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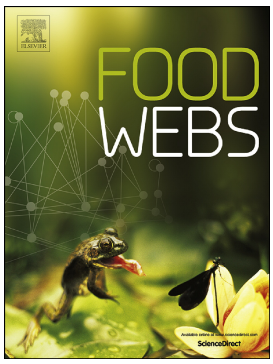

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Revisiting trophic cascades and aspen recovery in northern Yellowstone

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ABSTRACT

We revisit the nature and extent of trophic cascades and quaking aspen (*Populus tremuloides*) recovery in the northern range of Yellowstone National Park (YNP), where studies have reported on Rocky Mountain elk (*Cervus canadensis*) browsing and young aspen heights following the 1995-96 reintroduction of gray wolves (*Canis lupus*). A recent study by Brice et al. (2021) expressed concerns about methodologies employed in earlier aspen studies and that results from those studies exaggerated the extent to which a trophic cascade has benefitted aspen, concerns such as: (a) the selection of aspen stands, (b) young aspen sampling and measurements within stands, (c) the upper browse level of elk, (d) cause of increased young aspen height growth, (e) interpretation of browsing and height data, and others. We review these concerns but conclude that earlier aspen studies have provided important insights regarding the recovery of aspen that is underway in northern Yellowstone. We also found that Brice et al. (2021) misinterpreted or misrepresented

various aspects of those earlier studies, while failing to address potential biases and shortcomings of their own 2007-2017 study, including: (1) sampling aspen stands from only a portion of the park's northern range, (2) not randomly selecting aspen stands across their study area, but only within identified treatments, (3) varying sampling density (stands/km^2) by more than an order of magnitude between treatments, and (4) not sampling all stands in most years. Regardless of the advantages or disadvantages of the sampling designs and research methodologies employed in various aspen studies, they have consistently shown that decreased browsing has resulted in greater young plant heights in YNP's northern range, results supportive of an ongoing trophic cascade.

Key words: Wolves, Elk, Aspen, Herbivory, Trophic cascade, Yellowstone

1. Introduction

The potential for large mammalian predators to generate a trophic cascade in terrestrial ecosystems is a topic of considerable interest to the scientific community (Terborgh and Estes, 2010; Estes et al., 2011; Ripple et al., 2014; Natsukawa and Sergio, 2022), as well as the general public (Chadwick, 2010). In the mid-1990s, an opportunity to evaluate potential trophic effects of large predators upon ungulate prey and plants in the northern Rocky Mountains materialized when gray wolves (*Canis lupus*) were reintroduced into Yellowstone National Park (Smith et al., 2003). Prior to reintroduction, biologists were most interested in understanding and predicting possible changes in Rocky Mountain elk (*Cervus canadensis*) populations that might occur following the return of wolves (Varley et al., 1992). At the time there was little appreciation that restoring this apex predator might initiate a trophic cascade affecting woody plant communities, from a

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condition of height suppression by ungulate browsing for nearly all accessible young plants to one where such browsing no longer had a dominating influence.

Brice et al. (2021), hereafter referred to as simply "Brice et al.," recently reported on browsing and height trends of young quaking aspen (*Populus tremuloides*) for the period 2007-2017 in a portion of Yellowstone National Park's northern ungulate winter range, or "northern range", that lies within the park along its northern boundary. This area (Fig. 1) has provided a textbook example of a trophic cascade, based on studies showing that young aspen and other deciduous woody plants have responded to reductions in elk browsing following wolf reintroduction (see synthesis by Beschta and Ripple, 2016). While the results of Brice et al. supported the occurrence of a trophic cascade with aspen, they nevertheless claimed that earlier studies overstated these effects. First, at issue was the method of sampling employed to evaluate if any young aspen were growing taller and might eventually become overstory trees. Second, it was asserted that the interpretation of data as evidence for a trophic cascade was exaggerated and did not account for other possible explanations of observed trends. In the discussion that follows we address those concerns, as well as the sampling methods utilized and the interpretation of data in earlier studies. We also identify previously unacknowledged limitations regarding the underlying sampling design of Brice et al. and briefly compare their methodology to that used in recent aspen studies.

2. The northern range study area

Yellowstone National Park was established in 1872 and, over time, park administrators increasingly protected native ungulates while persecuting predators. By the mid-1920s wolves had been extirpated, and cougars nearly so. With few predators, and an absence of hunting in the park, the northern Yellowstone elk herd increasingly browsed

deciduous woody species, eventually preventing young aspen, cottonwoods (*Populus* spp.), willows (*Salix* spp.), and others from growing taller (Kay, 1990; Ripple and Larsen, 2000; Barmore, 2003; Wolf et al., 2007; Ripple et al., 2015; Peterson et al., 2020). Following the 1995-96 reintroduction of wolves (Smith et al., 2003), thus completing the park's large predator guild, the northern elk herd population decreased from record highs of nearly 20,000 animals in the 1990s to about 5,000 animals in recent years. The initial decline was likely due to a number of causes, such as a highly degraded winter range causing a shortage of forage, severe winters in 1996/97 and 1998/99, increased migration of elk out of the park, and human hunting outside the park, as well as predation from wolves and other large carnivores. In contrast, bison (*Bison bison*) numbers on the northern range increased seven-fold, from about 500 animals in the late 1990s to 3,500-4,000 animals by 2017 (Beschta et al. 2020).

3. Recent studies of young aspen

In the 1990s and preceding decades, intensive browsing by elk held nearly all young aspen plants in the northern range below a height of 100 cm (Ripple et al., 2001; Larsen and Ripple, 2005; Peterson et al., 2014), and overstory aspen trees were dying without new recruitment to replace them (Houston, 1982; Kay, 1990). When the park service reintroduced wolves in 1995-96, it was not known if they would sufficiently mediate the behavior or density of elk to reduce herbivory on young woody plants so that they could grow taller. Nevertheless, field observations in the early 2000s indicated that some young aspen were beginning to grow taller, thus raising several questions:

(1) Will any of these young aspen eventually grow tall enough to escape browsing by elk and, if so, were they a precursor to a more widespread release of other woody plants?

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(2) To what extent did a decline in browsing rate or other some factor contribute to increased heights?

(3) Was this the beginning of a trophic cascade involving large carnivores, elk, and woody plants that would release these plants from suppression by browsing?

Following the return of wolves, most early aspen studies within the park's northern range and adjacent areas (Table 1) employed a method of sampling that involved identifying the five tallest (5T) young aspen within a stand and then assessing their history of browsing and height growth, based on plant architecture measurements (Keigley and Frisina, 1998). The underlying purpose of this approach was to detect, as early as possible, any new trends in browsing and heights of young aspen. The method was first implemented in a 2006 field study designed to compare differences in young aspen growth between adjacent riparian and upland stands, against a background of near complete failure of aspen recruitment in previous decades (Ripple and Beschta, 2007). These 5T stems represented some of the earliest plants to release (i.e., increase in height from previously being suppressed by browsing) and the first to grow tall enough to potentially escape from elk browsing, thus suggesting that they might survive to become tall saplings and, eventually, overstory trees. A young aspen height >200 cm was used as an indication of new recruitment.

