter half of the 20th century was caused by high levels of ungulate herbivory and not a drying climate. Gray wolves (*Canis lupus* Linnaeus, 1758) were reintroduced during 1995–1996. For the period 1995–2012, we summarized annual predator–prey ratios, ungulate biomass, and drought severity. The average density of young aspen increased from 4350 aspen·ha⁻¹ in 1997–1998 to 8960 aspen·ha⁻¹ in 2012; during the same time period, those >1 m in height increased over 30-fold (from 105 to 3194 aspen·ha⁻¹). Increased heights of young aspen occurred primarily from 2007 to 2012, a period with relatively high predator–prey ratios, declining elk numbers, and decreasing browsing rates. Consistent with a re-established trophic cascade, aspen stands in Yellowstone's northern range have increasingly begun to recover.

Key words: aspen, elk, wolves, exclosure, drought.

Résumé : Cet article porte sur les patrons de recrutement à long terme du peuplier faux-tremble (*Populus tremuloides* Michx.) dans cinq exclos situés dans la partie nord de l'aire d'hivernage des ongulés dans le parc national de Yellowstone. Le recrutement du peuplier faux-tremble était faible (<3 tiges·ha⁻¹·an⁻¹) au milieu des années 1900, avant la construction d'exclos, à cause de l'herbivorisme du wapiti des montagnes Rocheuses (*Cervus elaphus* Linnaeus, 1758). Mais il a augmenté de plus de 60 fois en moins de 25 ans après la construction des exclos bien que le climat ait eu tendance à être plus sec depuis 1940. Les résultats supportent l'hypothèse selon laquelle le long déclin du peuplier faux-tremble dans la partie nord montagneuse de Yellowstone durant la deuxième moitié du 20e siècle était dû au niveau élevé d'herbivorisme des ongulés et non au climat plus sec. Le loup gris (*Canis lupus* Linnaeus, 1758) a été réintroduit au cours des années 1995 et 1996. Pour la période de 1995 à 2012, nous avons résumé sur une base annuelle le ratio prédateurs-proies, la biomasse des ongulés et la sévérité de la sécheresse. La densité moyenne des jeunes peupliers faux-tremble a augmenté de 4350 tiges·ha⁻¹ en 1997–1998 à 8960 tiges·ha⁻¹ en 2012. Durant la même période, le nombre de tiges plus hautes qu'un mètre a augmenté de plus de 30 fois, de 105 à 3194 tiges·ha⁻¹. L'augmentation de la hauteur des jeunes tiges de peuplier faux-tremble est survenue principalement de 2007 à 2012, une période durant laquelle le ratio prédateurs-proies a été relativement élevé, le nombre de wapitis a diminué ainsi que le taux de broutement. Avec le rétablissement de la cascade trophique, les peuplements de peuplier faux-tremble dans la partie nord montagneuse de Yellowstone ont de plus en plus commencé à récupérer. [Traduit par la Rédaction]

Mots-clés : peuplier faux-tremble, wapiti, loups, exclos, sécheresse.

Introduction

Quaking aspen (*Populus tremuloides* Michx.) are widely distributed across the western United States and Canada. Aspen normally occur in riparian areas or moist upland settings and their canopies transmit considerable light, thus these sites support a diverse understory plant community and provide habitat for a wide range of vertebrate and invertebrate species (DeByle and Winokur 1985). Young aspen seedlings and root sprouts are highly palatable to wild ungulates such as Rocky Mountain elk (*Cervus elaphus* Linnaeus, 1758) and bison (*Bison bison* (Linnaeus, 1758)) (Hudson and Frank 1987; Toweill et al. 2002), and high levels of ungulate herbivory can suppress recruitment of aspen and other woody browse species (White et al. 1998; Barmore 2003; Rogers and Mittanck 2014). In the western United States, aspen cover declined significantly during the 20th century (Bartos 2001).

Aspen trees can live to approximately 150 years of age, sometimes longer, and their stems are amenable to aging via tree ring counts. Thus, a "stem age" vs. "diameter" relationship, in conjunction with extensive sampling of aspen diameters, can illustrate general patterns of aspen recruitment over time. The resulting age structure (i.e., tree frequency vs. year of establishment) often provides important information regarding the influence of various factors upon long-term stand dynamics, factors such as fire regime, conifer competition, disease, ungulate herbivory, a changing climate, etc. (Howard 1996; Seager et al. 2013).

Aspen stands within the Greater Yellowstone Ecosystem occupy less than 2% of the area; nevertheless, they are considered ecologically important and there is ongoing concern about their ability to persist as older trees die without replacement (Brown et al. 2006). Recruitment of aspen and other deciduous woody species in the northern ungulate winter range (hereafter, northern range) of Yellowstone National Park decreased during much of the 20th century (Ripple and Larsen 2000; National Research Council 2002). Although some researchers suggested that climatic fluctuations,

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Fig. 1. Aspen age structure (percentage of aspen trees vs. year of establishment by 20 year intervals) in Yellowstone's northern range. Adapted from Ripple and Larsen (2000), Kauffman et al. (2013), and Painter (2013), with sample sizes of 98, 122, and 135 aspen, respectively.

