Exhibit B

Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA

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Summary

The decline of aspen (*Populus tremuloides*) in Yellowstone National Park (YNP) has been attributed to conifer encroachment, climatic influences, ungulate herbivory and more recently, a lack of grey wolves (*Canis lupus*) via trophic cascades. The current study explores evidence of a trophic cascade on aspen decline. We conducted the study in the Gallatin elk winter range of YNP, an area where aspen have not previously been studied. We approximated aspen origination dates from an age–diameter relationship to examine potential correlations between wolf presence and absence, elk (*Cervus elaphus*) herbivory and aspen recruitment. A comparative analysis was also conducted between the aspen data collected in the winter range and aspen data collected within two elk exclosures. Within the elk exclosures, aspen successfully recruited since fence construction in the 1940s. Outside the exclosures, aspen recruitment into mature stems began to decline in the 1920s (during wolf extirpation), completely ceased after the 1950s and has only been observed since the 1990s (post-wolf reintroduction). While a host of interacting biophysical factors may influence aspen recruitment and growth, the correlative results between aspen recruitment and historical elk browsing activities, coincident with the presence and absence of wolves, are consistent with a top–down trophic cascade.

Introduction

The ability of a predator to influence successively lower trophic levels beyond a predator's immediate prey base is known as a trophic cascade (Estes *et al*., 2001). Meta-analyses of trophic cascades have noted a dearth of long-term terrestrial trophic cascade studies linking large vertebrate predators and vertebrate prey (Shurin *et al*., 2002; Borer *et al*., 2005). Lack of terrestrial trophic cascades research involving large vertebrates can be attributed to the decades required to study trophic interactions at the scale of longer-lived terrestrial animals and tree species (rather than the few days to few years necessary to study aquatic and terrestrial invertebrate cascades). However, the removal of a terrestrial predator decades ago now affords investigators the opportunity to

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begin to fill this gap in the literature. Specifically, with the extirpation of the grey wolf (*Canis lupis*) by 1930 from Yellowstone National Park (YNP), an apex carnivore was removed from an ecosystem for more than six decades. Examining the period before and after wolf extirpation facilitates the study of top–down and bottom–up influences on trophic cascades at the temporal scale of elk (*Cervus elaphus*) herbivory and tree regeneration. The relatively long life (100 to150+ years) and high palatability of quaking aspen (*Populus tremuloides*) make this species suitable to study within such a context.

The lack of regeneration of quaking aspen in the Greater Yellowstone Ecosystem (GYE) has been documented for decades (Warren, 1926; Grimm, 1939; Barmore, 1965; Houston, 1982) and continues to be of concern to scientists and natural resource managers (Romme *et al.*, 1995; Yellowstone National Park, 1997; Meagher and Houston, 1998; National Research Council, 2002). Aspen decline has been variously attributed to conifer encroachment, natural stand dynamics, climate fluctuations, climate change and ungulate browsing (Houston, 1973; Loope and Gruell, 1973; Romme *et al.*, 1995; Yellowstone National Park, 1997; Meagher and Houston, 1998; Singer *et al.*, 1998). It is also possible that large carnivore presence can influence both ungulate population size and behaviour, and in doing so, affect aspen population dynamics (White *et al.*, 1998; Fortin *et al.*, 2005; Hebblewhite *et al.*, 2005, Mao *et al.*, 2005; Binkley *et al.*, 2006; Ripple and Beschta, 2007a).

To understand future aspen dynamics, a first and necessary step is to comprehend present and historic aspen dynamics and the associated forces that may contribute to aspen origination. The current study was conducted in the Gallatin elk winter range, an area where to our knowledge aspen have not previously been studied. The winter range also contains two elk exclosures erected in 1945, which allows the comparison of areas that experienced no ungulate browsing pressure to an area accessible to ungulates but not human hunters inside the park. Our study objectives were to:

1. Examine aspen recruitment during several establishment periods: an intact species-level trophic cascade involving wolf–elk–aspen (pre-1930s and post-1995); a truncated species-level trophic cascade of elk-aspen (1930s to 1995) and an aspen-only system inside the exclosures (post-1945).
2. Consider alternative hypotheses (conifer encroachment, climate trends and herbivory) in explaining the pattern of historic and current aspen recruitment during the various establishment periods.

Methods

Study area

The Gallatin is the main wintering area of the Gallatin elk herd (Lovaas, 1970). Based on incomplete data on early winter elk counts collected between 1929 and 1995 ($n = 40$) by the state of Montana, elk numbers have varied between 1214 and 3028 individuals, with an average of 1746 elk (SD = 440.1, ~9 elk km^{-2}). Following wolf reintroduction, from 1996 through the year 2003, elk numbers have averaged 1048 animals (SD = 209, ~5 elk km^{-2}). Creel and Winnie (2005) noted a trend towards lower calf recruitment and annual elk population counts following wolf reintroduction. Between 1997 and 2003, the number of wolves in the study area ranged from 8 to 13 (Smith, 1998, Smith *et al.*, 1999, 2000, 2001, 2003, 2004, Smith and Guernsey, 2002).