An underlying hypothesis of these studies was that the increased heights of these young aspen might signal the beginning of a trophic cascade. Within two decades of wolf reintroduction, 24 assessments of deciduous woody species in northern range riparian areas had been published (Beschta and Ripple, 2016). More than half of the studies evaluated ungulate browsing, and all found increased growth or cover of woody plants that occurred concurrently with a decrease in browsing.

4. Concerns of Brice et al.

4.1 *Selecting aspen stands*

Brice et al. suggested that aspen studies employing the 5T method did not use random selection of aspen stands and were therefore invalid, misleading, or unrepresentative. In fact, all 5T studies that sampled aspen stands within the park either (1) randomly selected stands or (2) selected all stands within a defined study area (Table 1), both acceptable experimental designs. Outside the park, Painter et al. (2018), used random selection in some treatment areas, but selected stands visible from roads and trails for two other areas.

Brice et al. also asserted that "by definition, 5T sampling measures only stands and locations within stands that produce young aspen." If the assertion is that stands were chosen based on the presence of young aspen, this is simply incorrect. As was the case for stands Brice et al. utilized in their study, which had been earlier chosen by Ripple et al. (2001), the selection process in all 5T aspen studies required each stand to have one or more overstory trees present and did not require the presence of young aspen. In no case was a stand rejected for sampling due to a lack of young aspen. While the repeated sampling of marked plots by Brice et al. allowed them to track stands where young aspen may have died out over time, this does not invalidate the methods of other studies.

4.2 *Selecting young aspen within a stand*

Brice et al. indicated that 5T sampling results have "exaggerated the aspen population response to wolf reintroduction," seeming to not understand that 5T studies were attempting to identify early changes in young aspen dynamics in the northern range and were not intended to characterize the population of all young aspen. There was no claim in any 5T study that all young aspen were growing taller, only that some young aspen in some stands were growing taller, potentially leading to new aspen recruitment for the first

time in decades (Table 2). Indeed, the average height of the five tallest young aspen selected from across a stand will always be greater than the average height of young aspen measured in a small 20 m^2 plot, such as that used by Brice et al. Painter et al. (2014, 2015) subsequently addressed this issue by measuring, in conjunction with 5T sampling, young aspen heights in random plots for 87 randomly selected stands across the northern range. The results of this random sampling in 2012 confirmed what had previously been suggested by 5T studies – that many, but not all, stands had new recruitment of tall young aspen associated with lower rates of browsing.

Painter et al. (2014) also established young aspen height trends over time based on random sampling plots. Plot data from stands in 1998, when browsing rates were consistently high and aspen regularly suppressed, were compared to the same stands in 2012 when average browsing rates were less and there was greater variation in young aspen heights. This comparison further demonstrated that a change in young aspen dynamics had begun, establishing trends over time by two different methods.

The data of Brice et al. show that variation in heights of young aspen has increased over time, which is another indication of changing growth patterns and a trophic cascade (Carpenter and Brock, 2006; Guttal and Jayaprakash, 2008). Furthermore, there is a strong correlation between average young aspen heights and average 5T heights ($r^2 = 0.95$, Fig. 2) in their sampled stands. Thus, contrary to the assertions of Brice et al., the 5T approach appears to have successfully functioned as a leading indicator of subsequent increases in average young aspen heights. We also suggest that 5T stem sampling is a more efficient and ecologically relevant measure of early recruitment success in a northern range aspen stand than is obtained from measuring the average height of young aspen within a small random plot. If at least some young aspen within a given stand can grow above the typical

upper browse level of elk, a situation that is easily detected by 5T sampling, this increases the likelihood that the stand may persist into the future, regardless of the average height of the remaining young aspen.

4.3 *Average height increases – 5T and plots*

Brice et al. indicated that a "weaker" trophic cascade was obtained from random plot data of average aspen heights than was indicated in earlier 5T studies, because the random plot data showed less increase in average height than the 5T data, though both increased over time. Certainly, the data from random sampling plots, such as from Painter et al. (2014) and Brice et al., add a valuable perspective to 5T data, but random sampling is not necessarily the best indicator of sapling recruitment. Any group of young aspen in Yellowstone's northern range normally contains many relatively small individuals that may be suppressed by a variety of factors (e.g., shading, site quality, browsing) and the small fraction of saplings that ultimately survive to regenerate a stand will most likely arise from any taller individuals that may currently be present. As some young aspen in a stand grow taller, the height distribution will become more skewed and result in greater variance. Thus, what may be considered an "unbiased" random sample from plots will generate data that are noisier and may be less relevant to the question of what is limiting stand regeneration than a method such as 5T that measures the leading edge of recruitment.

4.4 *Upper browse level of elk*

Brice et al. were concerned that recent northern range aspen studies (Table 1) assumed "that stems taller than 200 cm escape browsing [by elk]," and that this assumption exaggerated any claims of aspen recruitment. Clearly, elk browsing does not stop at an exact height, and elk will sometimes browse plants taller than 200 cm. The 5T studies critiqued by Brice et al. did not assume that all tall saplings would survive to become trees.

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Rather, the 200 cm threshold was used as a meaningful indicator that elk were no longer preventing growth of tall saplings, thus increasing the likelihood of new overstory trees in the future.

In an evaluation of nearly 3,900 aspen stands in and around Yellowstone National Park, Kay (1985) indicated that young aspen stems taller than 200 cm represented successful regeneration and recruitment because they "had grown beyond most ungulate use." A 200 cm height criterion has also been used in many western North American studies to evaluate recruitment success of young aspen in areas where elk browsing was an important factor (e.g., DeByle, 1985; Kay et al., 1996; Barnett and Stohlgren, 2001; Smith et al., 2001; Kay, 2001a; 2001b; 2003; Larsen and Ripple, 2005; Kimble et al., 2011; Taylor and Arends, 2012; Rogers and Mittanck, 2014; Rogers et al., 2021). These various studies employed a 200 cm height criterion because it has proven to be a useful indicator of recruitment success. Finally, we note that recently developed guidelines for restoring aspen in the Intermountain West specify a height of 183 cm (i.e., 6 ft) for determining recruitment success (Kitchen et al., 2019) and that some studies (e.g., Rhodes et al., 2017; 2018) have used an even lower height, that of 150 cm.

Results from Price et al. showed reduced browsing rates for plants taller than 200 cm, and even lower rates above 300 cm (their Fig. 2b, 2d), suggesting a greater likelihood of continued height growth for those plants. While they also noted that 400 cm more accurately represented the highest possible browse height of northern range ungulates, that height is less relevant as an early indicator of recruitment. We recommend future research to quantitatively test aspen height thresholds and their statistical probability of recruitment into the overstory at various intensities of browsing.