Fig. 2. Conceptual models of trophic-level interactions indicating the relative strength of top-down pressure (represented by arrow widths) in northern Yellowstone's aspen stands where elk have historically been the predominant large herbivore. Represented are the following scenarios: (*a*) an ungulate exclosure where both wolves and elk are absent, (*b*) wolves absent and elk present (i.e., mid-1920s to mid-1990s), and (*c*) wolves and elk present (prior to mid-1920s and after mid-1990s). In both (*a*) and (*c*), a full range of size and age classes of aspen are present, whereas young aspen in (*b*) are maintained in a browsing-suppressed state. We assume that bottom-up forces (i.e., resources) are the same and not limiting in all three models. For a more complete illustration of various direct and indirect effects of gray wolf reintroduction in the Greater Yellowstone Ecosystem, see Ripple et al. (2014*a*). Figure is provided in colour online.

lack of fire, or other factors might be involved (Houston 1982; Yellowstone National Park 1997), others pointed to high levels of herbivory by elk as the primary causative mechanism of decline (Kay 1990; Romme et al. 1995; Barmore 2003; Larsen and Ripple 2005). The role of fire was tested with the fires of 1988. After the burn, many new aspen appeared but herbivory remained intense, removing most of them (Romme et al. 1995).

Recent age-structure studies have provided an improved perspective of long-term aspen dynamics in Yellowstone's northern range (Ripple and Larsen 2000; Kauffman et al. 2013; Painter 2013). Although results of these studies varied somewhat, perhaps due to differences in stand selection, number of stands, and sampling within stands, all showed increasing numbers of aspen over time during the 1800s (Fig. 1). However, a pronounced decline in aspen numbers appears to have begun in the early 1900s and became increasingly severe in the mid to late 20th century. Since the early 1900s, Kay (1990) estimated that a decline of more than 90% has occurred in the area occupied by aspen. Recruitment of aspen largely ceased in the latter half of the 20th century (Fig. 1) as did that of cottonwood (*Populus* spp.) and willow (*Salix* spp.) (Beschta 2005; Wolf et al. 2007).

The deterioration of woody plant communities in northern Yellowstone largely occurred after gray wolves (*Canis lupus* Linnaeus, 1758) were extirpated and despite the culling of elk inside the park, as well as the hunting of those that seasonally migrated outside the park. Although recent studies (e.g., Kauffman et al. 2010; Painter et al. 2014) have generally confirmed that high levels of elk herbivory are the primary cause of reduced recruitment of deciduous woody species in Yellowstone's northern range, regional studies in the western United States have identified a drying climate as the major contributor to aspen decline (Rehfeldt et al. 2009; Hanna and Kulakowski 2012). For example, reduced growth of overstory aspen in Colorado and Wyoming was associated with high temperatures and low precipitation that, in turn, contributed to increased mortality (Hanna and Kulakowski 2012). Earlier, Rehfeldt et al. (2009) had found that aspen presence or absence in the western United States was primarily associated with temperature, precipitation, and dryness variables. Thus, questions remain as to whether climatic factors such as periods of drought may have caused or exacerbated the long-term decline in aspen recruitment across northern Yellowstone (Houston 1982; Yellowstone National Park 1958).

In the mid-1900s, the park service constructed fenced exclosures in Yellowstone's northern range to help understand aspen, willow (*Salix* spp.), and shrub–steppe dynamics in the absence of herbivory by wild ungulates. The Yellowstone exclosures allowed vegetation to be influenced primarily by site conditions (e.g., soil moisture and nutrients, temperature, and precipitation) and nat-

ural stand dynamics other than ungulate herbivory (e.g., stem competition and disease). We hypothesized that, in the absence of herbivory, aspen recruitment would increase over time within these exclosures regardless of climatic trends or fluctuations. Results could provide improved insights as to the relative importance of herbivory and climate on temporal patterns of aspen recruitment in Yellowstone's northern range during the 20th century (Fig. 1). Wolves were reintroduced into Yellowstone in the mid-1990s, and we summarized, on an annual basis, predator–prey ratios, ungulate biomass, and Palmer Z drought severity index values since their reintroduction. We also summarized annual browsing rates and heights associated with young aspen in northern range stands. We utilized these data to identify whether aspen plant community dynamics since the return of wolves were consistent with a re-established trophic cascade or, alternatively, largely influenced by contemporary climatic conditions.

To frame our results and discussion from a trophic cascades perspective, we considered three conceptual models of predator–prey–plant interactions. The simplest model of trophic interactions, typified by an ungulate exclosure (Fig. 2a), excludes any influence of large carnivores (predators) or large herbivores (consumers) upon plant communities (producers). In this situation, aspen are primarily regulated by resources and processes (other than herbivory). In our second conceptual model, elk are present but wolves are absent (Fig. 2b), which is a situation that occurred in northern Yellowstone from the mid-1920s through the mid-1990s; here, aspen are mediated by herbivory (top-down pressure).

