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Trophic cascades from wolves to alders in Yellowstone

William J. Ripple [a,*], Robert L. Beschta [a], Luke E. Painter [b]

[a] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA
[b] Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

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ABSTRACT

We explored possible interactions among gray wolves (*Canis lupus*), Rocky Mountain elk (*Cervus elaphus*), and thinleaf alder (*Alnus incana* spp. *tenuifoli*) in northern Yellowstone National Park. We developed an alder age structure based on annual growth rings for plants growing along six streams in areas accessible to ungulates on the northern range. Alder stems (n = 412) along the six streams originated only after wolf reintroduction. By 2013, 80% of the sampled alders along these streams were taller than 2 m, in contrast with a historical pattern of height suppression by ungulate herbivory. This pattern of alder recruitment is consistent with a trophic cascade whereby new alder growth occurred across all study streams within several years after wolf reintroduction. Although declines in elk density since wolf reintroduction likely contributed to the release of alder from herbivory, the immediate onset of new alder recruitment following wolf reintroduction indicates that behavioral responses to predation may also have been an important component in the resulting trophic cascade. These results suggest that predator conservation could play a role in the management and ecological restoration of riparian areas.

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1. Introduction

The removal of large carnivores from much of the world has had diverse ecological effects, often revealed through unexpected and complex interactions (Terborgh and Estes, 2010; Ripple et al., 2014b). One example of predator effects occurs in trophic cascades, where the effects of predators on prey are translated downward and across food webs (Estes et al., 2011). Yellowstone National Park (YNP) has been the focus of recent research on trophic cascades involving the extirpation and repatriation of gray wolves (*Canis lupus*) and represents a large-scale natural experiment that provides a unique opportunity to examine the interplay between predators, prey, and plants.

After wolves were extirpated from YNP in the mid-1920s, park biologists became concerned about the effects of increased Rocky Mountain elk (*Cervus elaphus*) browsing on vegetation in the northern and Gallatin ungulate winter ranges (Skinner, 1928; Rush, 1932; Wright et al., 1933; YNP, 1958; Lovaas, 1970; Ripple and Beschta, 2006). Analyses of the annual growth rings of deciduous tree species revealed that recruitment (i.e., growth of seedlings/sprouts into tall saplings or trees) occurred regularly in both of these YNP winter ranges when wolves were present, but declined and became rare after wolf extirpation (Ripple and Larsen, 2000; Beschta, 2005; Halofsky and Ripple, 2008a; Kauffman et al., 2010). These tree-ring study results are consistent with reports of YNP biologists (as cited above) about the decline of woody browse species in the early and middle 20th century. As a result of park service biologists' concerns, a program of elk reductions was initiated in the 1930s and continued through 1968. By the late 1960s, park service culling had reduced the northern range elk population to less than 5000 individuals (Fig. 1a), but with no resulting major recovery in recruitment of woody plants (Houston, 1982; Kay, 1990; Meagher and Houston, 1998; NRC, 2002; Barmore, 2003). After the elk culling program ended in 1968, elk numbers increased dramatically during the 1970s (Fig. 1a). In the 1980s and 1990s, elk numbers fluctuated widely due to winter starvation events (Garrott et al., 2003; Eberhardt et al., 2007). During this period of large population size (>19,000 elk in some years on the northern range), elk were limited by food resources and consumed relatively unpalatable species such as conifers (Kay, 1990; Meagher and Houston, 1998; NRC, 2002).

Wolves were reintroduced into YNP during 1995–96 following approximately seven decades of absence (Fig. 1b). Thirty-one wolves were moved from Canada to the northern range of YNP in January 1995 (n = 14) and January 1996 (n = 17). By 1996, five wolf pack territories covered nearly all of the northern range within the park (Fig. S1 in supplement, Fig. 1 in Phillips and Smith (1997)). During the fall of 1996, each of three different wolf packs on the northern range killed, on average, 1 elk every 2–3 days (Phillips

* Corresponding author.
E-mail address: bill.ripple@oregonstate.edu (W.J. Ripple).