4.5 *Growth conditions*

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Young aspen heights across the northern range in the decades prior to the return of wolves were generally restricted to <100 cm in height by intensive elk browsing, regardless of site quality, climate trends, or other factors (Barmore, 2003; Larsen and Ripple, 2005). However, Brice et al. contended that the tallest young aspen, as measured by the 5T method, likely occurred on the most favorable growing sites, thus realizing a level of recruitment unattainable for the average young aspen. A more plausible hypothesis for explaining increased heights of young aspen in the last two decades is a significant decrease in browsing, as has been measured in multiple studies of aspen and other woody species (Ripple and Beschta, 2007; Painter et al., 2014; Beschta et al., 2016; 2018) and confirmed by Brice et al.

Certainly, indicators of site productivity such as soil type, soil moisture, and sun exposure affect plant growth rates, and with a decrease in browsing these other variables may contribute to greater variability in young aspen heights. To assess the possible influence of site productivity on young aspen height increases, Ripple and Beschta (2007, 2012) compared current annual growth (CAG) of unbrowsed aspen leaders (a measure of site productivity) for two adjacent groups of stands that differed greatly in young aspen height. Surprisingly, they found that the average CAG was nearly identical in both groups of stands, but the group with a lower browsing rate had taller young aspen, demonstrating that differences in height were not due to differences in site quality but instead were due to differences in browsing. In addition, Painter et al. (2014, 2015) analyzed young aspen from random plots within randomly selected stands and found no relationship between productivity and young aspen height, but an inverse relationship between browsing and height.

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An inverse relationship between browsing and plant height is central to the trophic cascade hypothesis because it demonstrates the mechanism connecting the various trophic levels: carnivores cause a reduction in herbivory, resulting in greater plant growth (Beyer et al., 2007). Inverse relationships have been observed in all previous northern range aspen studies, as well as that of Brice et al., supporting the hypothesis that decreases in browsing, not differences in site productivity, have allowed young aspen to grow taller in Yellowstone's northern range.

Another hypothesis, suggested by Brice et al., was that 5[illegible] stems were likely browsed less because they were taller, and that previous studies simply assumed increased heights were the result of decreased browsing. This assertion ignores the recent ecological context of near complete suppression of aspen by browsing in the decades before wolf reintroduction and is a misreading of these previous studies, which recognized and addressed this causal ambiguity (e.g., Ripple and Beschta, 2007; Painter et al., 2014; 2015; 2018). If reduced browsing was the result rather than the cause of taller heights, then there should be a relationship between productivity (as indexed by annual leader length) and the height of young aspen, but as indicated previously this has not been the case. And, if browsing rates were mostly due to height preferences of elk, as Brice et al. suggest, then tall saplings would be heavily browsed on their lower branches; instead, tall saplings occurred in places where browsing was less (Painter et al., 2018). Based on a broad spectrum of northern range studies (Beschta and Ripple, 2016), decreased elk browsing remains the most plausible explanation for the ongoing release of young aspen and other deciduous woody plants that has been underway since the early 2000s.

5. An assessment of Brice et al.

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We agree with Brice et al. that evaluating trophic cascades associated with large mammalian predators is challenging. We also agree that it would be a mistake to confuse measurements of the tallest with the population average. However, sampling the 5T young aspen within northern range aspen stands, using randomly selected stands or all stands within a defined study area (Table 1), has not confounded our understanding of a trophic cascade in aspen, but instead has allowed for its early discovery and demonstration. And, as summarized in Table 2, 5T sampling was never intended to represent the average height of young aspen in Yellowstone's northern range, but instead to detect early changes and trends in young aspen dynamics.

The results of earlier 5T aspen studies (Table 1) were contextualized and supported by subsequent range-wide random sampling of Painter et al. (2014, 2015). We thus reject the broadly cast assertions of bias by Brice et al. regarding earlier Yellowstone aspen studies. For example, in 2012 Brice et al. sampled all of their 113 stands, and Painter et al. also sampled 87 randomly selected stands, so the two studies may be directly compared from published results. Painter et al. (2014) reported the mean height of young aspen in 2012 as 91 cm and 214 cm from random plots and 5T measurements, respectively. This compares to about 90 cm and 190 cm in Figure 3b of Brice et al. (2021), results that are very close and within the confidence intervals of the estimates. Furthermore, despite the claim that their data are more representative of young aspen on the northern range than other studies, the study design used by Brice et al. had possible sources of bias that could significantly limit the importance and utility of their results.

5.1 *Study area, sampling, and scope of inference*

Brice et al. indicated that they (1) "measured browsing and height of young aspen in 113 plots distributed randomly across the study area" which they had previously identified

as the 995 km^2 portion of the northern range that lies south of the park's northern boundary, and (2) that these stands were "selected from an inventory of stands with respect to high and low wolf-use areas." Both statements require significant qualification.

Regarding the areal extent of their study, the stands utilized by Brice et al. were originally selected by Ripple et al. (2001) using a sampling design that excluded portions of the northern range and utilized stands in locations intended to represent specific treatments, not overall conditions across the northern range (Fig. 3). For example, approximately 225 km^2 in the western portion of the northern range within the park was outside of the designated study area. Another 162 km^2 were classified as "wolf pack buffer zones," and these areas were also excluded from sampling. Thus, the aspen stands sampled by Brice et al. came from only 61% of the 995 km^2 of northern range that lies within the park. Furthermore, not all stands were sampled each year. While all 113 stands were sampled in 2011 and 2012, none were sampled in 2015. For the remaining 8 years, an average of 16% and 28% of their stands were not sampled for young aspen in plots or for 5T stems, respectively.

With regard to the sampling of "high and low wolf-use areas," their data sets were actually based on a stratified random sampling design with disproportionate sampling densities between three strata. Ripple et al. (2001) identified three treatment categories for sampling aspen stands: (1) high human presence (Mammoth village, YCC Complex, and Roosevelt Lodge), (2) high wolf use (Leopold, Rose Creek, and Druid packs), and (3) low wolf use. The total area associated within the high human presence, high wolf use, and low wolf use treatments was 20 km^2, 84 km^2, and 505 km^2, respectively (Fig. 3b), and the number of stands within each area was subjectively designated to provide enough stands to adequately characterize young aspen within each treatment. Although stands within each

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treatment were randomly chosen, sampling densities (stands/km^2) varied by more than an order of magnitude between treatments, with average densities of 0.84, 0.71, and 0.07 stands/km^2 for the high human presence, high wolf use, and low wolf use treatments, respectively (Fig. 3b) and wolf pack buffer zones within the study area were not sampled (Fig. 3a). The relatively high sampling densities in the vicinity of Mammoth (i.e., Mammoth Village and the YCC Complex), an area of high human presence, are easily discerned by a tight cluster of sampled stands in Fig. 3b. It is unclear why Brice et al. did not use their data sets to assess potential treatment effects, but instead used them in an attempt to represent aspen stands across the northern range, an analysis for which they were not intended. To date, only the study of Larsen and Ripple (2005) has randomly selected aspen stands from across the park's portion of the northern range, stands that were subsequently resampled by Painter et al. (2015).