Fig. 3. (*a*) Lamar East exclosure (dashed lines indicate location of exclosure fencing) in the Lamar Valley; young aspen outside the exclosure continue to be suppressed by browsing, primarily from bison. (*b*) An example of a two-tiered aspen stand along Crystal Creek in Yellowstone's northern range consisting of relatively old overstory trees and a recovering understory of young aspen 3–4 m in height following the return of wolves; note the lack of intermediate diameter classes due to decades of intensive elk herbivory. Although understory aspen in this stand exceed a recruitment threshold of 2 m (the upper browse level of elk), many northern range stands have not yet done so. Photo credits: (*a*) R.L. Beschta (September 2013) and (*b*) R.L. Beschta (September 2010).
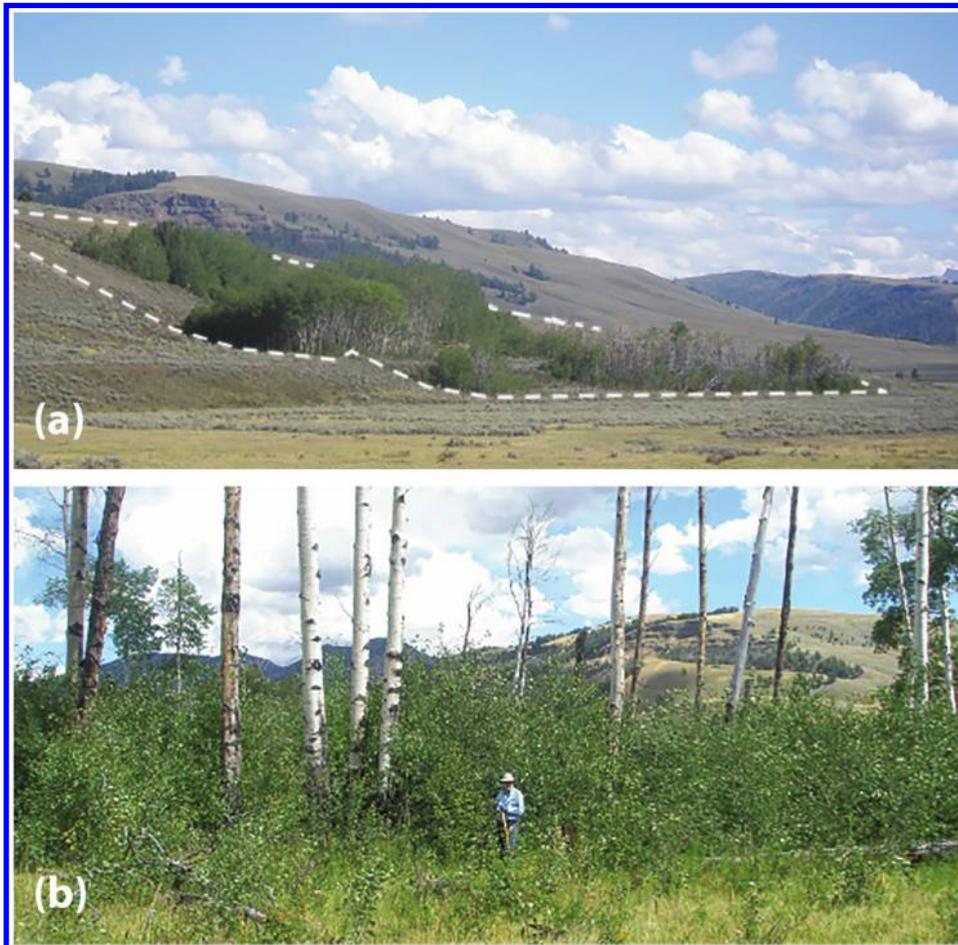
Our third model (Fig. 2*c*) represents a carnivore–ungulate–aspen trophic cascade whereby wolves, in conjunction with other large predators, mediate elk behavior and (or) density (top-down pressure), thus reducing any effects of this large herbivore on aspen community dynamics. Although we emphasize wolves as an apex predator in Fig. 2*c*, predation by bears (*Ursus* spp.; Barber-Meyer et al. 2008), cougars, and human hunting outside the park (Eberhardt et al. 2007) represent additional factors exerting top-down pressure on elk, thus potentially influencing their populations and use of habitat in northern Yellowstone.