Elevation varies from 2400 to 3000 m. Winter precipitation normally occurs as snow. Annual valley snowfall is ~250 cm, with over 750–1000 cm of annual snowfall at higher elevations. Heavy, deep snows in the fall and winter force the elk herd to move to lower elevations that include both the Daly Creek and Black Butte watersheds, core winter range areas for the Gallatin elk herd (Lovaas, 1970). Both the Daly Creek and Black Butte watersheds lie in the north-west corner of YNP. In the current study of the core Gallatin elk winter range, we examined all aspen stands within the Daly Creek and the northern half of the Black Butte watersheds, encompassing an area of ~35 km^2 (Figure 1).

The coniferous vegetation of the Gallatin is comprised of pure stands of lodgepole pine (*Pinus contorta*) or mixed stands of lodgepole pine, Douglas fir (*Pseudotsuga menziesii*) and Engelmann spruce (*Picea engelmanni*). Willow

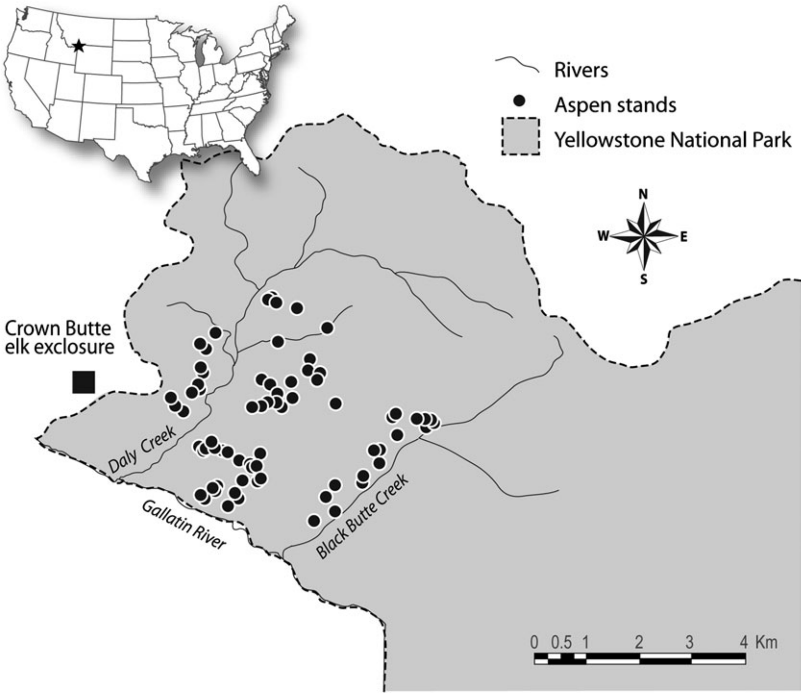

Figure 1. Study location. All data were collected within the Gallatin elk winter range, southwestern Montana. Porcupine exclosure is ~10.7 km north of study area.

(*Salix* spp.) is the most prevalent deciduous tree in the Gallatin valley bottom, and aspen is the dominant deciduous tree at higher elevations. Both willow and aspen are minor forest components in comparison to the coniferous species. On open hillslopes, sagebrush (*Artemisia* spp.), rabbitbrushes (*Chrysothamnus* spp.), Idaho fescue grass (*Festuca idahoensis*), wheatgrasses (*Agropyron* spp.) and bluegrasses (*Poa* spp.) are commonly found. Winter elk diets are dominated by grasses and forbs (Stock, 1936). As snow depth and snow hardness increases, browse species such as willow and aspen become more heavily used (Stock, 1936) although aspen stems greater than 2 metres in height tend to be out of the browsing reach of elk.

European Americans first settled in the Gallatin basin in 1863 (Lovaas, 1970), although the Native American use of the area was present before this time. While wildlife protection was more successful beginning in the 1880s, market hunting of elk and wolves in the 1860s and 1870s was widespread and could have continued until the early part of the twentieth century. 'Abundant signs' of Native Americans were observed in the region as late as 1863 (Lovaas, 1970), and Native American presence may have also influenced animal abundance. Today, hunting is permitted outside the park in the adjacent Gallatin National Forest.