The (a) exclusion of 23% of northern range from their study area and another 16% associated with wolf pack buffer zones, (b) large differences in aspen response between treatments, (c) a wide range of sampling densities between treatments, and (d) the fact that not all stands were sampled each year create an unknown degree of bias that directly affects the scope of inference regarding how well results of Brice et al. represent northern range aspen stands, issues that were not addressed in their study. In other words, their dataset was not designed as a random or representative sample of aspen stands from across the northern range, nor should it be characterized as such. Therefore, their dataset should be viewed cautiously with these limitations in mind.

5.2 *Comparing methods*

There is little doubt that 5T sampling has provided an early indication of increased young aspen heights following the return of wolves. As shown in Fig. 5, a relatively

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systematic pattern of increasing heights occurred for each time series, where average 5T heights, as expected, increased well in advance of average young aspen heights. For example, an average 5T height of ~120 cm occurred in 2007, whereas the equivalent average young aspen height on plots was not realized until 2015, some eight years later. Although Brice et al. asserted that their results "do not support the hypothesis that the tallest young aspen represent a 'leading edge' indicator of a "broader shift in plant community dynamics," Fig. 5 indicates otherwise.

Brice et al. compared browsing rates obtained from random sampling plots to the 5T method and concluded that the 5T method exaggerated the decrease in browsing rates. However, they included young aspen taller than 200 cm in these estimates, something Painter et al. (2014, 2015) did not do. Even so, Brice et al. (Fig. 3a) found the two methods yielded similar browsing estimates in 2007, likely because there were few tall saplings in 2007 to bias the 5T data. As saplings grow above 2 m, browsing rates decrease rapidly with height, so including these tall saplings does not accurately measure browsing rates that may be suppressing shorter plants. The similarity of results for the two methods during the early years of aspen recovery validates the use of the 5T method for estimating browsing rates in 2006 and 2010 field studies by Ripple and Beschta (2007, 2012), when results from the two methods were remarkably close even with the inclusion of tall saplings.

Painter et al. (2018) also compared browsing rates obtained with random sampling plots to those from the 5T method. When only aspen <200 cm in height were included, browsing rate estimates for the two methods were almost identical, differing by only a few percentage points. This again illustrates that the 5T method was a useful and efficient method of estimating browsing rates during the early years of aspen recovery. However, in

recent years the 5T young aspen have been less useful as indicators of overall browsing because many have grown taller than 200 cm and so must be excluded to avoid biasing measures of browsing rates, as occurred in the results of Brice et al. To resolve this issue, Painter et al. (2018) used random sampling of aspen <200 cm tall to estimate browsing, in conjunction with the 5T method for assessing aspen recruitment.

Young aspen may sometimes be absent within a small plot, such as the 20 m^2 plots of Brice et al., resulting in no young aspen measurements as well as no recruitment, although both may be present elsewhere in the stand. Others have used considerably larger plots (e.g., 202 m^2) when trying to accurately characterizing aspen within a given stand (e.g., St. John, 1995; Kimble et al., 2011). Even if young aspen are present on a plot, the likelihood that they include some of the taller plants in the stand may be relatively small. Thus, if a research goal is to identify early recruitment of young aspen that were previously suppressed by browsing, the 5T method has a distinct advantage over the use of small plots (Fig. 4), and the results are "exaggerated" only if the purpose and limitations of the study design are misunderstood.

We also propose that the 5T method provided considerable efficiencies in time and resources for evaluating the early stages of aspen recovery. For example, the 5T approach required visiting an aspen stand only once and, with plant architecture measurements, allowed time series of annual browsing rates and plant heights of the 5T young aspen to be constructed for previous years, reaching back nearly a decade (Ripple and Beschta, 2007, Painter et al., 2014; Beschta et al., 2018). In contrast, repeat annual sampling of plots was required by Brice et al. for establishing temporal patterns of browsing and height.

Both methods, 5T vs. small plots, have strengths and weaknesses that go beyond mere efficiency of data collection, and using both can help provide a more complete view of

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aspen stand conditions and dynamics. In 1998 when browsing levels were exceptionally high and aspen recruitment was almost completely suppressed by intensive elk browsing (Larsen and Ripple, 2005), both methods would have yielded a similar result. However, average heights obtained by these two methods have increasingly diverged in recent years, as shown in Fig. 5. While the average 5T height for the stands sampled in 2017 by Brice et al. was 313 cm, indicating significant recruitment of tall young aspen, heights measured in their small plots that same year averaged only 141 cm (Fig. 5). While the 5T method does not capture the degree to which many young aspen might remain suppressed by browsing, or other factors such as pathogens, shading, and nutrient availability, the small random plot method is unable to confirm the degree to which many stands have experienced new recruitment that is of historical, biological, and ecological importance for sustaining northern range aspen communities.

In northern Yellowstone, annual browsing and height information associated with young aspen has largely been obtained via two approaches: (a) 5T sampling and plant architecture measurements (Table 1) and (b) small plots with annual plant measurements (Brice et al. 2021). Additional methods of evaluating ungulate browsing effects have been used in other studies, such as evaluating the age of terminal twigs since browsing, tracking the growth and survival of planted herbaceous plants or seedlings palatable to ungulates, and using lateral twigs for browsing and growth information (Blossey et al. 2017, Waller et al. 2017, Waller 2018). The use of such techniques in future studies could provide an improved basis for understanding browsing and plant growth in the northern range.

5.3 *Other ungulates*

Although Brice et al. acknowledged the presence of other large ungulates in the northern range, their discussion did not address the extent to which they might be

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suppressing young aspen heights (e.g., bison) or affecting upper browse levels (e.g., moose [*Alces alces*]). Browsing by elk has continued to suppress young aspen in some portions of the northern range (e.g., around Mammoth), yet in other areas (e.g., the Lamar Valley) increased bison herbivory has begun to limit the growth of young aspen (Painter et al., 2015; Beschta et al., 2018), much like elk did in previous decades. With the decrease in elk numbers and the increase in bison numbers during recent decades, overall foraging pressure by bison began to exceed that of elk in 2007 and it was 10 times greater than that of elk by 2018 (Beschta et al., 2020). Even though young aspen may represent a minor component of this large herbivore's diet, a greatly increased bison herd since 2004 is now suppressing the growth of many young aspen, willows, cottonwoods and perhaps other plant species across the Lamar Valley and other low-elevation portions of the northern range (Painter and Ripple, 2012; Beschta et al., 2020; Painter and Tercek, 2020).