Methods

Study area

Yellowstone National Park's northern range consists predominantly of shrub–steppe terrain and covers an area of 1500 km², of which approximately two-thirds lies within the park along its northern border. Wolves were historically present in the park but extirpated by the mid-1920s. After an absence of approximately seven decades, 41 wolves were released in 1995–1996 again completing the park's large predator guild. Grizzly bear (*Ursus arctos* Linnaeus, 1758) numbers increased following wolf reintroduction, providing additional predation pressure on elk (Smith et al. 2003; Barber-Meyer et al. 2008). Annual elk and bison counts in the northern range have been conducted by the park service since the

early 1900s, and over the last decade (2003–2012), these counts indicated a decline in elk from 9200 to 4200 animals, whereas bison increased from 890 to 2670 animals (annual census counts, Yellowstone National Park). Mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), pronghorn (*Antilocapra americana* (Ord, 1815)), and moose (*Alces alces* (Linnaeus, 1758)) are also present on the northern range but in relatively small numbers.

Four ungulate exclosures, each ~2 ha in area and containing one or more aspen stands, were constructed in the northern range in the late 1950s and early 1960s (Fig. 3*a*; Table 1). A smaller exclosure (~0.13 ha) was constructed in 1980–1981 at Tower Junction. Except for Mammoth, where aspen were growing in competition with conifers, aspen stands in these exclosures occurred within a landscape of shrub–steppe vegetation. Willows were present to varying degrees within the exclosures (Kay 1990) but were absent at Tower Junction. A prescribed fire occurred in the Junction Butte exclosure following the 1986 growing season; additional information regarding exclosure plant communities is provided by Kay (1990).

Data collection and analysis

Exclosures

In late summer of 2013, we measured the diameter at breast height (DBH, 1.5 m), to the nearest centimeter, of all aspen within

Table 1. General characteristics of northern range ungulate exclosures and associated aspen stands.

Year installed	Exclosure name	Area (ha)	Elevation (m)	Aspect	Latitude	Longitude	Aspen cover (ha)	Density of stems >1.5 m in height (no. per hectare)
1957	Lamar East	2.3	2020	S	44°52′20″	110°12′14″	0.62	2750
1957	Mammoth	2.0	1930	N	44°57′36″	110°41′55″	0.28	665
1962	Lamar West	2.4	2040	S	44°53′05″	110°13′00″	0.94	1580
1962	Junction Butte	1.7	1890	SW	44°54′43″	110°22′04″	0.14	9340
1980–1981	Tower Junction	0.13	1910	N	44°55′00″	110°25′15″	0.01	8390
			$\bar{x} = 1960$					$\bar{x} = 4545$

the five northern range exclosures. An exception to this protocol occurred within the Lamar East exclosure where one aspen stand contained numerous jack-strawed dead trees with branches still attached, making it difficult to inventory the entire stand. For this one stand, we measured DBHs within 2 m wide belt transects installed perpendicular to the long axis of the stand and spaced at 10 m intervals (a 16.4% area-based sample); the number of aspen associated with each DBH class was thus multiplied by a factor of 6.1 for this stand. We delineated the area (in hectares) of most aspen stands in the field but utilized aerial photographs for relatively large stands (e.g., Mammoth exclosure). The inventory of DBHs and corresponding area of each stand were used for calculating an average aspen density (number of aspen per hectare) by DBH class for each exclosure. We estimated the age (AGE_{yr}) of each DBH class from a scaling formula developed in the northern range by Kay (1990): $AGE_{yr} = 2.89 \times DBH + 4.86$, with $r^2 = 0.84$ and $n = 895$. Aspen densities by year of establishment (i.e., $2013-AGE_{yr}$) were used to develop an age structure for each exclosure.

Monthly values of the Palmer Z drought severity index (PZI; Karl 1986) were obtained for the location of each exclosure from the Western Regional Climate Center (2014) and then averaged to index annual soil moisture conditions for the study area. PZI represents the departure of soil moisture levels from a long-term average and is based on monthly values of precipitation, temperature, and evapotranspiration; negative values of PZI indicate relatively droughty conditions (Palmer 1965; Heim 2002). We used linear regression to illustrate any trends in the annual PZI over the period 1941–2007. We also regressed average aspen densities (using the four oldest exclosures: Lamar East, Lamar West, Junction Butte, and Mammoth) against PZI values to help identify their possible association with climate.

Aspen after wolf reintroduction

To index the potential ecological effectiveness of wolves, we calculated an annual predator–prey ratio (wolves per 1000 elk) based on northern range counts of wolves and elk, their primary prey, for the period 1995–2012 (Hebblewhite 2013). We also calculated annual ungulate biomass (kg·ha⁻¹) of northern range elk and bison from 1995 to 2012, based on ungulate counts by the park service in conjunction with representative winter weights of female elk (225 kg; Dean et al. 1976) and female bison (430 kg; Meagher 1973). We did not adjust elk counts to account for sightability (see Houston 1982; Eberhardt et al. 2007).

