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Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction

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ABSTRACT

The 1995/1996 reintroduction of gray wolves (*Canis lupus*) into Yellowstone National Park after a 70 year absence has allowed for studies of tri-trophic cascades involving wolves, elk (*Cervus elaphus*), and plant species such as aspen (*Populus tremuloides*), cottonwoods (*Populus* spp.), and willows (*Salix* spp.). To investigate the status of this cascade, in September of 2010 we repeated an earlier survey of aspen and measured browsing and heights of young aspen in 97 stands along four streams in the Lamar River catchment of the park's northern winter range. We found that browsing on the five tallest young aspen in each stand decreased from 100% of all measured leaders in 1998 to means of <25% in the uplands and <20% in riparian areas by 2010. Correspondingly, aspen recruitment (i.e., growth of seedlings/sprouts above the browse level of ungulates) increased as browsing decreased over time in these same stands. We repeated earlier inventories of cottonwoods and found that recruitment had also increased in recent years. We also synthesized studies on trophic cascades published during the first 15 years after wolf reintroduction. Synthesis results generally indicate that the reintroduction of wolves restored a trophic cascade with woody browse species growing taller and canopy cover increasing in some, but not all places. After wolf reintroduction, elk populations decreased, but both beaver (*Caster canadensis*) and bison (*Bison bison*) numbers increased, possibly due to the increase in available woody plants and herbaceous forage resulting from less competition with elk. Trophic cascades research during the first 15 years after wolf reintroduction indicated substantial initial effects on both plants and animals, but northern Yellowstone still appears to be in the early stages of ecosystem recovery. In ecosystems where wolves have been displaced or locally extirpated, their reintroduction may represent a particularly effective approach for passive restoration.

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1. Introduction

In a system with three trophic levels (tri-trophic) involving predators, prey, and plants, predators can indirectly affect plant communities by influencing prey behavior and density, thus releasing plants from herbivory (Strong and Frank, 2010). In Yellowstone, wolves (*Canis lupus*) were extirpated from the park by the mid-1920s, absent for a period of seven decades, and reintroduced in the winters of 1995/1996. The historical presence, then absence, and now presence of wolves in Yellowstone National Park (YNP) represents a natural experiment through time and an opportunity to study cascading trophic interactions. During the seven-decade wolf-free period, the collapse of a tri-trophic cascade allowed elk (*Cervus elaphus*) to significantly impact wildlife habitat, soils, and woody plants. For example, species such as aspen (*Populus tremuloides*) and willows (*Salix* spp.) were generally unable to successfully recruit young stems into the overstory on Yellowstone's northern winter ranges, except in fenced exclosures (Grimm, 1939; Lovaas, 1970; NRC, 2002; Barmore, 2003).

Recent studies of aspen and cottonwood (*Populus* spp.) age structures, based on assessments of tree rings and diameter classes, have shown that the extirpation of wolves and subsequent increase in elk herbivory was linked to the long-term decline in the recruitment of these deciduous species (Ripple and Larsen, 2000; Beschta, 2005; Halofsky and Ripple, 2008b). With wolves now back on the Yellowstone landscape for 15 years, we ask the question: How has the reintroduction of wolves affected the recruitment of woody browse species? Our objectives were to (1) collect new data on the recruitment status of both aspen and cottonwood in the Lamar River catchment on the northern winter range of YNP, and (2) synthesize the existing body of work on tri-trophic cascades (i.e., wolves, elk, and changes in woody plants) in Yellowstone since wolf reintroduction 15 years ago.

2. Methods

In September of 2010, we repeated an aspen recruitment survey originally conducted in 2006 in the Lamar catchment of YNP's northern range where riparian and adjacent upland aspen stands had been surveyed along four streams; the Lamar River and Slough, Crystal, and Rose Creeks (Ripple and Beschta, 2007b). This pairing

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originally allowed us to compare browsing levels and aspen heights between upland and riparian (stream side) areas. We returned to the same 98 stands measured in 2006 using a global positioning satellite (GPS) system. In order to document any early aspen recruitment, we measured the browsing status and heights of the five tallest young aspen (ramets) in each stand using a methodology similar to that of our original survey (Ripple and Beschta, 2007b). In our 2006 survey, we used plant architecture methods to inspect individual leaders for terminal bud scars and browsing to retrospectively determine annual aspen heights and the percentage of leaders browsed over time (1998–2006). In 2010, we successfully measured 485 young aspen in 97 of our 98 original stands where we recorded aspen height, current annual growth, and current browsing status. One site was excluded because a conifer had been felled by the park service, thus potentially impacting the young aspen. We recorded the presence and absence of downed logs (aspen and conifer >30 cm in diameter) within a 3 m radius of each measured aspen because downed logs represent potential impediments for ungulates [e.g., bison (*Bison bison*)], potentially causing less browsing and more aspen growth (Ripple and Beschta, 2007b; Halofsky and Ripple, 2008a). Our aspen sampling design defined four different site categories: upland and riparian areas and sites with and without logs. We merged our aspen browsing and height data from 2006 with that collected in 2010. Combining these two data sets allowed us to plot browsing and aspen height for the years 1998–2006 and 2010. We photographed each of the 97 sampled aspen stands in 2010.

In September of 2010, we also surveyed cottonwood recruitment in the Lamar and Soda Butte Valleys. We searched for and enumerated all young cottonwood trees ≥ 5 cm diameter at breast height (DBH) using the same methods as earlier described by Beschta and Ripple (2010). We plotted the number of young cottonwood trees ≥ 5 cm DBH for 2001, 2002, 2003, 2004, and 2006 as reported by Beschta and Ripple (2010) along with the number of cottonwood trees ≥ 5 cm DBH that we found during our survey in 2010. Further information on study areas and methods of surveying aspen and cottonwood can be found in Ripple and Beschta (2007b) and Beschta and Ripple (2010), respectively. See Despain (1990) for a detailed description of the vegetation communities.

Two potential bottom-up factors that might influence tree recruitment, snowpack amount and site productivity were considered for this study. In order to analyze trends in snowpacks, we obtained the accumulated daily snow-water equivalent data by year [SWE_{acc} , see Garrott et al. (2003) for methods] from two National Resources Conservation Service SNOTEL sites nearest the northern range (Northeast Entrance Site and Canyon Site). As an index for site productivity, we summarized the current annual growth of all sampled aspen leaders that were unbrowsed in 2010. We used a Student's *t*-test to check for difference in current annual growth between upland and riparian sites. Aspen plant height was also regressed against current annual growth to determine if there was a relationship between this index of productivity and aspen height. A positive relationship would indicate that site productivity differences could be contributing to the variability in aspen height.