Brice et al. indicated browsing rates of young aspen at heights above 200 cm were relatively low in 2007 but had increased by 2017, calling into question the use of 200 cm as an indicator of the upper browse level by elk. In their supplemental material they indicated that moose comprised about 10% of all ungulate sightings, based on camera records. Given their relatively large body size, studies of moose browsing have variously considered browsing effects up to 250 cm, and sometimes higher (Saether, 1990; Ericsson et al., 2001; Hornberg, 2001). Perhaps the recent but relatively small increase in browsing above 200 cm is due to a greater presence of moose as woody plant communities in various portions of the northern range continue to recover, providing improved foraging habitat for this large herbivore (Painter et al., 2014; Beschta and Ripple, 2016). If browsing by moose becomes a significant factor affecting aspen recruitment, future studies may need to take this into account, but so far moose have been a minor influence.

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6. Concluding remarks

We appreciate the efforts of Brice et al. in systematically collecting and analyzing young aspen browsing and height data from Yellowstone's northern range, and their results have augmented our understanding of those variables relative to 5T sampling vs. random plot sampling. However, we question the use of their publication as a vehicle to devalue previous aspen studies, the conclusions of which their new data actually support. We have also identified potential sources of bias in their sampling design and field measurements that should be considered when interpreting their findings.

In general, characterizations of young aspen in Yellowstone's northern range following the return of wolves, whether using 5T samples or those from plots, indicate that many previously suppressed young aspen plants have become taller each year and that recruitment above the upper browse height of elk is increasingly more widespread. It would thus appear that the reintroduction of wolves into the northern Yellowstone ecosystem has caused a shift in the dynamics of aspen communities, as well as those of other deciduous woody species (e.g., Beschta and Ripple, 2016). Yet, from an ecological perspective, the recovery of aspen stands is still in an early stage and the effects of a changing climate and increased bison population may affect how that recovery proceeds into the future. Thus, a continued effort by the scientific community will be needed to monitor and evaluate the dynamics of ungulates and aspen in northern Yellowstone National Park, and perhaps the Greater Yellowstone Ecosystem, as the ongoing trophic cascade continues to unfold.

Declaration of Competing Interest

None.

Acknowledgements

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TABLES

Table 1

Aspen studies in and around Yellowstone National Park (YNP) that, following the 1995-96 return of wolves, selected the five tallest (5T) young aspen within a stand for measuring annual browsing and heights; Halofsky et al. (2008) sampled the three tallest (3T) young aspen. In addition to 5T sampling, Painter et al. (2014, 2015) used random sampling plots in each stand.

General Location **Publication authors (year)**	**Study Area** **- treatments**	**Data Collection (year)**	**No. of Stands**	**Stand Selection***
Northern Range (inside park)				
Ripple and Beschta, (2007, 2012)	Eastern Sector of NR** - riparian stands - upland stands *Total number of stands*	2006 2006	44 54 *98*	All All
Painter et al., (2014, 2015)	NR *Total number of stands*	2012	87 *87*	RS
Beschta et al., (2018)	Western Sector of NR	2015	60	RS

	- Glen Creek drainage - near Mammoth *Total number of stands*	2016	38 *98*	All
Northwest Portion of Park				
Halofsky et al., (2008)	- unburned - burned *Total number of stands*	2004 2004	21 23 *44*	All All
North of Park				
Painter et al., (2018)	- Northern Sector of NR - Dome Mountain - Gallatin Canyon, #1 - Gallatin Canyon, #2 - Sunlight-Crandall *Total number of stands*	2015 2015 2014 2014 2011	22 7 30 46 43 *148*	RS R/T RS R/T RS

* All = all aspen stands within study area were selected

RS = aspen stands within study area were randomly selected

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R/T = stands visible from roads and trails were selected

** NR = Northern range

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Table 2

General conclusions from northern range studies that utilized measurement of the five tallest (5T) young aspen in stands as part of their study design. These quotes refute claims made by Brice et al. (2021) that earlier studies exaggerated changes occurring in plant communities. Contrary to their claim, none of these earlier studies reported that the deterioration of all aspen stands has been reversed.

Ripple and Beschta (2007)

"Our results indicate the first significant growth of young aspen in over half a century."

"Our data are only representative of the first recovering aspen (5 tallest per clone) and not an estimate of the aspen population response across Yellowstone's northern winter range."

Halofsky et al. (2008)

"Broadly, our results suggest aspen numbers and recruitment can be affected by multiple processes including top-down influences from large predators, pulse (fire) vs. chronic (herbivory in a wolf-free environment) disturbances, and bottom-up influences resulting from fire such as changes to apical dominance and shading."

Ripple and Beschta (2012)

"It should be noted that because we measured the five tallest young aspen in each stand, our results represent the ''leading edge'' of aspen recruitment."

"When documenting recruitment [of woody species], authors [of other northern range studies] consistently reported (1) that plant height increases were inversely related to browsing levels and (2) increased growth/recruitment was 'spatially patchy' and only found at some sites and not others."

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"Even so, none of the studies we reviewed indicated recruitment of woody browse species across all potential sites during the first 15 years after wolf reintroduction and it appears Yellowstone may still be in the early stages of ecosystem restoration resulting from a trophic cascade caused by wolves."

Painter et al. (2014)

"In the last decade some saplings survived to grow above the reach of elk, in contrast with the absence of tall saplings in sampling plots in 1997–1998."

"Many aspen stands are in the early stages of recovery as indicated by decreased browsing and increased height of young aspen."

Painter et al. (2015)

"Recent growth of aspen saplings above the browsing height of elk is evidence of a beginning aspen recovery in northern YNP [Yellowstone National Park]."

"The resulting increase in aspen recruitment is evidence of a trophic cascade at a landscape scale."

Beschta et al. (2018)

"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."

"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."

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Painter et al. (2018)

"As elk densities have decreased more in some areas than others, spatial variation in browsing has increased, resulting in a patchy increase in aspen recruitment."

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LIST OF FIGURES

Fig. 1. The northern ungulate winter range comprises approximately 1,500 km^2 of mountainous terrain of which 995 km^2 (comprising primarily the West, Central, and East Sectors) occur mostly inside Yellowstone National Park.

Fig. 2. Average height of young aspen in small random plots (y-axis) vs. the average annual height of the five tallest (5T) young aspen (x-axis) in northern range aspen stands for years 2007-2014, 2016, and 2017 (data source: Brice et al., 2021).

Fig. 3. Yellowstone's northern range (inside the park) identifying (a) a portion of the west sector outside the study area of Brice et al. (2021) study area and wolf pack buffer zones within the study area, both of which were not sampled, and (b) the location and density of sampled aspen stands within the study area, by treatment (see Ripple et al., 2001).

Fig. 4. Percent of aspen stands in 2017 where the average height of the young aspen from small plot or five tallest (5T) sampling equaled or exceeded the indicated height (data source: Brice et al., 2021).