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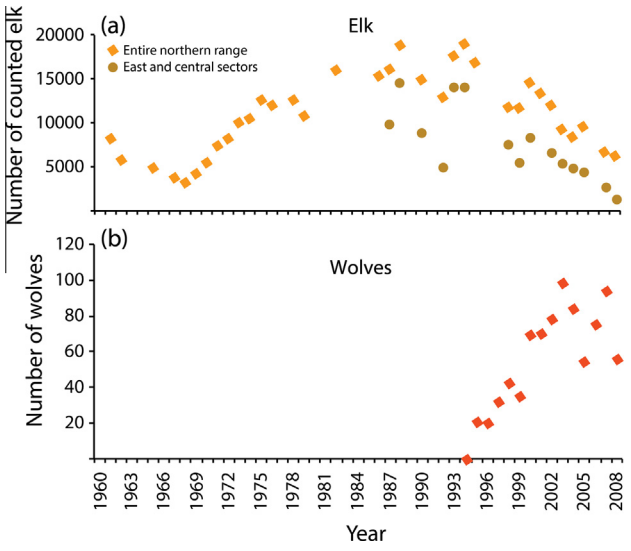

Fig. 1. Number of counted (a) elk and (b) wolves on the northern range. Not shown for elk are poor count years of 1977, 1989, 1991, and 2006. The field sites for this study were all located in the eastern and central sectors of the northern range (as defined by Painter et al. (2015)) and the elk counts for these two sectors were summed and shown with circles as a second series in (a). The eastern and central sectors include the portions of the northern range east of and including the Blacktail Creek drainage. Elk data for the eastern and central sectors were not available prior to 1987.

and Smith, 1997). Following reintroduction, wolf numbers on the northern range increased until 2003 and thereafter declined, while the elk population decreased steadily during this period (Fig. 1a and b). The initial decline in elk numbers in the mid-to-late 1990s was due in part to starvation caused by a degraded winter range and a severe winter in 1996–97; other factors included predation by wolves, bears, and continued hunting by humans of elk that left the park (Eberhardt et al., 2007; White and Garrott, 2013).

Research on the effects of predators, ungulates, and other factors on the establishment and growth of deciduous trees in northern Yellowstone has focused on aspen (*Populus tremuloides*) and cottonwood trees (*Populus* spp.) (reviewed by Ripple and Beschta (2012). Recruitment of these tree species has increased since the reintroduction of wolves, although the magnitude of the recovery is spatially variable (Beschta and Ripple, 2014; Painter et al., 2015). Over the same period, deciduous shrubs in some areas of northern Yellowstone have increased in height, biomass, or cover including willows (*Salix* spp.) (Beyer et al., 2007; Tercek et al., 2010; Baril et al., 2011; Marshall et al., 2014) and various berry-producing shrubs (Beschta and Ripple, 2012; Ripple et al., 2014a).

Herein we report on the first extensive field study of thinleaf alder (*Alnus incana* spp. *tenuifoli*) in Yellowstone's northern range. Thinleaf alder, a small tree or tall shrub, commonly occurs in riparian areas throughout western North America and can grow up to ~12 m tall (Fryer, 2011). Through its nitrogen fixing properties, it enriches soil and facilitates the establishment of other native plants. Thinleaf alder spreads both vegetatively and from small winged seeds, although vegetative reproduction is thought to be more common. It sprouts primarily from root crowns, but can also sprout from roots. Dense alder thickets can provide cover for fish, thermally modify microclimates and stream temperatures via shading, and protect streams from bank erosion. Songbirds eat thinleaf alder seeds, squirrels consume catkins, beaver use stems to build lodges and dams, and various small and large mammals use alder as cover (Fryer, 2011). Thinleaf alder has low palatability as ungulate forage, but it is consumed by ungulates especially when other forage is limited (Gaffney, 1941; Nelson and Leege, 1982; Case and Kauffman, 1997). Northern Yellowstone alders, as well as conifers, were affected by browsing in the 1950s (Jonas, 1955) indicating that elk were using low-quality forage even with densities lower than those of the 1980s–90s. Also, before wolf reintroduction Keigley (1997) observed heavy herbivory effects on various woody browse species on the northern range, including alder.