Aspen analysis

During the summer of 2004, we enumerated and visited all aspen stands we could locate within the study area (35 km^2) with 1:24 000 scale aerial photography acquired in 1999 and field reconnaissance. We defined a stand as a minimum of three aspen stems greater than breast height, with each stem in the stand less than 30 m away from any other stem in the stand. In small stands (<9 aspen trees), we measured the diameter at breast height (d.b.h.) of every tree. In larger stands (≥9 aspen trees), we measured all stems <20 cm in d.b.h. and a subset of nine stems representing a range of diameters ≥20 cm in d.b.h.. In addition to d.b.h. information, we obtained increment cores from aspen trees representing a range of diameters.

To explore potential sampling bias, we compared the age distribution (see age-structure methods below) of all trees in stands that had fewer than nine total aspen trees and were therefore completely sampled (69 per cent of all stands sampled) to the age distribution of all stands with ≥9 total stems. Results of the Kolmogorov–Smirnov two-sample goodness of fit test indicated the age distributions of our sampled population (stands with ≥9 aspen trees) was not significantly different from the distribution of ages in stands where all aspen trees were measured (ks = 0.25, *P* value = 0.75). We therefore assumed there was no bias in our sampling protocol and pooled all our data.

We established a 2 × 20 m belt transect in every third aspen stand to examine current aspen reproduction levels, running this transect from the stand edge towards the stand centroid and randomly selecting the direction of the belt transect with a random number table. Within each transect, we collected aspen sprout information, defining aspen sprouts as immature aspen less than breast height. We recorded the total number, height and previous year's browsing (yes/no) for all aspen sprouts within each transect. Both aspen basal area and current conifer encroachment was quantified by collecting aspen and conifer basal area information from the approximate stand centre using a basal area gauge with a basal area factor of five. We conducted a regression of aspen sprout density and conifer basal area to ascertain the relationship between the two variables. We noted the presence or absence of fire from fire scars on Douglas fir and from historic documents.

Within the same elk winter range, we collected additional data on aspen within two fenced elk exclosures erected in 1945. Crown Butte exclosure is ~2.0 ha and 0.3 km from the park boundary, and Porcupine exclosure is ~1.9 ha and 10.7 km north of the park boundary. Both exclosures were erected to 'determine the effect of grazing by big game on winter ranges.' We collected d.b.h. measurements on all aspen stems greater than 1 cm in d.b.h. and extracted additional increment cores from a variety of tree sizes ≥5 cm. Trees cored at breast height were also cored 0.2 m from the tree base to derive an estimate of time required to grow to breast height.

All tree cores were stored, air dried, mounted and sanded following procedures outlined by Stokes and Smiley (1968). We used a dissecting microscope and standard dendrochronological procedures (Stokes and Smiley, 1968) to count the rings on each core. Due to low variability in ring width, cross-dating was unsuccessful. From the aspen tree ring counts and corresponding d.b.h. measurements, we created an aspen age–diameter relationship. We used 59 complete cores to create the aspen age–diameter relationship. Five years were added to each age based on the difference in tree age calculated from seven 0.2 and 1.5 m cores (mean = 5 years, SD = 1) located within the exclosures. The final age–diameter equation was as follows: age = 2004 − (2.50 d.b.h. + 0.02 d.b.h.^{2} + 5) ($R^2 = 0.90$). We used the regression equation to approximate aspen origination years for all d.b.h. measurements collected in the field.

To examine climate trends, we averaged two Palmer Drought severity indices (Cook *et al.*, 2004) downloaded from the International Tree Ring Databank website (http://www.ncdc.noaa.gov/paleo/treering.html). This long-term record is based on climatically sensitive tree-ring chronologies. Negative values are indicative of drought conditions (moderate (−2), severe (−3), extreme (−4)), whereas positive values are associated with above average precipitation. The two records used were grid points 84 and 100 from the International Tree Ring Databank website.

Results

We collected a total of 476 d.b.h. measurements from the 73 enumerated aspen stands in the winter range, 353 d.b.h. measurements within Crown Butte exclosure and 653 d.b.h. measurements within Porcupine exclosure (Figure 2). From the 476 d.b.h. measurements collected outside of the two exclosures, we found that aspen recruitment began declining during wolf extirpation (1920s), completely ceased in the 1950s and has only begun to occur again since wolf reintroduction (1990s, Figure 3), illustrating a large gap in tree recruitment. In contrast, the number