Fig. 5. Annual time series of the average height (cm) of the five tallest (5T) young aspen (cm) and the average height of young aspen measured on 20 m^2 plots in northern range aspen stands [data sources: 1999-2006 from Peterson et al. (2014); 2007-2017 from Brice et al., (2021)]. The horizontal arrow indicates that the average 5T height in 2007 preceded an equivalent value of average young aspen height by approximately eight years. Dashed

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lines and coefficients of determination (r^2) from fitted exponential equations for purposes of illustrating general trends.

Conflict of interest

None.

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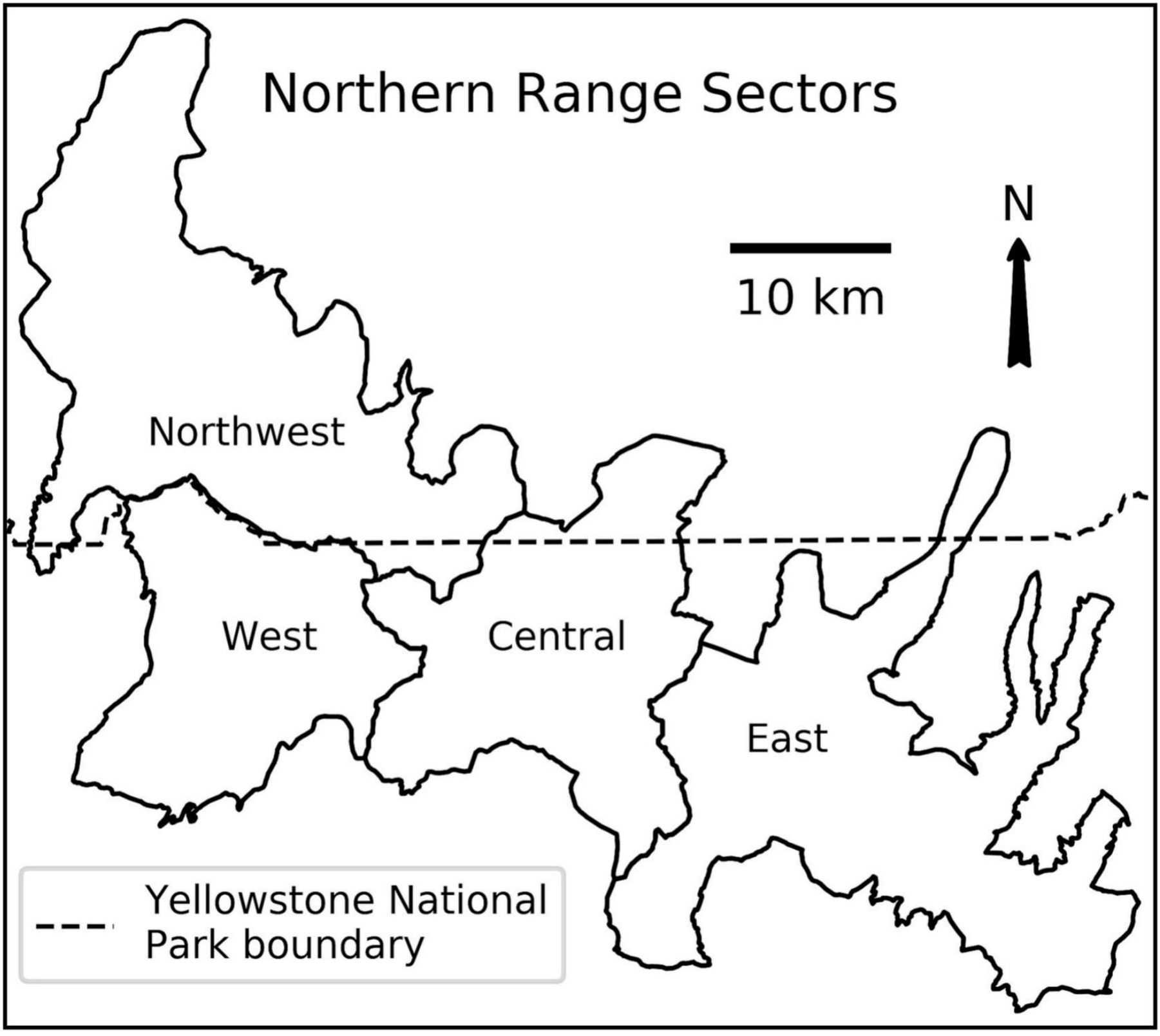
Northern Range Sectors
N
10 km
Northwest
West
Central
East
Yellowstone National Park boundary

Figure 1

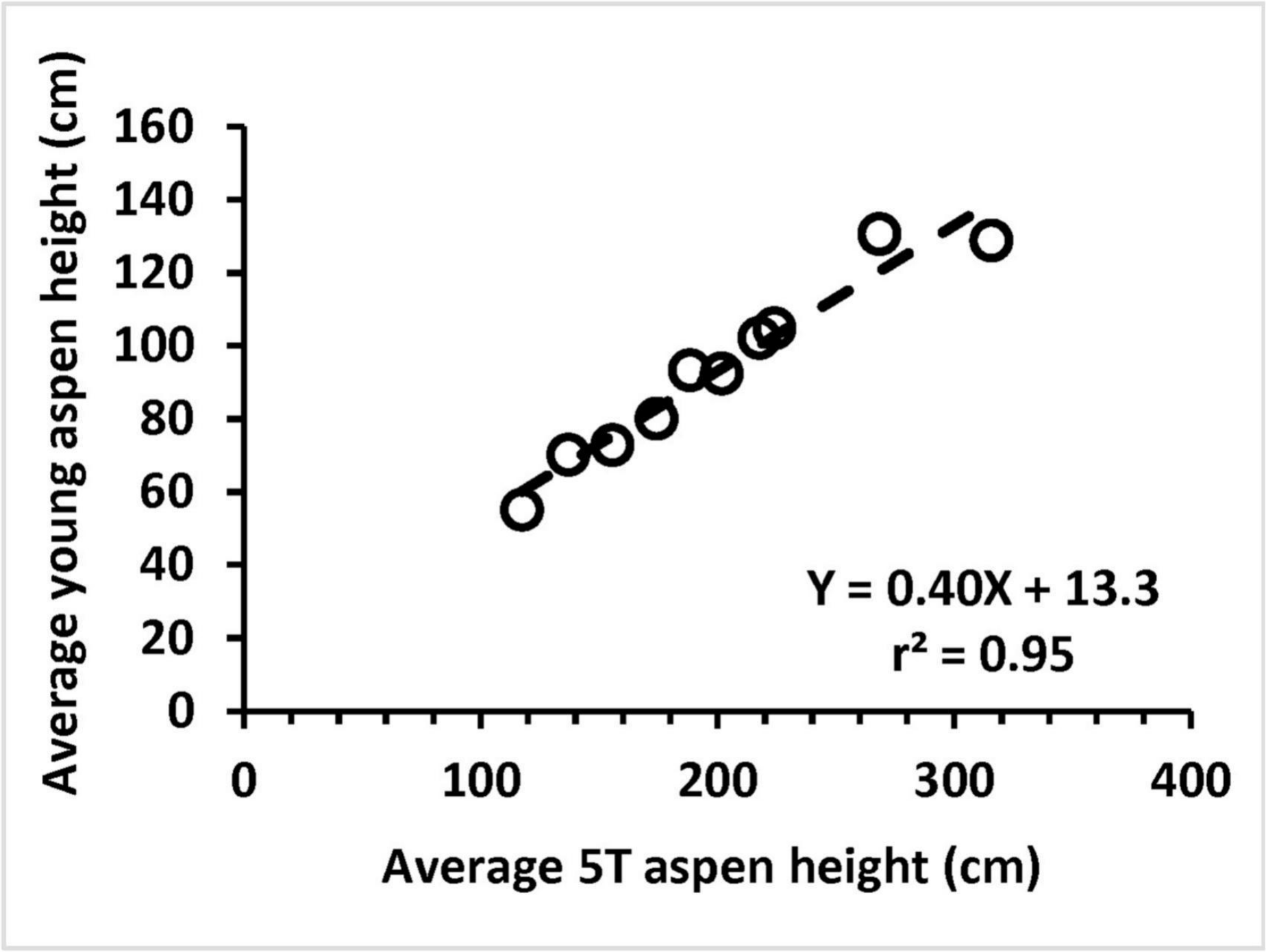
Average young aspen height (cm)
160
140
120
100
80
60
40
20
0
0
100
200
300
400
Average 5T aspen height (cm)
Y = 0.40X + 13.3
r² = 0.95