Because little is known about Yellowstone's thinleaf alder, our main objective was to analyze temporal patterns of thinleaf alder stem establishment on the northern range of Yellowstone National Park. In light of previous research showing changes in cottonwood and aspen recruitment following wolf reintroduction, we hypothesized that thinleaf alder exposed to ungulate browsing would also increase in recruitment over this same time period.

2. Methods

This study took place on the northern ungulate winter range, comprising more than 1500 km^2 of mountainous terrain and open valleys, approximately two-thirds of which occurs within the northeastern portion of YNP in Wyoming (NRC, 2002). Much of the winter range is shrub steppe, with patches of intermixed lodgepole pine (*Pinus contorta*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmanni*), and aspen. Thinleaf alder, and various species of willow, cottonwood, and other woody browse plants occur within riparian zones. See Houston (1982) and NRC (2002) for a more detailed description of the northern range study area.

We determined the age structure of alder stems (frequency distribution of number of stems by year of establishment) growing along small streams, and then compared the number of alder stems established before wolf reintroduction versus after wolf reintroduction. This research design provided two predator treatments: (1) wolves absent (pre-1995) followed by (2) wolves present (post-1995).

We located small perennial streams (4th–5th order) on the northern range within the park that intersected the North Entrance road, the Grand Loop, and the Northeast Entrance road. We excluded streams where riparian areas had burned in the large fires of 1988 (i.e., Lava, Lupine, Elk, Lost, and Tower Creeks). For the remaining streams (Glen, Blacktail, Oxbow, Geode, Crystal, Rose, Indian, and Pebble Creeks), we searched for alder 1000 m upstream and downstream of the road. We found alder along six of these streams: Blacktail, Oxbow, Geode, Crystal, Rose, and Pebble Creek representing a west-east gradient across the northern range. All six streams intersect the main west-east road and were within the central and eastern portions of the northern range within the park (Fig. 2).

Within the search area associated with each of the six streams, we measured the diameter at breast height (DBH, cm) of the tallest stem of each alder plant (breast height = 1.4 m). We measured only plants that were accessible to ungulate browsing; this excluded any individuals growing in or adjacent to woody debris that might inhibit ungulate access. From each of the six riparian areas we haphazardly selected four alder stems (24 total stems mostly from the larger size classes) to develop an age/diameter regression equation. The larger size classes were more frequently sampled because, as the first recruits, they would be the most critical in determining when any increase in alder growth began to occur. We cut the selected stems at 1.4 m above the ground level with a hand saw and counted the number of growth rings in the field using a hand lens after sanding the sections. From this set of data we developed an age/diameter relationship equation with 95% confidence intervals (CI). To determine the number of years it took for alder stems to reach breast height, we haphazardly located alder stems ~1.4 m