In 1997–1998, Larsen (2001) measured the frequency and heights of young aspen (<5 cm DBH) in 79 randomly selected northern range stands within the park. A 2012 assessment of northern range aspen stands (all stands were also inside the park) by Painter et al. (2014, 2015) replicated Larsen's (2001) methods in 87 stands (including 76 of Larsen's original stands from 1997–1998). We compared young aspen densities and heights from these two time periods (1997–1998 vs. 2012). Painter et al. (2014) also measured annual browsing and spring heights for the five tallest young aspen in each stand. The five tallest young aspen provided a "leading edge" indication of any recent improvement in young aspen heights and were positively correlated with the average heights of all young aspen in a given stand (Painter et al. 2014); heights of the

five tallest aspen also have been found to be positively correlated with the heights of several species of berry-producing shrubs (Beschta and Ripple 2012). We calculated an average PZI for 2007–2012, the period during which young aspen height increases have been observed in northern range aspen stands (Painter et al. 2014).

Results

Exclosures

The density of aspen ≥ 1.5 m in height for the five northern range exclosures ranged from 665 to 9340 aspen·ha⁻¹ ($\bar{x} = 4545$ aspen·ha⁻¹; Table 1; Supplementary Table S1); exclosure elevations ranged from 1890 to 2040 m. The highest aspen densities occurred at Junction Butte and Tower Junction, whereas the density at Mammoth was relatively low, perhaps due to competition with conifers at this site. Aspen cover ranged from a low of 0.01 ha at Tower Junction to a high of 0.94 ha at Lamar East.

During the 25 years prior to the installation of elk-proof fences at each exclosure site, aspen recruitment was relatively low, averaging < 3 aspen·ha⁻¹·year⁻¹. Following fence construction, aspen recruitment increased in all exclosures although the magnitude and timing of increase varied. For example, the 1957 Lamar East exclosure along the north side of the Lamar Valley had only a modest increase in aspen recruitment during the first 20 years following its installation (Fig. 4a). Aspen recruitment in the 1957 Mammoth and 1962 Lamar West exclosures underwent a sharp increase within a decade of construction, remained at a nearly constant rate over the next 25 years, and recently increased again (Figs. 4b and 4c). The 1962 Junction Butte exclosure was located in open, hummocky terrain, and although increased aspen recruitment was not apparent in this exclosure following fence construction, likely due to the mid-1980s prescribed burn that may have removed most established plants, relatively high recruitment occurred in the 1980s and 1990s followed by a decline after 2000 (Fig. 4d). Aspen recruitment at the 1980–1981 Tower Junction exclosure increased for about a decade after its construction and has since remained relatively constant (Fig. 4e). We presented results only for 2007 and earlier because ~5 years, on average, were required for aspen to attain breast height (author's unpublished data).

By the 25th year following fence construction, average aspen recruitment for the five exclosures was 62 times greater (standard error (SE), ±30) than that occurring in the years prior to construction. A significant downward trend in annual PZI ($r^2 = 0.14$, $p = 0.002$) during 1941–2007 indicated increasingly droughty conditions in the later portion of this 67 year period (Fig. 4f). Regression analysis of average aspen density (using the four largest and oldest exclosures) and PZI, over time, indicated an inverse relationship between these two variables (aspen·ha⁻¹ = –95 × PZI + 205, with $r^2 = 0.19$ and $p = 0.083$).

Aspen after wolf reintroduction

Following the 1995–1996 wolf reintroductions, the predator–prey ratio increased until about 2003, as the number of wolves increased and the number of elk decreased. However, due to declines in both wolf and elk numbers after 2003, the predator–prey ratio (Fig. 5a) has since averaged ~9.8 wolves per 1000 elk (SE,

Fig. 4. Aspen age structure (number of aspen ≥ 1.5 m in height per hectare vs. year of establishment) from 1941 to 2007 within northern range ungulate exclosures (arrows identify year of exclosure construction): (*a*) Lamar East (*n* = 1701 aspen), (*b*) Mammoth (*n* = 627 aspen), (*c*) Lamar West (*n* = 449 aspen), (*d*) Junction Butte (*n* = 1298 aspen), and (*e*) Tower Junction (*n* = 193 aspen). (*f*) Annual Palmer Z drought severity index (PZI) for the northern range exclosure sites (dashed line represents linear regression; PZI = −0.017 × year + 33.3, with r^2 = 0.14 and *p* = 0.002). Because aspen DBHs were measured to the nearest centimeter and their ages (years) were calculated as 2.89 × DBH + 4.86, aspen densities are plotted at 2.89 year intervals. Annual PZI values are from Western Regional Climate Center (2014).

Fig. 5. Northern range (*a*) predator–prey ratio (wolves per 1000 elk), (*b*) ungulate biomass of elk and bison (kg·ha⁻¹), (*c*) annual browsing (%) for aspen ≤ 1 m in height (% of stems browsed = −4.23 × year + 8606.3, with r^2 = 0.95 and *p* < 0.001), and (*d*) proportion of aspen stands (%) with at least five young aspen ≥ 1 m and ≥ 2 m in height. Since 2004, the year that wolves attained their greatest numbers in the northern range, the predator–prey ratio has averaged 9.8 wolves per 1000 elk (SE, ±0.84). Annual wolf and elk counts from National Park Service, Yellowstone National Park; aspen browsing and height adapted from Painter et al. (2014).