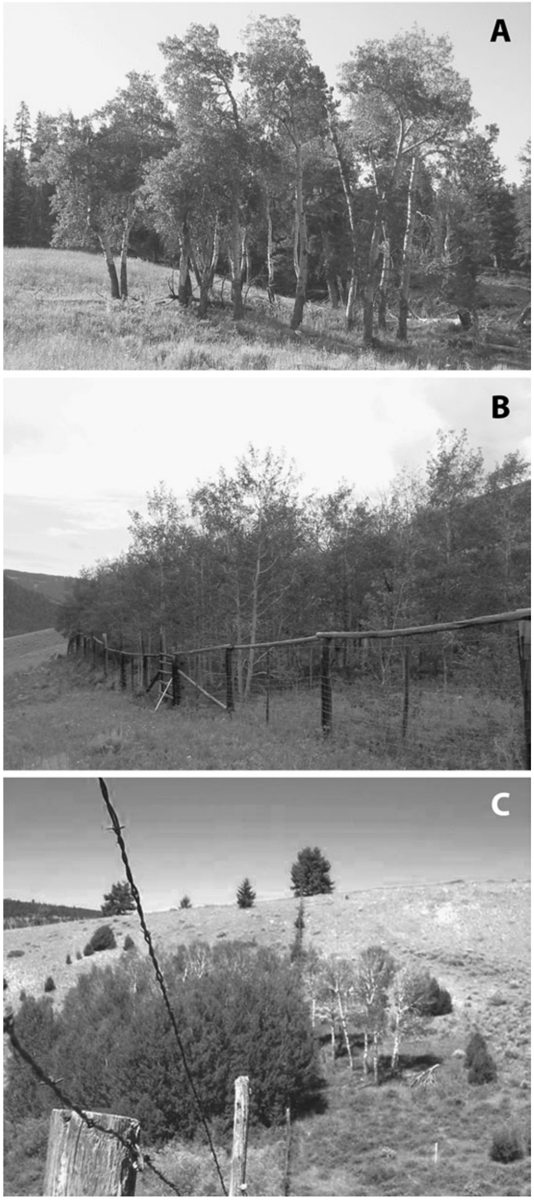

Figure 2. A typical aspen stand in the Gallatin elk winter range (A), Crown Butte exclosure (B) and Porcupine exclosure (C). Note the lack of aspen recruitment in the typical winter range stand and the lack of aspen recruitment outside (left) of Crown Butte exclosure and outside (right) of Porcupine exclosure.

of aspen originating within the exclosures began to increase after the fences were constructed, and aspen have continued to establish inside the exclosures through to the present day (Figure 4). Within both the Crown Butte and Porcupine exclosures, over 90 per cent of the aspen originated after the exclosures were erected in 1945 (Figures 2 and 4).

In our assessment of current aspen recruitment outside of exclosures in the winter range, we found a total of 262 aspen sprouts within the 23 transects situated in aspen stands, with a mean aspen sprout density of 2837 ha^{-1} (lower and upper 95 per cent confidence limit (CL) = 1571, 4102). Ninety-five per cent of these aspen sprouts had been browsed between the 2003 and 2004 measurements. Mean aspen sprout height was 26.3 cm (lower and upper 95 per cent CL = 24.3, 28.4).

In addition to the 262 aspen sprouts, we also found 14 recruiting aspen stems outside the exclosures that originated in the 1990s. All 14 stems were located along forest edges adjacent to scree. On average, these stems were browsed 3.9 times between 1998 and 2003. The percentage of stems browsed consistently declined from 100 per cent in 1998 to ~7 per cent in 2003 (Figure 5a). In 1998, mean ± SE stem height was 98.8 ± 14.5 cm (Figure 5b). By the end of 2003, the last full year each stem was exposed to herbivory, mean ± SE stem height was 229.9 ± 18.6 cm and only one stem had been browsed (Figure 5b). No stems were browsed after reaching 200 cm in height.

We examined other potential causes of aspen decline in the study area, including conifer encroachment, fire suppression and climate. We found that within the 23 measured aspen stands, mean conifer basal area was 14.7 m^2 ha^{-1} (lower and upper 95 per cent CL = 10.0, 19.5), and mean live aspen basal area was 21.3 m^2 ha^{-1} (lower and upper 95 per cent CL = 14.8, 27.7). We found little association between the current proportion of conifer basal area (conifer encroachment) in a stand and current aspen sprout densities ($F_{1,21}$ = 1.52, P value = 0.23, R^2 = 0.07).