We summarized trends in wolf, elk, and bison populations on the northern range. Other ungulate species were present on the northern range [i.e., moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*)], but their densities were considerably lower than elk and bison (see Table 1 in Ripple and Beschta, 2004a) and annual counts were not available for them. We plotted beaver (*Castor canadensis*) population trends because these herbivores could benefit from improving woody plant communities. We did not initiate any new willow surveys, but we included temporal trends in willow stem ring area from Beyer et al. (2007). Stem ring area represents the annual cross-sectional growth of willow stems and can

be useful for documenting the timing of willow release (i.e., growing taller), with an increase in annual ring areas indicating more willow growth and a release from browsing suppression.

Finally, for the 15 year period since wolf reintroduction of 1995/1996 through 2010, we searched the literature for tri-trophic cascades studies that attempted to measure vegetation change in Yellowstone. We summarized articles that included data regarding changes in height, cover, or size (i.e., stem diameter or growth ring area) of woody browse species.

3. Results

Between 1995 and 2003, northern range wolf numbers increased from 0 to 98 (Smith et al., 2011). However, since 2003 the population has generally declined, but has fluctuated substantially (Fig. 1A). According to annual elk census data, the northern range elk counts decreased from highs >15,000 individuals during the early 1990s before wolf reintroduction to approximately 6,100 in 2010 (Fig. 1B) (White and Garrott, 2005; unpublished data – Yellowstone National Park).

Based on plant architecture measurements, 100% of aspen leaders were browsed in 1998, but this percentage declined considerably during the next 12 years for all four site categories: (1) uplands without logs, (2) uplands with logs, (3) riparian areas without logs, and (4) riparian areas with logs (Fig. 1C). Browsing intensity diminished at differing rates depending on site category and as of 2006 browsing remained greater in the uplands relative to riparian areas. Between 2006 and 2010, browsing had decreased for all site categories and the percentage of aspen leaders browsed declined from 84% to 24% for uplands without logs, 67% to 20% for uplands with logs, 49% to 18% for riparian sites without logs, and 16% to 4% for riparian sites with logs. As browsing levels decreased, aspen heights increased across all site categories. Average heights of the five tallest young aspen in each stand in 1998 were ≤ 40 cm regardless of site category (Fig. 1D). Most of the decrease in browsing and increase in aspen heights happened since 2004. By 2006, average aspen height for riparian areas with logs increased to 230 cm which is above the normal browsing reach of elk. As of 2010, mean aspen heights had increased for all site categories to a mean of 176 cm for uplands without logs, 224 cm for uplands with logs, 237 cm for riparian areas without logs, and 350 cm for riparian areas with logs. In terms of recruitment status of the 485–490 total aspen trees measured in our surveys, we found no aspen taller than 200 cm in 1998 (0%), 171 aspen above 200 cm in 2006 (35%), and 289 aspen above 200 cm in 2010 (60%). Overall, mean height of the five tallest young aspen increased from 154 cm in 2006 ($n = 490$) to 265 cm ($n = 485$) in 2010 ($p < 0.0001$). Photographs of each of the sampled 97 stands resurveyed in 2010, the majority of which show releasing aspen, were archived in ScholarsArchive@OSU for long-term storage and can be viewed at <http://www.hdl.handle.net/1957/20842>.

In terms of productivity, there was no significant difference ($p = 0.53$) in mean current annual growth of aspen in 2010 for upland sites ($\bar{x} = 46.7$ cm, $n = 214$) versus riparian areas ($\bar{x} = 45.6$ cm, $n = 202$). Additionally, there was very little correlation between site productivity, as measured by current annual growth, and aspen plant height ($r^2 = 0.02$).

Using ≥ 5 cm diameter at breast height (DBH) as an indication of successful recruitment of young trees into the overstory, recruitment inventories in 2001 and 2003 yielded “zero” cottonwoods that met the ≥ 5 -cm DBH criteria (Beschta and Ripple, 2010). However, since 2004 cottonwood recruitment has steadily increased, attaining a total of 156 recruiting trees in 2010 for the Soda Butte and Lamar Valleys (Fig. 1E), almost all of these along Soda Butte Creek or the upper Lamar River, above the confluence of the two