±0.8). From 1995 to 1999, elk comprised more than 90% of the northern range's ungulate biomass. With declining elk numbers and increasing bison numbers occurring after 1995, by 2012, the total biomass of bison utilizing the northern range exceeded that of elk (Fig. 5*b*).

In 1997–1998, the density of young aspen < 5 cm DBH in northern range stands averaged 4350 aspen·ha⁻¹ (Larsen 2001) compared with 8960 aspen·ha⁻¹ in 2012 (Painter et al. 2014). In 1997–1998, young aspen 1–2 m and > 2 m in height had average densities of 105 and 0 aspen·ha⁻¹, respectively (Larsen 2001), but by 2012, these

densities had increased to 2656 and 538 aspen·ha⁻¹, respectively (Painter et al. 2014). With regard to the five tallest young aspen in each stand, browsing rates declined after 2003 (Fig. 5*c*). The proportion of northern range stands with five or more young aspen ≥ 1 m or ≥ 2 m in height has exhibited an upward trend since 2006, and by 2012, these proportions were 59% and 25%, respectively (Fig. 5*d*). For 2007–2012, a period of increasing young aspen heights, the PZI averaged −1.02 (SE, ±0.29), indicating relatively dry conditions.

Discussion

Exclosures

At about the time that the four largest northern range exclosures were being installed, the park's elk management plan (see pp. 1–2 in Yellowstone National Park (1958)) indicated a concern that "the cumulative effects of grazing and trampling by excessive

numbers of elk for many decades are obvious today" and that "former groves of aspen now have only a few trees which cannot be replaced while elk consume reproduction." Exclosure results confirmed that relaxation of ungulate herbivory was the only requirement for improved long-term recruitment of aspen in northern Yellowstone; similar improvements in recruitment were found within Gallatin elk winter range exclosures that were erected in 1945 near the northwestern corner of Yellowstone National Park (Halofsky and Ripple 2008). Variations in age structure associated with the northern range exclosures (Figs. 4a–4e) are probably due to factors such as stem competition and exclusion (DeByle and Winokur 1985). Approximately one-half of a century after fence construction, aspen densities within the exclosures (range = 665–9 340 aspen·ha⁻¹; Table 1) are beginning to approach those found in aspen stands from northwestern Wyoming (range = 3 500–10 400 aspen·ha⁻¹) (Bartos et al. 1991).

The inverse relationship between aspen recruitment inside the exclosures and drought severity over time (Fig. 4) indicates that a drying climate was unlikely to have caused the major decrease in recruitment that occurred across northern Yellowstone aspen stands (outside of the exclosures) in the latter half of the 20th century (Fig. 1). These results were therefore consistent with a hypothesis that herbivory, and not climate, was the dominant factor affecting declining northern range aspen recruitment during the mid- to late-1900s. However, this result is in direct contrast with recent regional studies that have identified a warming climate as the major factor contributing to widespread aspen decline in the western United States (e.g., Rehfeldt et al. 2009; Hanna and Kulakowski 2012), a decline that is supposed to accelerate in coming decades based on climate projections (Rehfeldt et al. 2009). Unfortunately, these regional climate-based studies of aspen dynamics did not concurrently address the potential long-term effects of ungulate herbivory upon aspen stand dynamics, even though domestic and wild ungulates are common across much of the western United States (Beschta et al. 2013) and both are capable of causing long-term reductions in aspen recruitment (e.g., Kay 2011; Rogers and Mittanck 2014).

Various deciduous woody species in Yellowstone's northern range, in addition to aspen, also have responded once protected from ungulate herbivory. For example, willows previously suppressed by browsing increased in height following exclosure construction (Kay 1990). Kay (2001) also found that understory vegetation inside exclosures was dominated by tall, palatable shrubs and forbs, whereas understory vegetation outside consisted mostly of unpalatable, low-growing forbs and exotic grasses. The results of other northern range exclosure research by Singer (1996), Barmore (2003), Kauffman et al. (2010), Ripple et al. (2014b), and others have generally indicated improved growth and diversity of plant communities once ungulate herbivory was curtailed (Fig. 2a).

Exclosure studies elsewhere in North America, where large predators have been removed or displaced, have also provided critical information for understanding the effects of native ungulates on plant communities. For example, in a mixed-hardwood forest of northeastern Pennsylvania, aspen seedlings inside exclosures had the highest density relative to 13 other woody species, whereas outside of exclosures, aspen seedlings were entirely absent due to high levels of herbivory by white-tailed deer (Shafer et al. 1961). Similarly, herbivory by elk and moose outside of ungulate exclosures at Elk Island National Park restricted aspen regeneration and the heights of palatable shrubs (Milner 1977). At Rocky Mountain National Park, aspen inside exclosures continued to regenerate over time, whereas young aspen outside of exclosures occurred at low densities, remained short, and were heavily branched due to intensive browsing, predominantly by elk (Hess 1993).