While fire can influence conifer presence and basal area, no fire scars were observed on any Douglas fir trees we came across in the study area. In his history of the Gallatin elk herd, Lovaas (1970) did not document any historic fires in the Gallatin elk winter range. We therefore concluded there was a low likelihood of high intense

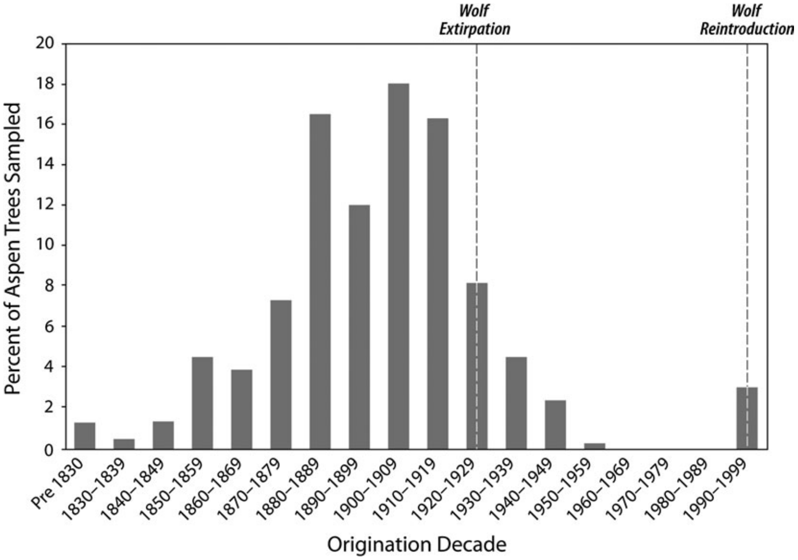

Figure 3. Winter range aspen origination ($n = 476$). While declining in the 1920s, 1930s and 1940s, essentially no aspen trees were found originating between the 1950s and 1980s during a time of wolf absence. Recent recruitment in the 1990s is coincident with wolf reintroduction.

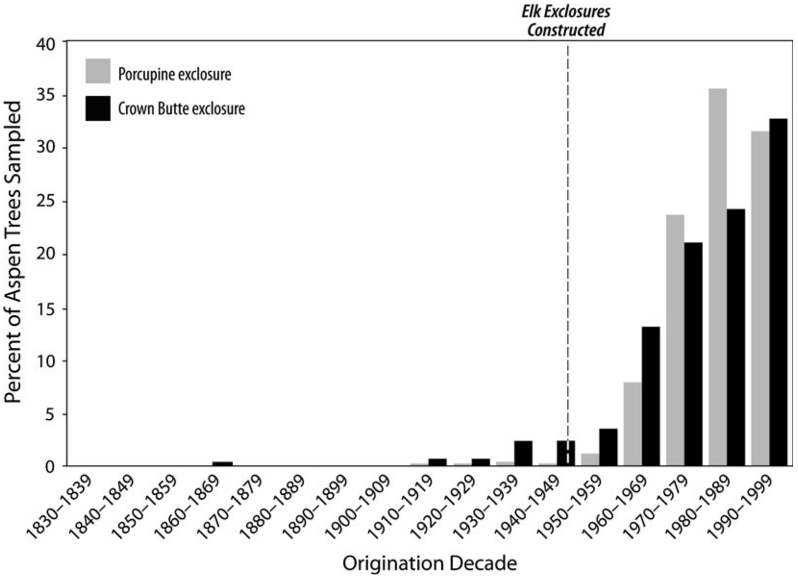

Figure 4. Aspen origination inside Crown Butte ($n = 353$) and Porcupine ($n = 653$) exclosures. Aspen have consistently recruited inside the fences since their erection in 1945.

and severe fires, typically necessary for a flush of aspen recruitment, in the study area during the twentieth century. Over a longer temporal scale, climate trends do not appear to correspond to periods of aspen recruitment and decline (Figure 6) either within or outside of the exclosures.

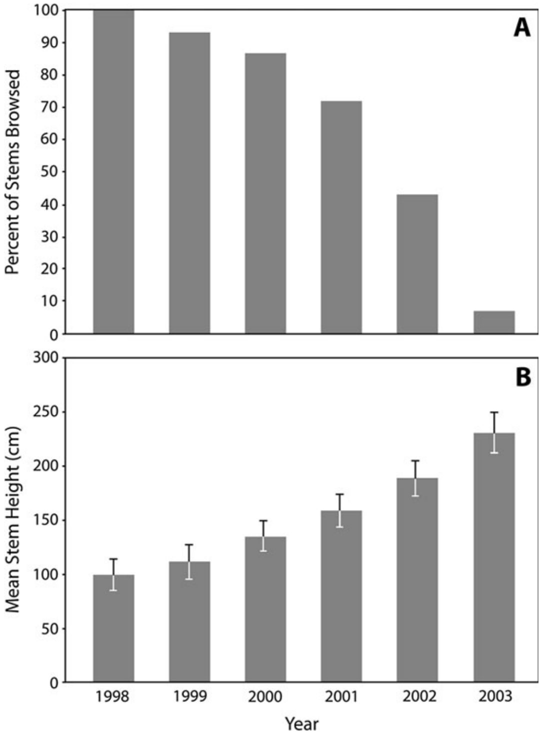

Figure 5. Aspen recruitment originating in the 1990s ($n = 14$). (A) The percentage of the stems browsed in a given year. (B) Average height and standard error bars for recruiting aspen stems.