Figure 2

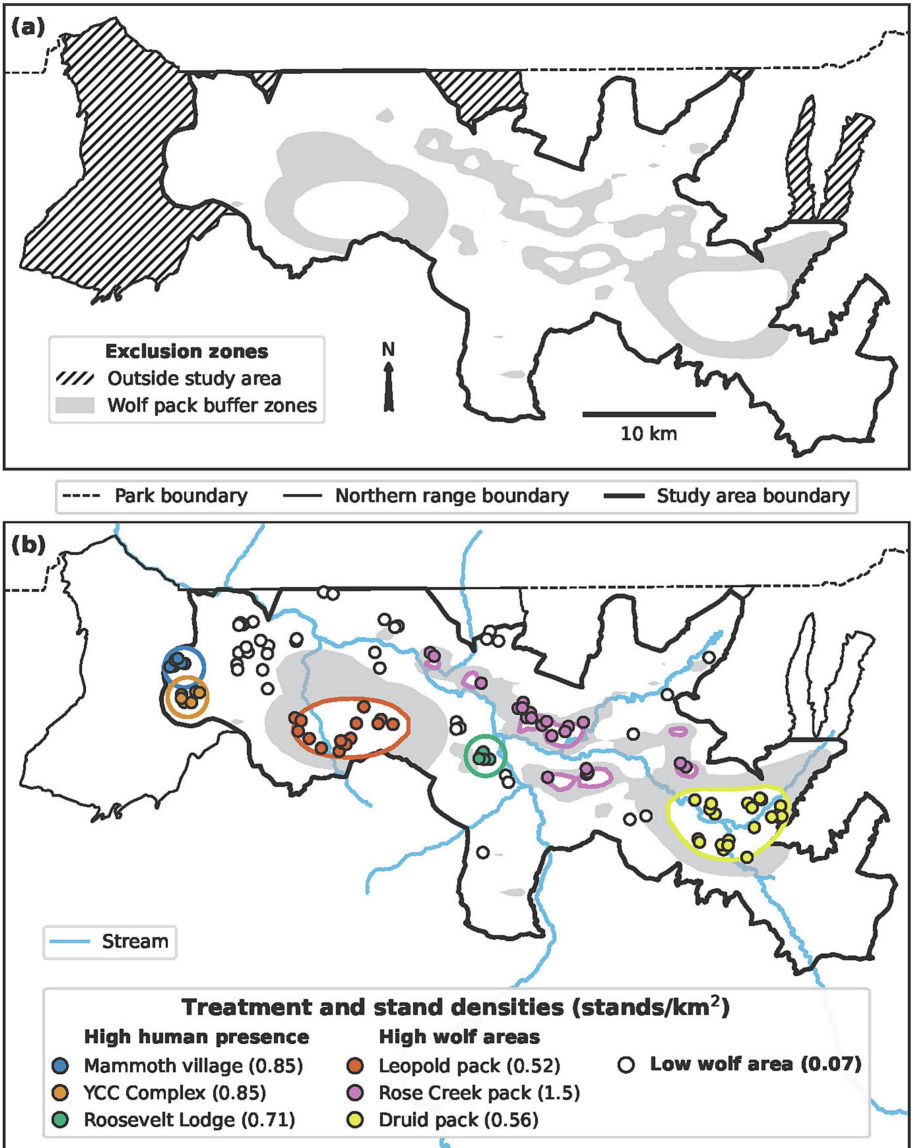
(a)
Exclusion zones
Outside study area
Wolf pack buffer zones
N
10 km
Park boundary
Northern range boundary
Study area boundary
(b)
Stream
Treatment and stand densities (stands/km²)
High human presence
Mammoth village (0.85)
YCC Complex (0.85)
Roosevelt Lodge (0.71)
High wolf areas
Leopold pack (0.52)
Rose Creek pack (1.5)
Druid pack (0.56)
Low wolf area (0.07)