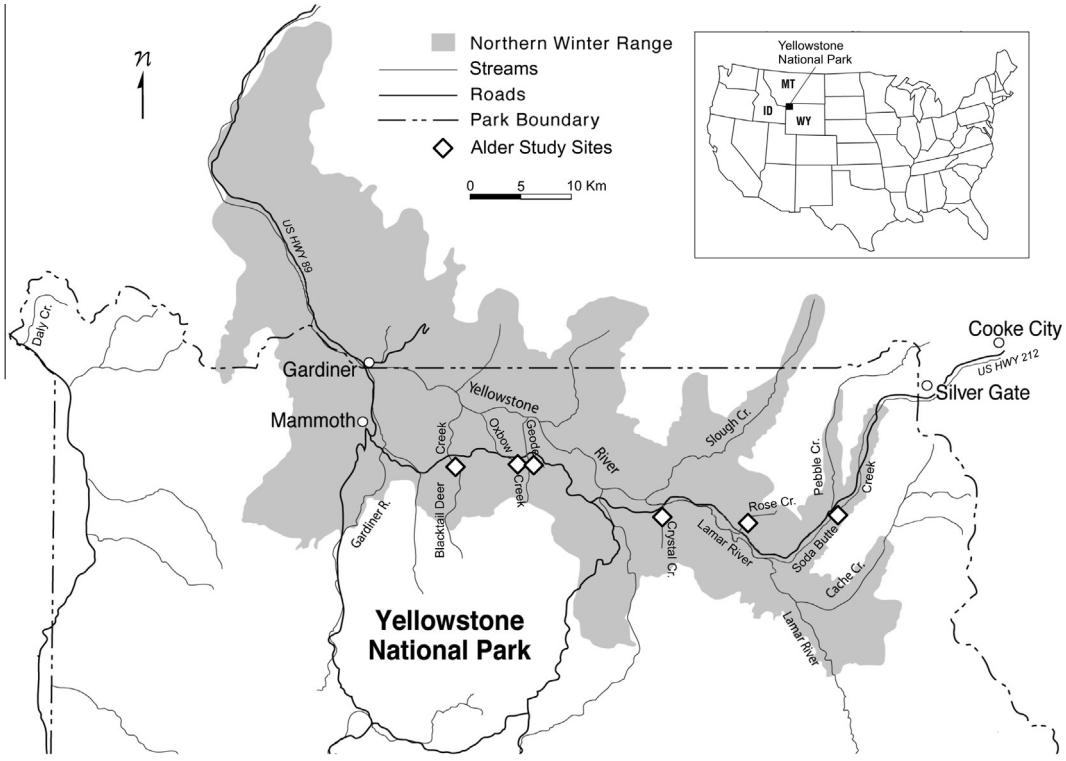

Fig. 2. Northern ungulate winter range (northern range) study area showing the locations of six riparian study sites.

tall along our stream study reaches and aged them by counting the number of annual bud scars along the stems. Both of these approaches, the age/diameter regression and the counting of bud scars, were undertaken to minimize destructive sampling because alder were not abundant at our study sites.

We determined the distance to the nearest road for each measured alder. We tested for a road effect because of the potential for road disturbance to affect ungulate behavior, although our previous work in northern Yellowstone showed no effect of roads on the amount of ungulate browsing (Ripple and Beschta, 2007). We used regression analysis to inspect for a significant relationship between distance to roads and alder size classes.

Finally, we gathered long-term snow water equivalent (SWE) data from established snow courses. Annual snowpack accumulations can influence ungulate foraging and predation rates in winter (Garrott et al., 2009) and low snowpacks can exacerbate summer drought conditions. To index snow conditions in northern YNP, we obtained SWE data (January 1–April 1) for the Lupine Creek and Northeast Entrance snow-recording locations (data obtained from USDA National Resource Conservation Service); these locations are ~48 km apart and bracket our study sites. From these data we calculated the average annual SWE for the period 1960–2008. We also calculated the long-term average SWE and compared SWE for the years before and after wolf reintroduction to this mean.

3. Results

We measured the DBH of 412 ungulate-accessible alders along the six study streams and found only young saplings (DBH range = 0.2–5.2 cm) with no larger overstory alders. The DBH of the 24 sectioned alder stems included <2 cm ($n = 3$), 2–3 cm ($n = 4$), 3–4 cm ($n = 5$), and 4–5 cm ($n = 12$). We evaluated linear and non-linear age/DBH relationships for least squares fit. We selected a linear model because non-linear models were not significantly better fits than the linear model (log transformed $r^2 = 0.70$, quadratic $r^2 = 0.77$, and power function $r^2 = 0.78$). The linear age–DBH relationship was: age = 2.55 × DBH ($r^2 = 0.75$, $p < 0.001$, $n = 24$). For our largest measured alder stems of 5.2 cm DBH, the regression predicted age was 13.3 years (95% CI + 0.9 years). The linear regression was applied to all measured alders stems for determining dates of establishment. The average age of stems at breast height was 4 years ($n = 17$, 95% CI ± 0.2). Establishment year (EY) for individual stems was estimated as follows: EY = 2013 − (2.55 × DBH) + 4 years.