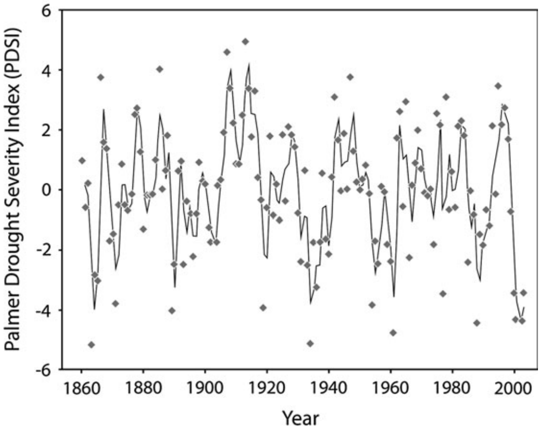

Figure 6. Palmer drought severity index (PDSI) values through time with a fitted moving average line. The more negative the PDSI value, the dryer the year. The more positive a PDSI value, the wetter the year. A PDSI value of zero indicates an average year.

Discussion

To best examine the different reasons for aspen decline, we will address each factor, including conifer encroachment, fire suppression, climate, herbivory and trophic cascades, individually.

Conifer encroachment

It has been shown that, as stands change from aspen to conifer dominated, aspen recruitment will often decline as a consequence of increased shading (Jones and DeByle, 1985). Thus, aspen stands with greater conifer basal area could have less current aspen recruitment than those aspen stands with lower conifer basal area. Our aspen sprout density results, however, are inconsistent with expectations from increasing conifer encroachment although it is likely that if conifer basal area continues to increase resulting in more shade, future aspen regeneration in the study area will be negatively effected.

Fire suppression

If fire suppression is the main factor causing aspen decline, few aspen should recruit without fire. While historic fire records for the study area are limited, both the successful recruitment of aspen inside the exclosures and the recent aspen recruitment adjacent to scree illustrate that fire is not a necessary requirement for aspen to recruit in this area. Additionally, although studies have documented vigorous aspen sprouting occurring immediately after a fire (Jones and DeByle, 1985), under heavy browsing, sprout numbers rapidly return to pre-fire levels (Bartos and Mueggler, 1981; Romme *et al.*, 1995). Hessl and Graumlich (2002) found that under high browsing levels, the positive relationship between fire severity and aspen recruitment was lost. Bartos (1994) and White *et al.* (1998) have questioned whether the addition of fire under high browsing levels actually hastens the demise of aspen stands. Therefore, even if a fire had occurred in the Gallatin within the ~40–50 year age gap

(1950s–1990s), due to high elk densities, the fire effect on aspen recruitment may not have been a positive relationship.

Climate

Climate can influence forage production and the ability of plants to successfully regenerate. Researchers have therefore suggested that the decline in aspen is attributable to a drier climate (Houston, 1982; Singer *et al.*, 1994; Romme *et al.*, 1995; Yellowstone National Park, 1997; Singer *et al.*, 1998). If the overall regional climate influence is towards drying, then a decrease in aspen over the entire winter range would be expected. However, three lines of evidence suggest climate is insufficient in and of itself to explain aspen decline:

1. With the exclosures in the same elk winter range as the rest of the study, it is unlikely that those plants inside the fenced areas would respond differently to climate than would aspen stands outside of the fenced areas.
2. Only aspen within the exclosures consistently recruited from the late 1940s to the present, irrespective of general climate conditions.
3. Aspen sprout densities indicate that aspen are successfully establishing within the study area.

Other researchers have similarly found weak associations between climate and aspen, willow and cottonwood (*Populus deltoids*) growth throughout the Rocky Mountains (Baker *et al.*, 1997; White *et al.*, 1998; Hessl and Graumlich, 2002; Ripple and Larsen, 2000; Barmore, 2003; Beschta, 2003, 2005; Ripple and Beschta, 2004).

Herbivory

If contemporary levels of herbivory were significantly influencing aspen growth, recruitment of aspen trees should be minimal within the elk winter range and extensive within the elk exclosures. This pattern is supported by the data (Figures 3 and 4). Currently, the only multi-aged aspen stands successfully recruiting in the entire winter range study area lie inside the elk exclosures and adjacent to scree outside of the exclosures. It is only inside both fences that the distribution of aspen origination ages follows the expected J-shape of a reproducing plant population where stand replacement disturbance events have been absent. The unimodal distribution of aspen origination outside the exclosures, as evinced by a recruitment gap, is indicative of a declining aspen population.