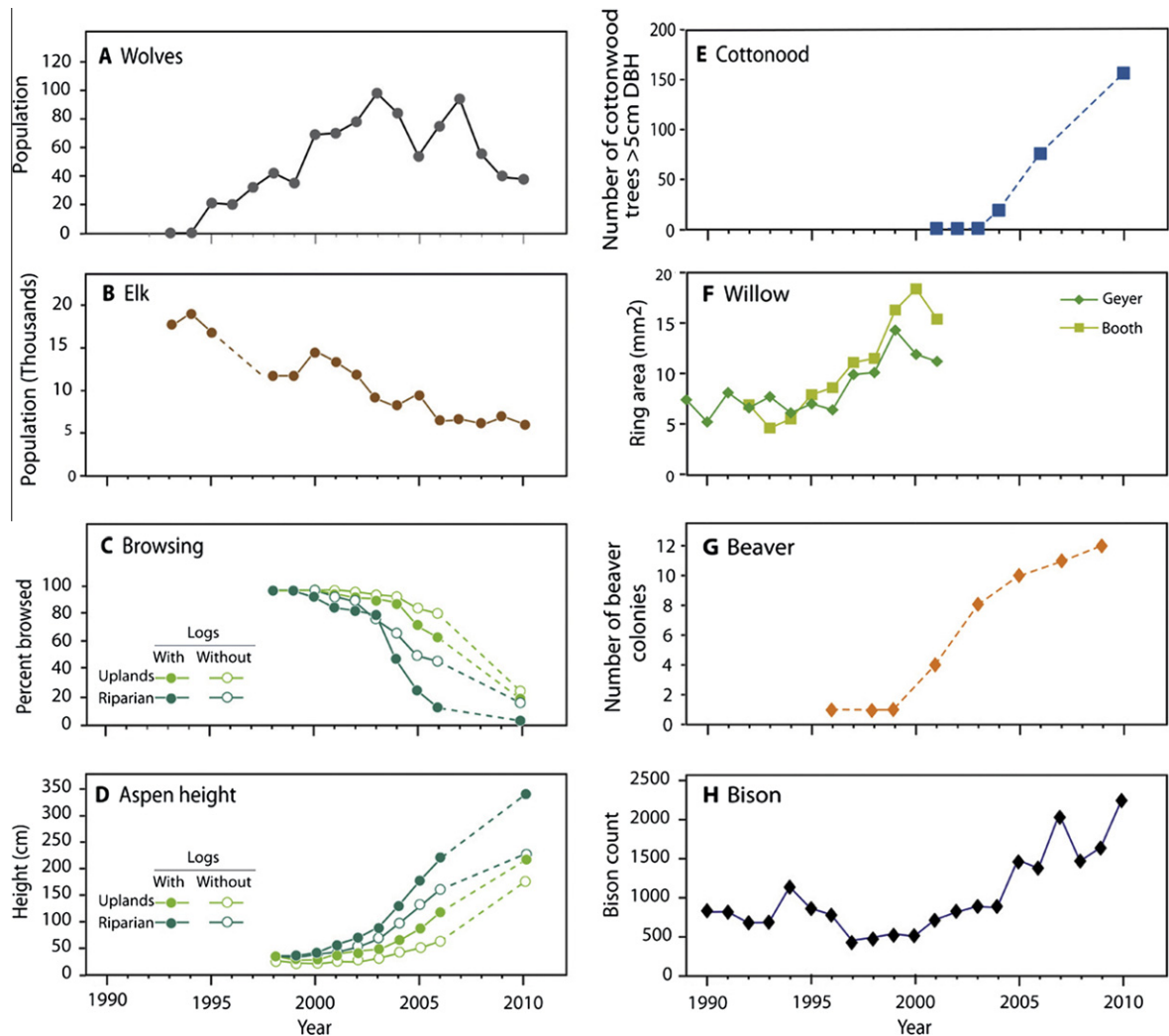


Fig. 1. Trends in (A) wolf populations, (B) minimum elk populations from annual counts, (C) percentage of aspen leaders browsed, (D) mean aspen heights (early springtime heights after winter browsing but before summer growth), (E) cottonwood recruitment, (F) willow ring area, (G) number of beaver colonies, and (H) summer bison counts. Wolf data were obtained from [Smith et al. \(2011\)](#). Elk data for the period 1993–2004 from [White and Garrott \(2005\)](#); 2005–2010 elk data as well bison data unpublished from Yellowstone National Park. The elk count for 2006 is believed to be inaccurate due to poor weather conditions during the count. Animal data presented here are based on reporting year protocol suggested by [White and Garrott \(2005\)](#). Recent changes in the distribution of elk to more use of conifer cover ([Mao et al., 2005](#)) indicate that continuing efforts to conduct the traditional complete counts of elk may not be adequate. Willow data from [Beyer et al. \(2007\)](#); beaver data from [Smith and Tyers \(2008\)](#) and Yellowstone National Park. Dashed lines represent time periods with at least 1 year of missing data. Panels A, G, and H represent animal population counts for the northern range in the park; B the entire northern range; and C, D, E, and F from selected plant study areas within the northern range inside the park.

streams. Mean willow stem ring area was as much as two times greater after wolf reintroduction compared to before wolves suggesting a willow release ([Fig. 1F](#)). The number of beaver colonies on the northern range increased from 1 in 1996 to 12 in 2009 ([Fig. 1G](#)). Summer counts of bison on the northern range have greatly increased since wolf reintroduction. The number of counted bison between 2001 and 2010 ($\bar{x} = 1,385$) averaged nearly two times greater than between 1990 and 2000 ($\bar{x} = 708$) ([Fig. 1H](#)).

Mean annual snow water equivalent (SWE_{acc}) was 34.7 m for the period of 1981–2009. During the late 1990s (1995–1999), representing the early years of wolf recovery in Yellowstone NP, annual SWE_{acc} averaged 49.7 m which was more than 40% above the long term mean. During more recent years (2000–2009), the average SWE_{acc} was 30.6 m or approximately 14% below the long term mean.

During the 15 years since wolf reintroduction (1995/1996–2010), we found 13 field studies and 2 remote sensing studies of change in woody browse species in Yellowstone ([Table 1](#)). Twelve of 13 field studies reported taller plants over time. For example, some valley-bottom willows showed evidence of release from high

browsing pressure by about 1997 on the northern range ([Beyer et al., 2007](#)) and by about 1999 on the Gallatin winter range ([Ripple and Beschta, 2004b](#)). Two remote sensing studies of willow cover also showed significant increases in willow canopy cover since wolf reintroduction ([Groshong, 2004](#); [Baril, 2009](#)). Cottonwoods on the northern range showed evidence of a release at just a few sites in 2002 ([Ripple and Beschta, 2003](#)), had increased by 2006, and increased further by 2010 ([Fig. 1E](#)). Evidence for a release of riparian aspen appeared at some sites by 2004 ([Ripple and Beschta, 2007b](#)) and by 2010, even upland aspen were at early stages of a release ([Fig. 1D](#)).

When documenting recruitment, authors 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. Most authors attributed these plant responses, at least partially, to spatial variation in perceived predation risk; relatively risky sites received less browsing and experienced more plant growth. Perceived predation risk relates to prey antipredator behavior ([Lima and Dill, 1990](#)) and can be inferred from foraging patterns (browsing) and space use by

Table 1

Synthesis of trophic cascades studies in Yellowstone National Park for the 15 year period from when wolves were first reintroduced in 1995/1996 to the end of 2010. Only trophic cascades studies that included an analysis of potential plant changes over time are included.