Our analysis indicates that alder stems growing along the six study streams originated from approximately1996 through 2008 (Fig. 3). Age estimates of the oldest alder stems (i.e., 1996, Fig. 3) had a 95% CI of ± 0.9 years, indicating the initial onset of alder growth most likely occurred around 1995–97. Alder stems originating since 2008 were too small for obtaining DBH measurements. In 2013, 80% of the measured alders along the study streams were taller than 2 m, generally considered to be above the normal browse level of elk (Fig. 4). We do not know the proportion of alder stems that established from seeds versus roots in our study sites, but in some cases we observed that visible old root systems were the obvious source of stem establishment.

There was no significant relationship between distance to road and alder stem diameter size ($r^2 < 0.01$, $p = 0.55$, $n = 412$). SWE was above average for the two years immediately following wolf reintroduction (1996–97; Fig. 5). However, the annual SWE was below average most years after 1997, consistent with the fact that the region was in a drought (Painter et al., 2014).

4. Discussion

To the best of our knowledge, our results for alder represent the first published study of this woody species in Yellowstone's northern range, and the first to evaluate the possible effects of wolf reintroduction on alder. Comparing alder recruitment rates before and

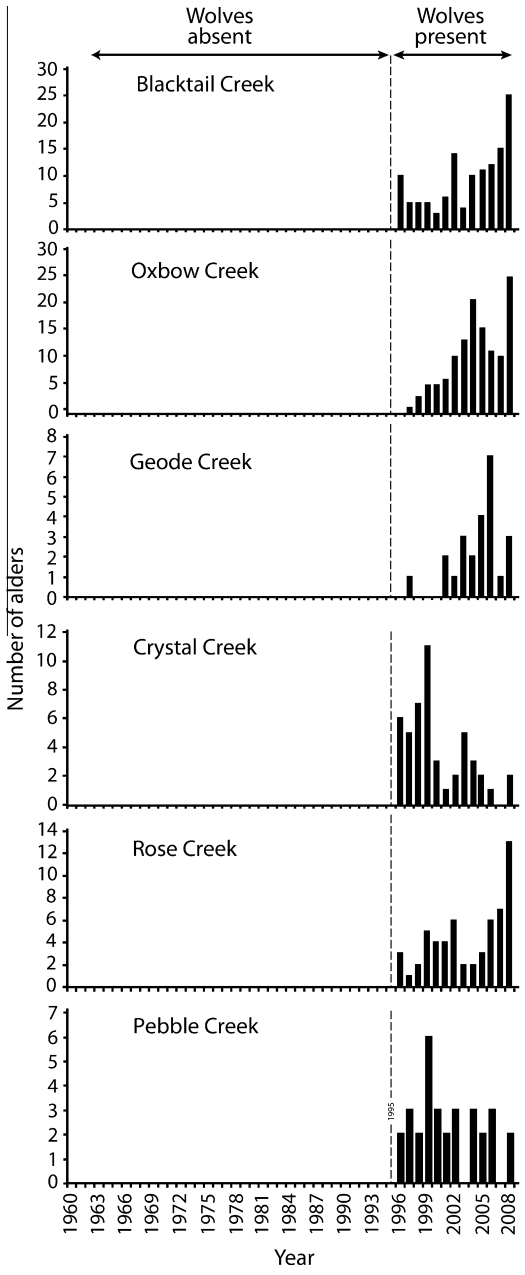

Fig. 3. Alder age structure (number of established stems by year) in ungulate-accessible riparian areas along six study streams on the northern range of YNP (Blacktail Deer Creek, $n = 128$ alder; Oxbow Creek, $n = 123$ Geode Creek, $n = 24$; Crystal Creek, $n = 48$; Rose Creek, $n = 57$; Pebble Creek, $n = 32$). Note the absence of stem establishment before wolf reintroduction (vertical scales vary).