Studies of long-term changes in vegetation within several national parks of western Canada found that deciduous woody plant species often experienced high levels of herbivory and declining recruitment following the loss of wolves (Trottier and Fehr 1982;

White et al. 1998; Hebblewhite et al. 2005; Beschta and Ripple 2007b). In the western United States, recruitment levels of deciduous woody plants were found to decrease by nearly 90%, on average, within two decades following the loss of an apex predator, with declines in recruitment becoming more severe in subsequent decades and occurring independently of climatic regime (Beschta and Ripple 2009). On lands outside of national parks, herbivory by livestock can also have major effects on plant community composition and structure (Donahue 1999; Fleischner 2010; Beschta et al. 2013).

Aspen after wolf reintroduction

More than a decade after the return of wolves and concurrent with high predatory–prey ratios and a decline in browsing, increased heights of young aspen are increasingly occurring in northern range stands inside the park, even during a period of relatively dry conditions (Figs. 3b and 5d). Thus, the warming and drying climate currently underway in northern Yellowstone does not appear to represent a major limitation on the establishment and growth of young aspen at this time. Height increases of young aspen are an important ecosystem metric in Yellowstone's northern range because studies undertaken prior to wolf reintroduction commonly found that ungulate herbivory held them and other deciduous woody plants to < 1 m in height. For example, northern range studies inside the park that were conducted between 1935 and 1989 (Kay 1990; Singer 1996; Barmore 2003) found that heights of young aspen accessible to wild ungulates averaged 0.3 m (SE, ±0.1); heights of young willows and other browse species averaged 0.4 m (SE, ±0.2). In contrast, Barnett and Stohlgren (2001) reported 227–370 stems·ha⁻¹ of young aspen > 2 m in height for an elk winter range in the southern Greater Yellowstone Ecosystem, where browsing rates were 21%–22%.

Following the return of wolves, declines in winter habitat use by elk within the park have mostly occurred in the eastern and central portions of the northern range (White et al. 2012; Painter et al. 2015). It is also in the eastern portion of the northern range that studies first indicated that young aspen were beginning to increase in height, particularly within riparian areas (Ripple and Beschta 2007; 2012). Although Kauffman et al. (2010) sampled 16 aspen stands in 2004–2007 from across the northern range and found young aspen continued to be heavily browsed and short, more recently, Peterson et al. (2014) reported that young aspen in 113 northern range aspen stands went from average heights of 0.4–0.6 m during 1999–2007 to > 1 m by 2013. Painter et al. (2014) found that as browsing of young aspen in the northern range decreased after 2003 (Fig. 5c), young aspen heights began to increase after about 2006 (Fig. 5d); these trends have continued through 2012. Thus, observed reductions in browsing and increases in the average height of young aspen in the northern range appear to have largely occurred after the 2004–2007 field measurements of Kauffman et al. (2010). Kimble et al. (2011) in 2006 found no significant increase in young aspen on the portion of the northern range that occurs north of the park boundary, consistent with Painter et al.'s (2014) results indicating that the increases tended to occur after that time. Increased aspen heights and recruitment following the return of wolves have also been documented for Banff (Hebblewhite et al. 2005) and Jasper (Beschta and Ripple 2007b) national parks.

Any increase in growth and recruitment of young aspen that might be attributed to climatic variables implies that these plants are growing faster because of improved site productivity. Based on measurements in 2006 from 98 aspen stands in the eastern portion of the northern range, Ripple and Beschta (2007) found no significant difference in the current annual growth of unbrowsed aspen leaders (an index of site productivity) for riparian and upland stands, perhaps because aspen stands normally occur on relatively moist sites (DeByle and Winokur 1985). Remeasurement of these stands in 2010 (Ripple and Beschta 2012) again found that

the current annual growth of unbrowsed leaders of riparian and upland stands were not significantly different. Similarly, Painter et al. (2014) found no relationship between current annual growth of unbrowsed leaders and young aspen height. In each of these studies, it was concluded that reduced herbivory, and not potential differences in site productivity or climatic variables, represented the major factor associated with observed increases in young aspen heights during recent years. If current levels of herbivory continue to decline, future fires may stimulate aspen reproduction and recruitment resulting in a different outcome than in the decades when wolves were absent (Romme et al. 1995).