Field date	Species	Location	Metric	Synthesis comment	Citation
1995–1999	Mostly willow	Soda Butte Creek	% cover	Between 1995 and 1999, a 279% increase in deciduous woody vegetation cover	Groshong (2004)
2001	Willow	Northern range	Growth rings	Twofold increase in willow stem growth rings following wolf reintroduction. Willows started releasing in 1997	Beyer et al. (2007)
2002	Cottonwood	Lamar and Soda Butte Valleys	Height	Cottonwood started releasing in 2002 at three sites to maximum heights of 200–400 cm	Ripple and Beschta (2003)
2003	Willow	Gallatin Range	Height	Between 1998 and 2002, heights of tallest willows increased from 75 cm to 200 cm. Willows started releasing in 1999	Ripple and Beschta (2004b)
2004	Willow	Northern and Gallatin Range	Height	Between 1999 and 2003, mean heights of tallest willow increased <150 cm to more than 300 cm	Ripple and Beschta (2006)
2004	Willow	Blacktail Creek	Height % cover	Between 1997 and 2003, tallest willows increased from <50 cm to >250 cm, canopy cover over streams increased from 5% to 14–73%	Beschta and Ripple (2007a)
2004	Aspen	NW Yellowstone	Height	Between 1995 and 2004, mean aspen heights increased from <100 cm to >300 cm in 1988 burn area	Halofsky et al. (2008)
2002–2005	Willow	Northern range	Height	Between 2001 and 2005 willows increased in height, but continued to be suppressed at <100 cm	Bilyeu et al. (2008)
1991–2006	Mostly willow	Northern range	% cover	Between 1991 and 2006, tall deciduous woody vegetation cover increased 170%	Baril (2009)
2002–2006	Cottonwood	Lamar and Soda Butte Valleys	Height	Between 2002 and 2006, median heights for tallest cottonwoods increased from 100 to 300 cm	Beschta and Ripple (2010)
2003–2006	Willow	Gallatin Range	Height	Between 2003 and 2006, median heights for tallest willows increased from approximately 125 cm to over 200 cm	Beschta and Ripple (2010)
2006	Aspen	Northern Range	Height	Between 1998 and 2006 mean heights for tallest riparian aspen increased from <50 cm to >200 cm. Riparian aspen started releasing by 2004	Ripple and Beschta (2007b)
2004–2007	Aspen	Northern Range	Height	Between 2004 and 2007, sampled aspen were not releasing. Mean Aspen heights were between 25 and 75 cm	Kauffman et al. (2010)
2010	Aspen	Northern Range	Height	Between 2006 and 2010 mean heights for tallest riparian aspen increased from 164 to 265 cm. Upland aspen started releasing by 2010	This study
2010	Cottonwood	Lamar and Soda Butte Valleys	Diameter	The number of young cottonwoods trees ≥ 5 cm DBH increased from 0 in 2001 to 156 in 2010	This study

prey over time. With the exception of one early study with field work conducted in 2001 (Beyer et al., 2007), all of the studies that reported plant recruitment and trophic cascades attributed the woody browse release primarily to a combination of behavioral and density effects of wolves on ungulates. Beyer et al. (2007) concluded that their results were consistent with a behaviorally mediated trophic cascade. One northern range field study of 16 aspen stands did not detect increased plant heights or recruitment over time (Kauffman et al., 2010).

4. Discussion

Since wolf reintroduction, Yellowstone northern ecosystems have responded as predicted by classic ecological theory with alternating biomass levels across adjacent trophic levels (i.e., more wolves, fewer elk with altered behavior, more plant biomass). Over a 13-year period from 1998 to 2010, we found a strong inverse relationship between browsing intensity and heights of young aspen in that as browsing decreased, aspen height increased (Fig. 1C and D). Browsing on aspen has been declining in both uplands and riparian areas and aspen heights increased significantly since our last survey in 2006. One reason that recent browsing percentages were low for our sampled aspen in 2010 is that many of them had grown above the browsing reach of elk (~200 cm). Furthermore, aspen recruitment in 2010 was spatially less variable than

in 2006, since recruitment has now started occurring on more upland sites (Fig. 2). 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.

We found no evidence that differences in site productivity as indexed by aspen current annual growth was the main cause for the aspen recruitment that we report herein, or in our previous study (Ripple and Beschta, 2007b). Furthermore, we detected no significant difference in our index of site productivity in uplands compared to riparian areas. This lack of difference may have been due to the fact that many of the upland sites were located in relatively moist areas, many with seeps. We also found little correlation between our index of site productivity and aspen height.

While more widespread aspen recruitment would suggest an increasing influence from a density-mediated trophic cascade because elk numbers have trended significantly lower since wolf reintroduction, it is difficult to separate density effects from behavioral effects because predation risk can be temporally dynamic and exist at multiple spatial scales, from a few meters to very large landscapes (Laundré et al., 2001). Sometimes large-scale shifts in behavior due to predation risk may locally appear to be density effects. For example, in recent years elk have reduced their use of the high elevation winter range in and around the Lamar Valley compared to low-elevation winter range both in and out of the park (White et al., 2010, *in press*). This landscape-scale shift in elk space use was likely caused by higher predator densities, more predation, deeper snow, and increased risk levels in the Lamar Valley compared to low elevation sites (White et al., 2010, *in press*). For example, elk are more vulnerable to wolf attacks at higher elevations in winter due to relatively deep snowpacks.

Researchers have documented major behavioral effects whereby elk in YNP, under the risk of predation by wolves, have altered their habitat use, movements, group sizes, vigilance, and other traits (Laundré et al., 2001; Childress and Lung, 2003; Wolff and Van Horn, 2003; Ripple and Beschta, 2004a; Creel et al., 2005; Hernández and Laundré, 2005; Fortin et al., 2005; Beyer, 2006; Gude et al., 2006; Halofsky and Ripple, 2008a). At least some of these behavioral effects, in addition to density effects, have likely contributed to a trophic cascade in Yellowstone (Table 1). Early on and before a significant prey population decline, we would conceptually expect any trophic cascade to be dominated by behavioral mediation and, as prey populations decline over time, to become dominated by density mediation (see Fig. 6 in Beschta and Ripple, 2010). Conversely, Kauffman et al. (2010) did not find evidence for a behaviorally mediated trophic cascade on the northern range, but it should be noted they did not document a release of plants at their sample sites (i.e., no trophic cascade was found, thus no behaviorally mediated trophic cascade would be expected). We are uncertain why Kauffman et al. (2010) did not find recruitment of young aspen but it may have been due to methodological differences in measurements of young aspen relative to other studies, increased heights of young aspen were just beginning, or other factors (Beschta and Ripple, 2011a).

Even with the occurrence of increased recruitment within existing aspen stands, full recovery of aspen to historical conditions may not be possible during the next few decades because most stands (approximately 2/3rds) have already died out and were lost due to heavy elk herbivory during the seven-decade period of wolf absence (Renkin and Despain, 1996; NRC, 2002). Furthermore, a recent modeling study has predicted there will be an aspen snag deficit during the second half of the 21st century corresponding to the aspen recruitment gap that was created during the long wolf-free period of the 20th century (Hollenbeck and Ripple, 2008). It should be noted that future aspen restoration is also possible with sexual reproduction now that wolves are again present in the Yellowstone ecosystem. For example, aspen may again regenerate following fire



Fig. 2. (A) August 2006 photograph showing a lack of recent aspen recruitment (aspen <1 m tall) in an upland site and (B) September 2010 photograph of recent aspen recruitment (some aspen >2 m tall) in same upland site. The dark, furrowed bark comprising approximately the lower 2 m of aspen boles represents long-term damage due to bark stripping by elk.

from seed sources rather than from extant clones (Turner et al., 2003).