after wolf reintroduction, provides an important tool for understanding temporal patterns of alder recruitment. Furthermore, our survey of alder across much of the northern range of Yellowstone allows for a broad scope of inference within the range. Below we discuss our results in the context of trophic cascades, whether behaviorally or density-meditated, and also consider climate fluctuations as a possible explanation (alternative hypothesis) for new recruitment and increased alder height.

4.1. Trophic cascades

Our results are consistent with the hypothesis of a wolf-ungulate-alder trophic cascade in northern Yellowstone, supported by comparisons of alder age structure across time, before and after wolf reintroduction at our study sites. This evidence demonstrates that alder stems recruited only after wolf reintroduction at our study sites. Thus, alder recruitment was likely linked to changes in top-down forces (reduced ungulate browsing).

Our finding that alder recruitment was rare or absent before wolf reintroduction, and greatly increased thereafter, is consistent with other studies on the northern range that found decreased herbivory and increased growth of aspen, cottonwood, willow and various berry-producing shrubs (Beyer et al., 2007; Tercek et al., 2010; Beschta and Ripple, 2014; Painter et al., 2014; Ripple et al., 2014a; but see Kauffman et al., 2010). Along some streams on the northern range, riparian willow, cottonwood, and aspen started growing taller by 1997, 2002, and 2004, respectively (Ripple and Beschta, 2012). Our results also agree with previous research in Yellowstone finding that woody browse species were severely suppressed, particularly in the last decades of the 20th century, a period during which wolves were absent from the area and elk densities were high. By comparing historical photos to modern photos of the northern range, for instance, Meagher and Houston (1998) found that the abundance of woody species decreased during the 20th century.

Predators can propagate cascading effects down trophic chains in at least two ways, by changes in prey density or behavior (Preisser et al., 2005). Because these effects can have similar impacts on prey resources, it can be difficult to determine their relative importance; many trophic cascades likely combine both density and behavioral effects.

4.1.1. Density effects

Following the reintroduction of wolves, northern range elk counts dropped from ~19,000 in 1994 to ~12,000 in 1998, due in part to the severe winter of 1996/97 (Fig. 5) (Garrott et al., 2003). Elk counts rebounded to 14,500 by 2000 before declining again to 6300 counted individuals in 2008. During this time (2000–08), elk numbers in the eastern and central sectors of the northern range decreased more than in the western and northwestern sectors (Painter et al., 2015). The steady reduction in elk numbers and their redistribution within the northern range is evidence that the elk population has been mediated by predation (top-down) following the return of wolves (Hamlin et al., 2009; Creel et al., 2013; White and Garrott, 2013). While researchers

Fig. 4. Photograph of Blacktail Creek's riparian area in September 2013. The tallest alder stem across the stream from the person was 4 m tall and had a DBH of 3.5 cm. Alder shown here are in the early stages of recovery and will likely get much taller and form dense thickets. Note the well-vegetated streambank and the on-going recruitment of both alder and willows in the background. Photo credit: W.J. Ripple.

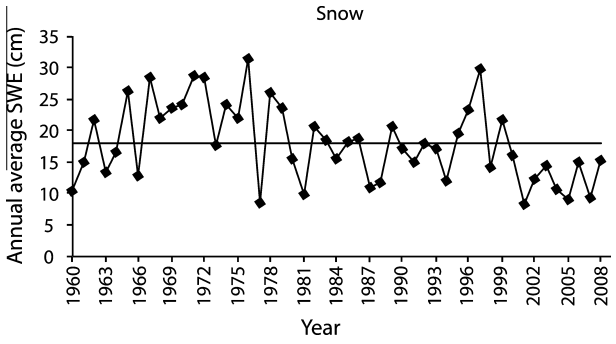

Fig. 5. Annual average snow water equivalent (SWE) for the Lupine and NE Entrance snow courses on the northern range for the period 1960–2008. The horizontal line indicates overall mean SWE for this period. See text for details.