Romme *et al.* (1995) and Ripple *et al.* (2001) reported mean aspen sprout heights between 25 and 43 cm in other portions of YNP, while Bartos (1994) reported a mean aspen sprout height of 50 cm 12 years after a fire in western Wyoming. All authors attributed the low aspen sprout heights to herbivory. With mean aspen sprout heights in the present study similar to those reported by other authors working in the GYE, it is probable that the same process noted elsewhere (high levels of chronic herbivory) is also influencing aspen sprout heights in the Gallatin elk winter range.

Looking over a longer time period, heavy grazing by elk was reported in Daly Creek watershed in 1920, 1921 and 1923 and in both Black Butte and Daly Creek watersheds in 1924 (White, 1924 as cited by Lovaas, 1970). A US Forest Service report encompassing the winters of 1934/1935 and 1935/1936 in the Gallatin notes, ‘in many places, the elk have eaten the willow and aspen so closely that they have driven the beaver out’ (Stock *et al.*, 1937). Another US Forest Service report from the winter of 1935–1936 estimates that, during critical winter periods, 80 per cent of the elk diet consisted of important browse plants, such as aspen and willow (Stock, 1936). The Conservation Committee of Bozeman noted in 1937 that elk had browsed much of the willow and aspen, while also stripping conifer needles and twigs as high as the animals could reach (Bozeman Daily Chronicle, 1937). The pattern of decline in aspen recruitment beginning in the 1920s in the current study is consistent with historic testimonies.

In the 1940s, the Conservation Committee of Bozeman noted the ‘almost complete absence of aspen reproduction’ within Buffalo Horn, Elk Horn and Porcupine drainages, areas north of the current study but within the same elk winter range (Upper Gallatin Conservation Committee, 1946 as cited by Lovaas, 1970). They further noted the ‘nearly normal’ vegetation within an exclosure and the ‘extremely short’ vegetation surrounding the exclosure. In the present study, outside of the elk exclosures, few measured stems originated in the 1940s.

In the 1950s, a report from a technician in the Fish and Game Department noted ‘the elk range (in the Upper Gallatin) definitely shows deterioration in the loss and size of vegetation … the forage was licked clean in the Black and Crown Butte areas during the past two falls and winters’ (Bozeman Daily Chronicle, 1953). In the present study, outside of the exclosures, almost no measured aspen originated in the 1950s.

The decline of aspen beginning in the late 1920s due to elk browsing (as reported in historical documents), the lack of aspen recruitment for more than half a century based on the current study and the ability of aspen to successfully recruit in the last half century within the exclosures, all lend strong evidence for the influence of herbivory on aspen recruitment in the Gallatin elk winter range. However, since we located aspen stems originating in the 1990s and a decline in browsing on these stems beginning in 1998, shifts in ungulate herbivory patterns may have occurred. We might therefore ask: (1) why was the increase in herbivory in the Gallatin only noted beginning in the 1920s, (2) why did we only locate new stems outside of the exclosures beginning in the 1990s and (3) why were all new stems outside of the exclosures adjacent to scree slopes?

Trophic cascades

Similar patterns of tree age gaps and suppressed woody growth have been noted in other studies in North America (Binkley *et al.*, 2006; Ripple and Beschta, 2006, 2007b). In South America, Terborgh *et al.* (2001, 2006) attributed the lack of small-stemmed individuals in Venezuela to increased herbivory. The authors concluded herbivory increased following predator removal, a top–down phenomenon. On Isle Royale, Michigan, McLaren and Peterson (1994) observed that as wolf numbers declined, moose numbers increased resulting in a suppression of balsam fir (*Abies balsamea*). According to historic documents and our tree origination data (Figure 3), an increase in aspen browsing in the Gallatin began in the 1920s, a time when wolves were being extirpated.

Other studies in YNP have shown similar patterns of tree species decline following wolf extirpation. Within the northern range of YNP, Ripple and Larsen (2000) observed a decline in aspen recruitment from the 1930s through 1995 in the park’s northern range. As with aspen, Beschta (2003, 2005) documented a decline in cottonwood (*Populus* spp.) beginning in the 1920s within YNP. The author also did not find a correlation between cottonwood decline and climate. Thus, two browse species in different winter ranges and growing under different conditions (riparian cottonwood *vs* upland aspen) concurrently declined during the time of wolf extirpation.

The only recruitment we found outside of the exclosures originated in the 1990s. The decline in per cent of stems browsed on the recruiting individuals began in 1998, coinciding with the presence of, and denning by, the Chief Joseph wolf pack in Daly Creek beginning in the winter of 1996/1997 (Smith, 1998). We therefore have evidence of recruitment when wolves were historically present, a gap in aspen recruitment following wolf extirpation coinciding with reports of increased herbivory and the start of aspen recruitment only since wolf reintroduction.