Aspen, as previously noted, is not the only species of concern in northern Yellowstone and thus it is important to consider whether recent growth patterns of other woody browse species are consistent with or different from that of aspen. An assessment of Booth (*Salix boothii*) and Geyer (*Salix geyeriana*) willow stem diameter growth from 1989 to 2001 in the northern range by Beyer et al. (2007) found that increases in growth occurred relatively soon after the 1995/1996 reintroduction of wolves (Fig. 1F). They also found an inverse relationship between browsing intensity and willow stem growth that suggested reduced browsing was the mechanism for the trophic cascades and that the presence of wolves on the landscape was a significant predictor of willow growth in their highest ranked models. Similarly, decreased browsing and increased willow height growth were found at various other locations in the northern range and the Gallatin winter range, beginning in the late 1990s (Ripple and Beschta, 2004b, 2006; Beschta and Ripple, 2007a, 2010). An example of willow releasing over time on the northern range is shown in Fig. 3.

Scattered groups of black (*Populus trichocarpa*) and narrowleaf (*Populus angustifolia*) cottonwoods, totaling some 700 trees in 2001, provided prominent overstory canopies along the Lamar River and Soda Butte Creek in the northern range (Beschta, 2005). However, contemporary mortality rates indicate half of them may be dead within approximately 25–30 years such that replacement of existing overstory cottonwoods with new recruits represents an increasing ecological concern (Beschta and Ripple, 2007a, 2010). Given these ongoing patterns of mortality, the emerging pattern of increasing cottonwood recruitment in some places in recent years, like that of aspen and willow, appears to represent fundamental change in the dynamics of riparian cottonwood communities following the reintroduction of wolves.

In summary, riparian willow appeared to start recruiting by 1997, riparian cottonwood by 2002, and riparian aspen by 2006. Recruitment of upland aspen has lagged behind that of riparian stands, but data from the current study in the higher elevations of the northern range show that even some upland aspen are now growing taller than 200 cm (~upper browse height of elk). With wolves back in northern range ecosystems, various bottom-up forces may now begin to influence woody plant recruitment. For example, sites with deeper snow may cause a decrease in browsing intensity (Creel and Christianson, 2009) whereas site productivity and water tables might affect plant recruitment levels (e.g., Bilyeu et al., 2008; Tercek et al., 2010).

Willows started recruiting before both cottonwoods and aspen most likely because of a combination of two factors: (1) they are found mainly at high risk sites in valley bottoms and riparian areas (Beyer, 2006) and (2) they can withstand greater browsing pressure due to the multi-stem protective structure of individual willow clumps. Nevertheless, the fact that multiple woody species (aspen, willows, and cottonwoods) with contrasting autecologies have begun recruiting since wolf reintroduction (Table 1), the timing of the increased recruitment, and that decreased browsing has been common where plants have begun to release, provides important evidence that a post-wolf trophic cascade is the main cause for woody browse recruitment, rather than variations in climate or weather, or some other factor. 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.

From the 1920s to the mid 1960s, when wolves were absent, the park service tried to attain improved recruitment of aspen and other woody browse species with decreased elk densities

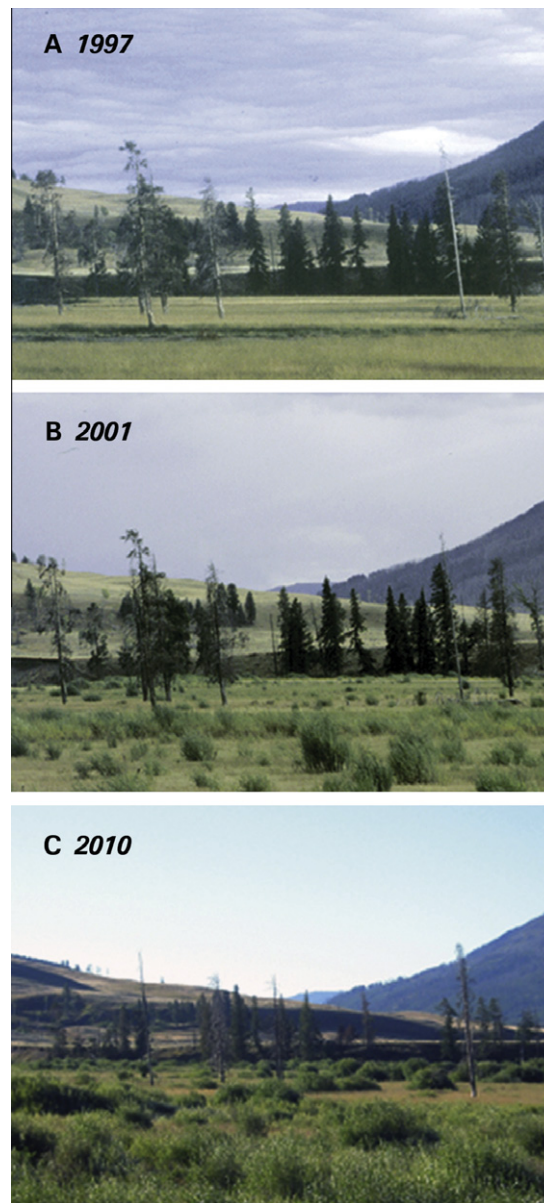


Fig. 3. Comparison photographs taken in 1997, 2001, and 2010 near the confluence of Soda Butte Creek with the Lamar River illustrating the stature of willow plants during suppression (A) from long-term browsing and their release (B and C) following wolf reintroduction in the winters of 1995–1996. As of 2010, both willow height and canopy cover increased compared to the earlier dates.

through culling of elk (NRC, 2002). In retrospect that experiment failed. While recruitment of multiple woody browse species appears to have begun in some areas of Yellowstone National Park in the presence of wolves, we might contemplate what will be required for a more complete and widespread recruitment of upland aspen in the coming years. The combination of behavioral and density effects from wolf presence (press disturbance) with periodic fire (pulse disturbance) may realistically portray how this system functioned historically. Fire reduces the dominance of aspen overstories, promotes the creation of dense young aspen thickets, and increases the occurrence of downed logs within the thickets. Researchers have also documented how elk, while under the risk of predation, skirt the edges of aspen thickets, avoiding their interiors (White et al., 2003). A photograph taken in the summer of 1900, before intensive herbivory from elk had become a problem on the northern range, provides visual evidence for this process



Fig. 4. Photograph taken in the summer of 1900 near Tower Junction on the northern range of Yellowstone National Park, showing aspen recruitment after wildfire and evidence of elk browsing on the outer stems of a 3- to 5-m-tall aspen thicket in the foreground and multiple recruiting aspen thickets on a distant hillslope. See text for hypothesis on the potential combined effects of wolves and fire on aspen recruitment and why browsing is evident only along the outer edges of the aspen thicket.