Figure 3

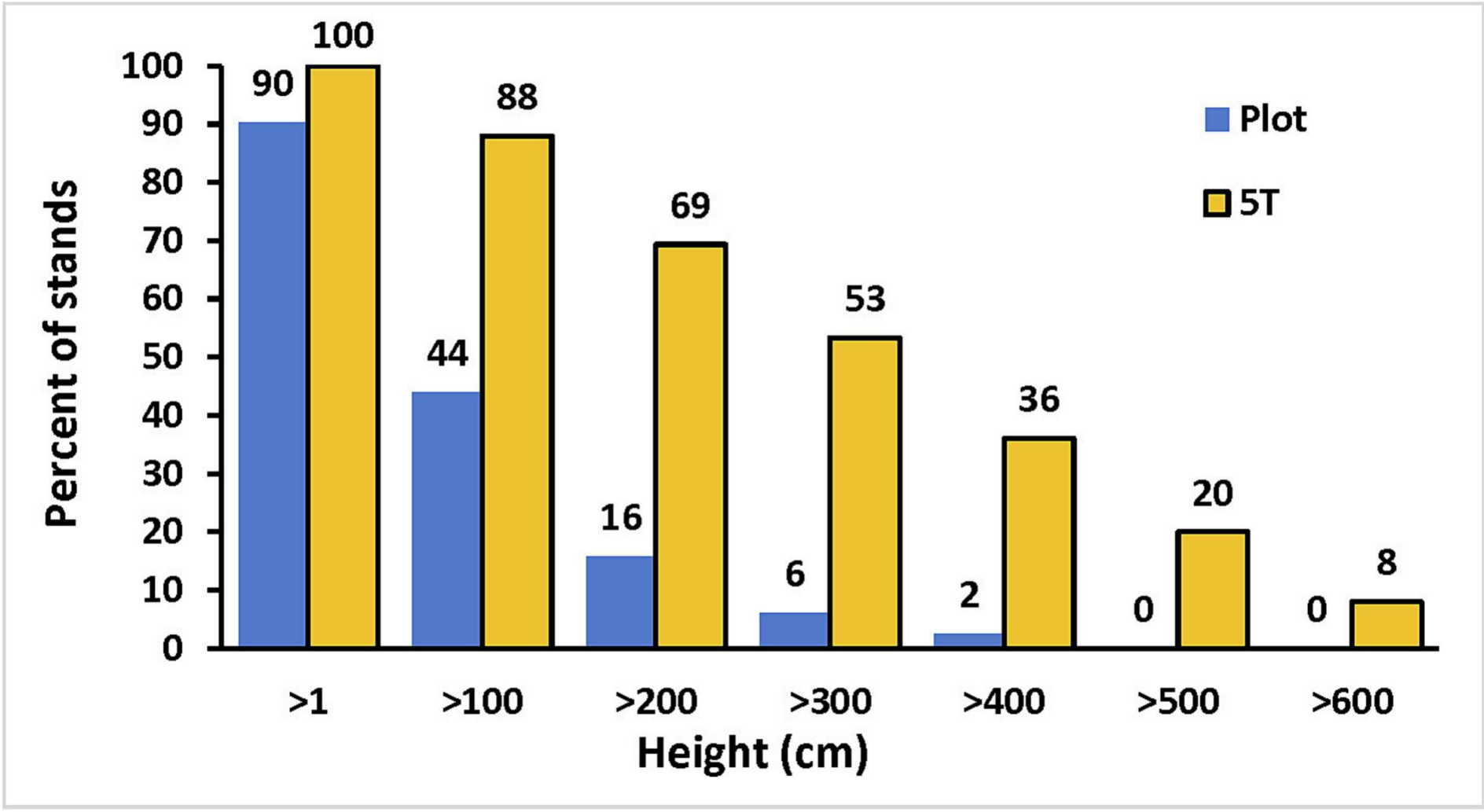
Percent of stands
100
90
80
70
60
50
40
30
20
10
0
90
100
44
88
16
69
6
53
2
36
0
20
0
8
Plot
5T
>1
>100
>200
>300
>400
>500
>600
Height (cm)

Figure 4

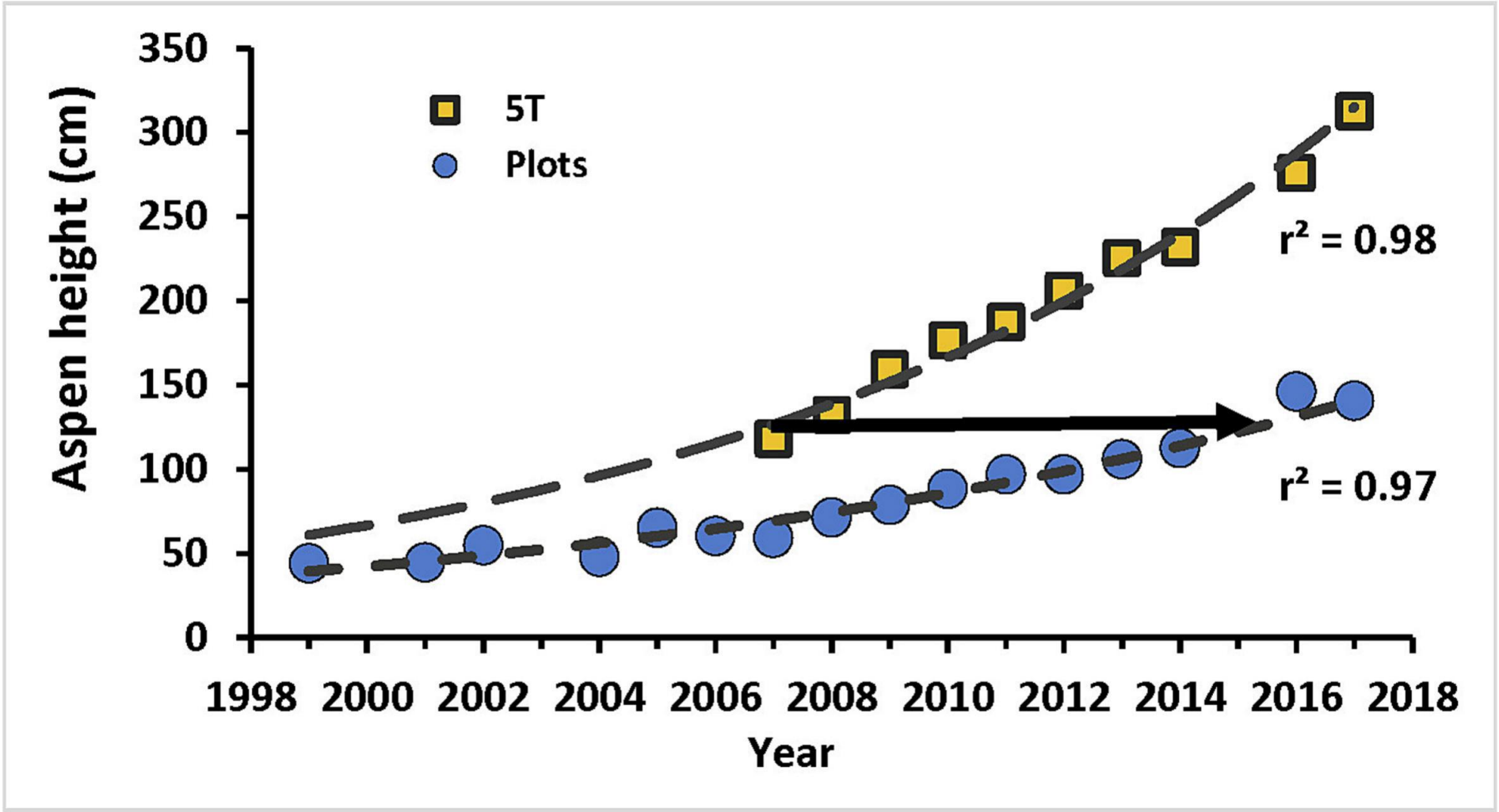
Aspen height (cm)
350
300
250
200
150
100
50
0
5T
Plots
r² = 0.98
r² = 0.97
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
Year

Figure 5