have debated the relative importance of factors affecting elk population dynamics, including increased bear predation (Barber-Meyer et al., 2008), large pre-2005 hunting harvests (Eberhardt et al., 2007), and a 2000–07 drought (White and Garrott, 2013), wolves have likely played a substantial role in the declining numbers and changing distribution of the northern Yellowstone elk herd (Hamlin et al., 2009). Elk hunting of those animals that seasonally left the park was greatly reduced after 2005 and the drought ended by 2007, yet through 2012 elk numbers within the park's northern range continued to decline under pressure from wolves and bears (White and Garrott, 2013; Painter et al., 2015), thus likely contributing to decreased herbivory of alder and other woody plants in recent years.

We asked why alder recruitment in the northern range occurred since the late 1990s, but was apparently lacking in the late 1960s when elk numbers were at their lowest. It is likely that some woody plant communities in riparian areas, including alder, began growing taller in the late 1960s but were subsequently suppressed by browsing and died as elk numbers increased dramatically after culling ended in 1968. Photographic evidence from the Lamar Valley supports this possibility in that it shows riparian plants starting to recruit in 1969 (Fig. S2).

Increased growth of young woody plants in the late 1960s does not explain a lack of alder recruitment in the 1950s when elk numbers (Houston, 1982; Painter et al., 2014) were comparable to those for the period 1998–2003, during which alder recruitment occurred. One possible explanation is that elk distributions were different between these two periods. In the 1950s most elk wintered within the park boundary with many in the eastern portion of the range (Houston, 1982). In contrast, elk distribution since wolf reintroduction has shifted west and north (White et al., 2012; Painter et al., 2015), resulting in lower elk densities for our six study sites (i.e., the central and eastern sectors of the northern range) than in the 1950s. This recent redistribution may represent a landscape-scale response of elk to changes in predation risk.

4.1.2. Behavioral effects

Prey animals foraging in risky environments must balance conflicting demands for food acquisition and safety (Lima and Dill, 1990; Brown et al., 1999). Predators can elicit a strong behavioral response in the prey population even with limited effects on prey density (Werner and Peacor, 2003; Creel and Christianson, 2008). For example, the foraging reduction by prey due to the presence of a predator can be strong, immediate, and widespread in the population of prey (Schmitz, 1998; Preisser et al., 2005). For prey, the risk of foraging is factored against maximizing the net rate of energy intake (Sih, 1980), but food varies in palatability, as well as nutritional and energetic content.

In Yellowstone, numerous researchers have shown that elk respond to the risk of wolf predation by altering their habitat use, movements, group size, vigilance, nutritional intake, and other traits (Laundré et al., 2001; Childress and Lung, 2003; Fortin et al., 2005; Hernandez and Laundre, 2005; Beyer, 2006; Gude et al., 2006; Halofsky and Ripple, 2008b; Christianson and Creel, 2010). In addition, reduced pregnancy rates can cause declines in elk densities, a dynamic that appears as a density effect, but is actually a predation risk effect (Christianson and Creel 2014).

As early as 1996 all of our study sites were within one or more wolf pack territories. The renewal of alder recruitment, a woody plant with low palatability, across all six study streams by the mid-late 1990s (immediately after wolf reintroduction), is consistent with the hypothesis that risk-induced shifts in elk foraging behavior contributed to reduced herbivory when elk densities were still relatively high. In contrast, predator-mediated reduction in prey numbers over time should lead to impacts occurring gradually, with the effect size generally related to the proportion of prey population removed (Werner and Peacor, 2003). Because new alder recruitment began soon after wolf reintroduction and occurred over a large portion of the northern range, our results for the years immediately following wolf reintroduction appear consistent with behavioral effects.