Theoretical implications

In ecosystems driven by bottom–up processes, plants dictate herbivore levels. Bottom–up theory predicts herbivores have a minimal impact on vegetation, and the stability of a system is largely independent of predators. Based on such logic, predators have a compensatory effect, meaning predators kill prey that would have died due to other causes if not predation. Bottom–up theory further predicts a positive relationship between plant biomass and herbivore density. In contrast, general top–down theory predicts that in a two-level trophic system, herbivores directly impact vegetation by reducing plant biomass (Fuller and Gill, 2001; Côté *et al.*, 2004; McShea, 2005). Thus, as herbivore numbers increase, plant biomass should decrease, indicating an inverse relationship between trophic levels. With a carnivore trophic level added, top–down theory predicts that predators force herbivore numbers down, which in turn increases plant biomass (Jędrzejewska and Jędrzejewski, 2005). Top–down theory therefore supports the concept that top carnivores, either alone or in conjunction with other predator species, can have an additive effect on prey mortality. Examination of aspen within the Gallatin elk winter range of YNP yielded little evidence of successful aspen recruitment outside of the elk exclosures in the absence of wolves. Thus, we observed a negative plant response to predator removal outside the exclosures, and a positive plant response under limited herbivory (inside the exclosures), consistent with top–down theory.

Trophic theory as originally stated was based on density-mediated effects of predators on prey. However, recent evidence suggests that behaviourally mediated trophic cascades may be equal to or greater than density-mediated effects (Schmitz *et al.*, 2004). While the recruiting aspen adjacent to scree may have been aided by a decline in elk densities since wolf reintroduction, the high browsing rates on and low mean height of aspen sprouts in the study area illustrate elk densities are still sufficient to browse nearly all aspen sprouts in a given year. Therefore, in addition to any density-mediated effect on elk due to wolf predation, the presence of recruiting aspen stems only adjacent to scree may represent a change in elk behaviour (Halofsky, 2007).

Evidence is mounting in the form of vigilance studies that perceived predation risk on elk has increased since wolf reintroduction (Laundré *et al.*, 2001; Childress and Lung, 2003), while other studies have illustrated changes in habitat preference by elk due to wolf presence (Fortin *et al.*, 2005; Mao *et al.*, 2005; Gude *et al.*, 2006). Ripple and Beschta (2004) list 'gravelly/rocky surfaces' as a potential terrain factor that might increase perceived predation risk and therefore could be areas elk avoid when browsing. Such gravelly surfaces would also include the scree slopes adjacent to the 14 recruiting aspen sprouts in the current study. Although our results are in agreement with the expected outcome from changes in elk behaviour, whether such behaviour shifts will result in woody plant release throughout the study area remains uncertain.

While Schmitz *et al.* (2000) tended to find the strongest top–down effect in terrestrial trophic cascades when plant damage, rather than plant biomass, was measured, the current study illustrates that in carnivore absence, herbivores negatively affect aspen biomass. Specifically, we document several decades of a gap in aspen recruitment. Therefore, aspen numbers, as well as biomass, have declined in the Gallatin.

With the small number of recruiting stems found outside of the exclosures, it is too soon to know if they portend the successful recruitment of future aspen or if they are more of an exception to the general rule of aspen decline. Consequently, if overall elk herbivory remains high, species loss and a conversion of available resources might occur potentially resulting in an alternative stable state (Schmitz *et al.*, 2006).

Although Native Americans probably influenced both historical wolf and elk populations, we were unable to quantify their impact. While wolves in and of themselves might not have the ability to indirectly increase the recruitment of woody browse species, with the full suite of top carnivores in YNP and no wolves for ~70 years, little aspen, willow or cottonwood recruitment has been documented (National Research Council, 2002). However, 60–70 years of documented willow and cottonwood suppression has begun to reverse itself only since the late 1990s, coincident with wolf reintroduction in the winter of 1995/1996 (Ripple and Beschta, 2003, 2004; Beyer, 2006).

Conclusions

Terrestrial trophic cascade studies involving large vertebrate mammals are rare. Humans have greatly altered animal migration routes and the structure and composition of vegetation on the earth through habitat modifications and also through the reduction and elimination of top predators. Because most terrestrial vertebrate systems are therefore not fully intact, the information gleaned from a time when the system was more complete becomes valuable. The correlative evidence presented in this study supports the positive top–down influence of wolf presence on aspen via additive predation pressure and a negative top–down influence on aspen when wolves are absent. Therefore, the presence of wolves may be integral to the long-term recruitment of this woody browse species within the study area.

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Conflict of Interest Statement

None declared.

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