(Fig. 4). The photograph, which was taken a few years after wildfire during a time when wolves were present on the northern range, shows elk browsing the outer stems of a 3- to 5-m-tall recruiting aspen thicket. The recoupling of fire disturbance with the behavioral and density effects of wolves on elk could again facilitate upland aspen recruitment that has been missing for many decades. Furthermore, there is recent evidence that this scenario has started to again play out in that the combined effect of fire and a subsequent decrease in elk browsing following wolf reintroduction appears to have facilitated recruitment in aspen thickets for an area in northwestern Yellowstone National Park (Halofsky et al., 2008).

The effects of new recruitment of woody browse species does not stop with plant communities, but continues to ripple through an ecosystem potentially changing abiotic processes, as well as biotic functions such as habitat and food-web support for a host of vertebrates and invertebrates with potential consequences for increased biodiversity (Hebblewhite and Smith, 2010). In an abiotic example, Frank (2008) suggested that a wolf-triggered trophic cascade on elk likely altered net nitrogen mineralization in northern range grasslands. Biotic scenarios are more numerous. For example, the predicted aspen snag deficit described above will likely affect populations of cavity nesting birds on the northern range for decades to come (Hollenbeck and Ripple, 2008). Conversely, small herbivores such as rodents and lagomorphs may already be benefiting from decreases in coyotes (*Canis latrans*) and additional cover and forage due to decreases in elk herbivory and changes to plant communities (Ripple et al., 2011; Miller et al., in press). Any increase in small herbivores could significantly affect the prey base for both avian and mammalian predators [e.g., red foxes (*Vulpes vulpes*), and badgers (*Taxidea taxus*)] that subsist on these smaller mammals. Direct and indirect effects of wolves on other animals in Yellowstone have also been suggested for scavengers such as ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and black-billed magpies (*Pica hudsonia*) due to subsidies from wolf-killed carcasses (Wilmers et al., 2003), and on smaller carnivores due to the killing of coyotes by wolves (Smith et al., 2003; Ripple et al., 2011). Wolves could have a positive effect on the diets of birds and bears through a decrease in ungulate browsing on berry-producing shrubs, resulting in higher berry production and more food for these taxa. In turn, birds and bears, can affect berry-producing shrub establishment by dispersing seeds after consuming the berries.

Wolves and bears may provide multiple and linked positive feedback loops in their sympatric predation effects such that wolves provide subsidies to bears through scavenging opportunities on wolf-killed carrion, thus supporting higher bear densities and increased predation by bears on neonatal elk, further lowering elk densities. In recent years, the bear population on the northern range has increased and in 2003–2005 bears killed more elk calves than wolves, coyotes, and cougars combined (Barber-Meyer et al., 2008).

It appears that songbird populations have already been affected by the resurgence of willow on the northern range. Specifically, Baril (2009) found that the increased willow growth on the northern range resulted in more structurally complex habitat that subsequently allowed for greater songbird richness, Shannon-Weiner diversity, and relative abundance for six of seven focal bird species that use willow (Fig. 5). She found greater abundances of common yellowthroat (*Geothlypis trichas*), Lincoln's sparrow (*Melospiza lincolnii*), warbling vireo (*Vireo gilvus*), yellow warbler (*Dendroica petechia*), song sparrow (*Melospiza melodia*), and willow flycatcher (*Empidonax traillii*) in released willows than in suppressed willows.

Beaver have also increased since wolf reintroduction; from one colony in 1996 to 12 in 2009 (Fig. 1G). Although beaver were reintroduced into the national forest just north of the park between 1986 and 1999, the park increase in beaver is likely due, at least in part, to the resurgence of willow communities, because beaver on the northern range have been almost exclusively feeding on the newly released willow (Smith and Tyers, 2008). Increases in beaver populations have tremendous implications for riparian hydrology and biodiversity. Beaver have important roles in the hydrogeomorphic processes of decreasing streambank erosion, increasing sediment retention, raising wetland water tables, modifying nutrient cycling, and ultimately influencing plant, vertebrate, and invertebrate diversity and abundance in riparian ecosystems (Naiman et al., 1988). Wyoming streams with beaver ponds were found to have 75 times more abundant waterfowl than those without beaver ponds (McKinstry et al., 2001). Other species groups likely to be positively affected by an increase in the number of beaver ponds include amphibians, reptiles, and fish. In addition, mammals such as muskrat (*Ondatra zibethicus*), and river otters (*Lontra canadensis*) could benefit from the recovery of willow, beaver, beaver ponds, and wetlands.

Riparian plant communities play an important role in affecting the stability and morphology of stream channels (Kauffman et al., 1997; Beschta and Ripple, 2006). Thus, recovering riparian vegetation can provide increased hydraulic roughness and root strength thereby increasing the stability of formerly eroding streambanks. With improving riparian plant communities, currently eroding channels are likely to stabilize (i.e., less bank erosion and lateral channel movement during periods of high flow), active channel widths decrease, and pool-riffle morphology to become more complex (Beschta and Ripple, 2011b). While plant community recovery

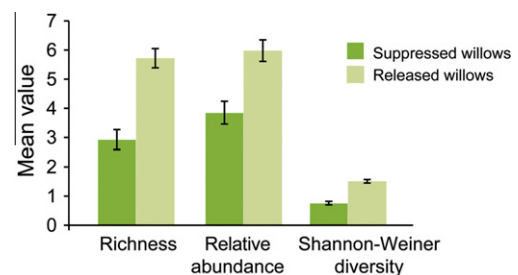


Fig. 5. Bird species richness, relative abundance, and Shannon-Weiner diversity on the northern range in suppressed versus released willows from browsing (Baril, 2009). Error bars represent standard errors.

can often proceed relatively rapidly in riparian ecosystems, channel recovery is likely to require a longer period of time.