Though low in palatability, wild ungulates will consume thinleaf alder during winter when forage is scarce (Gaffney, 1941; Nelson and Leege, 1982; Fryer, 2011). In Oregon, wild ungulates negatively affected the heights of thinleaf alder, but not as much as the heights of the more palatable willow and cottonwood (Case and Kauffman, 1997). In a northwest Montana study (Gaffney, 1941), thinleaf alder was characterized as a non-palatable species that elk only consumed when more palatable plants were overbrowsed. Gaffney (1941, p. 449) stated "Use of any of these species [alder and other less-palatable species] indicates an overbrowsed condition of the more palatable plants." Before wolves were reintroduced in 1995–96, young alder on the northern range were likely suppressed by elk browsing (Jonas, 1955; Keigley, 1997), as were other woody browse species (NRC, 2002), consistent with high elk densities and frequent starvation events. Therefore, if risk of predation by wolves after 1995 caused elk to give up some foraging opportunities, it is likely that alder, with low palatability, would have been abandoned before more palatable woody species.

4.2. Limitations to the study

While both behavior and density mediation may have contributed to the resurgence of alder since 1996, our ability to tease apart the relative importance of each is limited. The fact that ours was an observational study rather than a controlled experiment limits the strength and scope of inferences possible from our results.

There may be some error in the alder stem age structure data due to our minimally destructive sampling approaches (age–diameter regression, bud scars). However, any error due to predicting age from diameters is probably small because of the high correlation between alder diameter and age ($r^2 = 0.75$), a narrow 95% confidence interval (CI + 0.9 years) and a regression with an intercept through zero. While estimation errors for age are likely to increase with tree size, the alders we sampled were all small (DBH range $\leqslant$5.2 cm) leaving little possibility for a significant error regarding their ages.

4.3. Alternative hypotheses

An alternative to a trophic cascade mechanism as the cause of increased alder recruitment involves climate change or climatic

fluctuations. In this scenario, alder recruitment might improve due to factors such as a longer growing season, increased water availability, or deep snow that could protect plants from browsing and force elk to abandon high-elevation parts of the range. While the length of an average growing season in the region has increased slightly (Wilmers and Getz, 2005), the impact of this change on plants should be gradual rather than abrupt (i.e., the abrupt occurrence of alder recruitment post-1995; Fig. 3). Increased water availability is also an unlikely explanation since a regional drought occurred during 2000–07 (White and Garrott, 2013; Painter et al., 2014), and we detected no alder recruitment in the 1970s which was a period of greater moisture and relatively low elk densities. Although the deep snow in winter of 1996–97 may have temporarily protected alder from herbivory, snow accumulations were below average for most of the first decade following wolf reintroduction (Fig. 5). It should also be noted that previous high snowfall years in the absence of wolves before 1995 (Fig. 5) had no apparent effect on alder recruitment (Fig. 3).

5. Conclusion

The resumption and increase after 1995 of thinleaf alder recruitment in portions of northern YNP is consistent with a trophic cascade involving wolves, ungulates, and alder, mediated by a combination of behavioral and density effects. The timing of the onset of alder recruitment was nearly coincidental with wolf reintroduction, which suggests that behavioral mediation was a factor. However, the potential importance of this mechanism in recent years has been obscured by major shifts in elk space use across the northern range as well as a downward trend in elk numbers (density mediation). With the possible exception of any effects associated with the 1996–97 high snowfall, increased alder recruitment following wolf reintroduction was unlikely to have been caused by climate fluctuations or trends, as the recruitment continued through a decade of drought and low snowfall. The observed patterns of alder recruitment provide additional evidence of the far-reaching effects of predators and their prey on the structure and functioning of Yellowstone's ecosystem. The response of alder following the return of wolves suggests that predator conservation could be part of a management strategy to restore riparian areas and enhance biodiversity where forage plants have been suppressed by herbivores.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.06.007.

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