Increased areal cover, height, and recruitment of woody browse species other than aspen, including willow, cottonwood, alder, and berry-producing shrubs, also have been documented in the northern range during recent years and usually have been associated with a decrease in herbivory (Beyer et al. 2007; Baril et al. 2011; Beschta and Ripple 2007a, 2012, 2014; Ripple et al. 2014b; Marshall et al. 2014). An inverse relationship between browsing intensity and height of young woody plants is central to the trophic cascade hypotheses, as it clearly identifies the mechanism via which top-down pressure ensues (Beyer et al. 2007; Painter et al. 2014). With reduced browsing of young plants, spatial differences in site productivity may also begin to influence plant responses (e.g., increases in heights and recruitment). For example, Johnston et al. (2011), using small 0.02 ha exclosures in four northern range riparian areas, observed greater height increases of willow on sites with high water tables, indicating that bottom-up factors such as moisture availability can mediate height increases once the overriding effects of intensive ungulate herbivory have been removed.

Collectively, northern range vegetation responses from a variety of studies indicate that recent shifts in elk distributions and reduced elk densities (White et al. 2012; Painter et al. 2015) are likely to contribute to continued changes in woody plant communities into the future. Such changes include improved habitat and food-web support for various avian and terrestrial wildlife species (Beyer et al. 2007; Baril et al. 2011; Beschta and Ripple 2012; Ripple et al. 2014b). Thus, large carnivore recovery may be an important passive restoration approach (Kauffman et al. 1997) in ecosystems previously altered by high densities of native ungulates.

Although the reduction in browsing over time observed in many of the recent northern range studies is consistent with a re-established wolf-triggered trophic cascade, other factors may have influenced the strength of such a cascade. For example, increased predation of elk calves by bears during spring and early summer (Barber-Meyer et al. 2008; Hamlin and Cunningham 2009) may have affected elk recruitment and space use in recent years. Increased migration outside the park also could be influenced by changes in the availability of irrigated forage (Wilmers and Levi 2013) or altered hunting pressure; hunting north of the park has been greatly reduced since 2005 (White et al. 2012; Painter et al. 2015).

Aspen communities in northern Yellowstone appear to be increasingly shifting from an alternative stable state, a state dominated by ungulate herbivory (Fig. 2b), to one that includes the top-down pressure, via large predators, causing reduced ungulate effects upon vegetation (Fig. 2c). However, the rate of vegetation recovery has varied spatially and temporally. Factors contributing to this variability might include the following: (i) the predator–prey ratio (wolves per 1000 elk), a potential index of this large predator's capability to mediate elk (Mech and Boitani 2003; Hebblewhite 2013), has been relatively high and stable only after 2003; (ii) although elk numbers for the northern range have trended downward since the reintroduction of wolves, indicating incremental reductions in herbivory pressure over time, elk densities in the western portion of the range have decreased more slowly than in the central and eastern portions of the range (Painter et al. 2015); (iii) the growth form of young aspen (single leader) may allow ungulates to relatively easily maintain them in a suppressed state compared with multiple-stemmed woody species such as willow (Archer and Tieszen 1980); (iiii) even with declining elk populations, aspen may continue to experience considerable browsing pressure because these plants are highly palatable relative to other available woody species (Nelson and Leege 1982); and (iv) aspen suppressed by browsing may require several years for recovery to begin even when ungulate herbivory is entirely removed, as shown by age structure data for northern range aspen exclosures (Figs. 4a–4e). In addition, bison numbers in the northern range have trended upward since about 1997 and, therefore, may be contributing to aspen herbivory in those areas frequented by bison (Painter and Ripple 2012; Beschta and Ripple 2014; Painter et al. 2015). There is substantial dietary and habitat overlap between elk and bison on the northern winter range, suggesting that bison may have benefitted from reduced competition with elk (White and Garrott 2005).

Conclusions

More than one-half of a century after construction, fenced ungulate exclosures in northern Yellowstone National Park have provided an improved understanding of the potential roles of large carnivores, large herbivores, and bottom-up forces on aspen stand dynamics. Although temporal patterns of aspen recruitment varied within and between exclosures, all experienced a major increase in recruitment following the cessation of ungulate herbivory. This increase prevailed in spite of a long-term drying trend (i.e., a declining PZI) and confirms that climatic conditions since the mid-1900s were not a major limitation to aspen recruitment. These results are additionally important because they are the opposite of what was occurring in northern range aspen communities outside of exclosures. Here, in the absence of wolves, recruitment had been undergoing a long-term decrease since the early 1900s due to high levels of elk herbivory and essentially ceased in the later portion of the century.

The decreased browsing and increased height of young aspen that has become increasingly prevalent in northern range stands during the last two decades, following the return of wolves, has also been found in other northern range studies of cottonwoods, willows, alder, and berry-producing shrubs. These changes represent a fundamental departure from the sustained suppression of deciduous woody plants by ungulate herbivory that increasingly prevailed during the decades of wolf absence. If current trends continue, improved recruitment of deciduous woody species should eventually help recover the composition, structure, and function of aspen stands and riparian communities in Yellowstone's northern range even as these communities continue to be affected by a warming and drying climate. Collectively, our results are consistent with the re-establishment of an effective large predator guild following the return of wolves. Where wild ungulate herbivory is significantly affecting woody plant communities elsewhere in western North America, recovery of large predators may provide an important management option for reducing such effects.

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