Concurrent with the declining elk population, the bison population has been increasing on the northern range (Fig. 1H). Wolves may be allowing the bison population to increase through a decrease of inter-specific competition with lower elk numbers. Increased bison herbivory appears to be impacting young woody plants (e.g. willow, cottonwoods) on the northern range especially in the Lamar Valley where there is a relatively high year-round population (Painter and Ripple, 2012). Increased bison herbivory may explain why most cottonwood recruitment observed in recent studies has been on Soda Butte Creek and the extreme east end of the Lamar Valley, with little recruitment in the rest of the valley (Beschta and Ripple, 2010; Painter and Ripple, 2012). These secondary cascading effects may represent an example by which predators can influence multiple trophic levels through mediating the competitive interaction between the two prey species, elk and bison (Ripple et al., 2010a). Additional research in YNP is needed to examine the potential effects bison may be having on the structure and function of woody plant communities and riparian areas.

In terms of bottom-up influences, winter weather in Yellowstone can influence elk populations and seasonal patterns of herbivory (White and Garrott, 2005). While any changes in snowpacks and growing seasons may affect the release of woody browse plants, we suggest that such effects are of secondary importance relative to that of wolf presence and ungulate browsing. For example, during the seven decades when wolves were absent from northern Yellowstone's winter ranges and regardless of snowpack fluctuations, woody browse species were generally unable to grow above the browse level of elk, except in fenced enclosures. Therefore, snowpack depth, by itself, is unlikely to represent the main triggering mechanism regarding the ongoing release of woody browse species since wolf reintroduction because there has been plant recruitment regardless of snowpack depth, with recruitment occurring during both high snow and low snow periods.

5. Conclusions

Integrating top-down and bottom-up processes is a formidable challenge for ecologists and will require additional research on how potential bottom-up factors interact with top-down forces affect woody plant growth in Yellowstone. Examples of bottom-up factors include snow depth, precipitation (drought), and temperature (climate warming). More studies that sample multiple plant species across space and time are needed especially those that incorporate ungulate browsing levels and measures of site conditions and/or productivity. Additional research is a prerequisite for understanding differences in behavior of elk and bison, especially their patterns of browsing on deciduous woody species. Separating density and behavior effects of apex predators on prey, and subsequently on plant communities, in a dynamic landscape of fear is a continuing research need.

Based on studies of aspen, willow, and cottonwood in recent years, it appears that wolves have initiated a restructuring of northern Yellowstone's ecosystems via passive restoration (e.g., Kauffman et al., 1997). Improving recruitment of woody browse species during the first 15 years following wolf recovery has clearly begun, indicating that a tri-trophic cascade involving wolves-elk-plants has been re-established. Although these studies were conducted in Yellowstone National Park, the occurrence of trophic cascades involving wolves in other areas may have conservation implications for wolf management and ecosystem restoration.

The Yellowstone findings support other studies regarding the role of wolves in trophic cascades in northern Wisconsin (Callan,

2010), as well as Banff (Hebblewhite et al., 2005), Wind Cave (Ripple and Beschta, 2007a), Jasper (Beschta and Ripple, 2007b), and Olympic (Beschta and Ripple, 2008) National Parks. In fact, strong top-down forcing appears to be widespread in boreal and temperate ecosystems throughout the northern hemisphere, and this is the consistent conclusion from prehistoric, historic, and modern evidence from North America, Europe, Asia, and Oceania (Flueck, 2000; Beschta and Ripple, 2009; Ripple and Van Valkenburgh, 2010; Ripple et al., 2010b). Similarly, findings from apex predator research in the southern hemisphere indicate that dingos (*Canis lupus dingo*) appear to be biodiversity regulators (Letnic et al., 2011).

Taken collectively, the evidence provided by recent studies of top-down forcing and tri-trophic cascades caused by large predators with interacting bottom-up forces is becoming increasingly persuasive. Predation and predation risk associated with large predators appear to represent powerful ecological forces capable of affecting the interactions of numerous animals and plants, as well as the structure and function of ecosystems (Soulé et al., 2003; Terborgh and Estes, 2010; Eisenberg, 2010; Estes et al., 2011). Thus, the preservation or recovery of gray wolves may represent an important conservation need for helping to maintain the resiliency of wildland ecosystems, especially with a rapidly changing climate.

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References

- Barber-Meyer, S.M., Mech, L.D., White, P.J., 2008. Elk Calf Survival and Mortality Following Wolf Restoration to Yellowstone National Park. Wildlife Monograph No. 169.
- Baril, L.M., 2009. Change in Deciduous Woody Vegetation, Implications of Increased Willow (*Salix* spp.) Growth for Bird Species Diversity and Willow Species Composition in and around Yellowstone National Park's Northern Range. MS, Montana State University, Bozeman, USA.
- Barmore, W.J., 2003. Ecology of Ungulates and their Winter Range in Northern Yellowstone National Park; Research and Synthesis 1962–1970. Yellowstone Center for Resources, Yellowstone National Park, Mammoth, Wyoming, USA.
- Beschta, R.L., 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. *Ecology* 86, 391–403.
- Beschta, R.L., Ripple, W.J., 2006. River channel dynamics following extirpation of wolves in northwestern Yellowstone National Park, USA. *Earth Surface Processes and Landforms* 31, 1525–1539.
- Beschta, R.L., Ripple, W.J., 2007a. Increased willow heights along northern Yellowstone's Blacktail Deer Creek following wolf reintroduction. *Western North American Naturalist* 67, 613–617.
- Beschta, R.L., Ripple, W.J., 2007b. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research* 37, 1873–1885.
- Beschta, R.L., Ripple, W.J., 2008. Wolves, trophic cascades, and rivers in western Olympic National Park. *Ecohydrology* 1, 118–130.
- Beschta, R.L., Ripple, W.J., 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142, 2401–2414.
- Beschta, R.L., Ripple, W.J., 2010. Recovering riparian plant communities with wolves in northern Yellowstone, USA. *Restoration Ecology* 18, 380–389.
- Beschta, R.L., Ripple, W.J., 2011a. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade – comment. *Ecology*. doi:10.1890/11-0063.1.
- Beschta, R.L., Ripple, W.J., 2011b. The role of large predators in maintaining riparian plant communities and river morphology. *Geomorphology*. doi:10.1016/j.geomorph.2011.04.042.
- Beyer, H.L., 2006. Wolves, Elk and Willow on Yellowstone's National Park's Northern Range. MS, University of Alberta, Edmonton, Canada.
- Beyer, H.L., Merrill, E.H., Varley, N., Boyce, M.S., 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? *Ecological Applications* 17, 1563–1571.
- Bilyeu, D.M., Cooper, D.J., Hobbs, N.T., 2008. Water tables constrain height recovery of willow on Yellowstone's northern range. *Ecological Applications* 18, 80–92.

- Callan, R., 2010. Are Wolves in Wisconsin Affecting the Biodiversity of Understory Plant Communities via a Trophic Cascade? PhD Dissertation, University of Georgia, Athens, 151 p.
- Childress, M.J., Lung, M.A., 2003. Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour* 66, 389–398.
- Creel, S., Christianson, D., 2009. Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. *Ecology* 90, 2454–2466.
- Creel, S., Winnie Jr., J., Maxwell, B., Hamlin, K., Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86, 3387–3397.
- Despain, D.G., 1990. Yellowstone Vegetation. Consequences of Environment and History in a Natural Setting. Roberts Rinehart, Boulder, Colorado, USA.
- Eisenberg, C., 2010. The Wolf's Tooth: Keystone Predators, Trophic Cascades, and Biodiversity. Island Press, Washington, DC.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pickett, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soule, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet earth. *Science* 333, 301–306.
- Flueck, W.T., 2000. Population regulation in large northern herbivores: evolution, thermodynamics, and large predators. *Zeitschrift fuer Jagdwissenschaft* 46, 139–166.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330.
- Frank, D.A., 2008. Evidence for a top predator control of a grazing ecosystem. *Oikos* 117, 1718–1724.
- Garrott, R.A., Eberhardt, L.L., White, P.J., 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology* 81, 33.
- Grimm, R.L., 1939. Northern Yellowstone winter range studies. *Journal of Wildlife Management* 8, 329–334.
- Groshong, L.C., 2004. Mapping Riparian Vegetation Change in Yellowstone's Northern Range using High Spatial Resolution Imagery. MA Thesis, University of Oregon, Eugene, Oregon, USA.
- Gude, J.A., Garrott, R.A., Borkowski, J.J., King, F., 2006. Prey risk allocation in a grazing ecosystem. *Ecological Applications* 16, 285–298.
- Halofsky, J.S., Ripple, W.J., 2008a. Fine-scale predation risk on elk after wolf-reintroduction in Yellowstone National Park, USA. *Oecologia* 155, 869–877.
- Halofsky, J., Ripple, W., 2008b. Linkages between wolf presence and aspen recruitment in the Gallatin elk winter range of southwestern Montana, USA. *Forestry* 81, 195–207.
- Halofsky, J.S., Ripple, W.J., Beschta, R.L., 2008. Recoupling fire and aspen recruitment after wolf reintroduction in Yellowstone National Park, USA. *Forest Ecology and Management* 256, 1004–1008.
- Hebblewhite, M., Smith, D., 2010. Wolf community ecology: ecosystem effects of recovering wolves in Banff and Yellowstone National Park. In: Musiani, M.P.C., Paquet, P.C. (Eds.), *The Wolves of the World: New Perspectives on Ecology, Behavior, and Policy*. University of Calgary Press, Calgary, Alberta, pp. 69–120.
- Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86, 2135–2144.
- Hernández, L., Landré, J.W., 2005. Foraging in the landscape of fear and its implications for habitat use and diet quality of elk (*Cervus elaphus*) and bison (*Bison bison*). *Wildlife Ecology* 11, 215–220.
- Hollenbeck, J.P., Ripple, W.J., 2008. Aspen snag dynamics, cavity-nesting birds, and trophic cascades in Yellowstone's northern range. *Forest Ecology and Management* 255, 1095–1103.
- Kauffman, J.B., Beschta, R.L., Otting, N., Lytjen, D., 1997. An ecological perspective of riparian and stream restoration in the Western United States. *Fisheries* 22, 12–24.
- Kauffman, M.J., Brodie, J.F., Jules, E.S., 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91, 2742–2755.
- Landré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology* 79, 1401–1409.
- Letnic, M., Ritchie, E.G., Dickman, C.R., 2011. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study, in press. doi: 10.1111/j.1469-185X.2011.00203.x.
- Lima, S.L., Dill, L.M., 1990. Behavioural decisions made under the risk of predation. *Canadian Journal of Zoology* 68, 619–640.
- Lovaas, A.L., 1970. People and the Gallatin Elk Herd. Montana Fish and Game Department, Helena, Montana, USA.
- Mao, J.S., Boyce, M.S., Smith, D.W., Singer, F.J., Vales, D.J., Vore, J.M., Merrill, E.H., 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69, 1691–1703.
- McKinstry, M.C., Caffrey, P., Anderson, S.H., 2001. The importance of beaver to wetland habitats and waterfowl in Wyoming. *Journal American Water Resources Association* 37, 1571–1577.
- Miller, B., Harlow, H.J., Harlow, T., Biggins, D., Ripple, W.J., in press. Trophic interactions linking wolves, coyotes, and small mammals. *Canadian Journal of Zoology*.
- Naiman, R.J., Johnston, C.A., Kelley, J.C., 1988. Alteration of North American streams by beaver. *BioScience* 38, 753–762.
- National Research Council (NRC), 2002. *Ecological Dynamics on Yellowstone's Northern Range*. National Academy Press, Washington, DC.
- Painter, L.E., Ripple, W.J., 2012. Effects of bison on willow and cottonwood in northern Yellowstone National Park. *Forest Ecology and Management* 264, 150–158.
- Renkin, R., Despain, D., 1996. Notes on postfire aspen seedling establishment. In: Greenlee, J.M. (Ed.), *Ecological Implications of Fire in Greater Yellowstone*. International Association of Wildland Fire, Fairfield, WA, pp. 95–103, 105–106.
- Ripple, W.J., Beschta, R.L., 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184, 299–313.
- Ripple, W.J., Beschta, R.L., 2004a. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* 54, 755–766.
- Ripple, W.J., Beschta, R.L., 2004b. Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecology and Management* 200, 161–181.
- Ripple, W.J., Beschta, R.L., 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecology and Management* 230, 96–106.
- Ripple, W.J., Beschta, R.L., 2007a. Hardwood tree decline following the loss of large carnivores on the Great Plains, USA. *Frontiers in Ecology and the Environment* 5, 241–246.
- Ripple, W.J., Beschta, R.L., 2007b. Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138, 514–519.
- Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* 95, 361–370.
- Ripple, W.J., Van Valkenburgh, B., 2010. Linking top-down forces to the Pleistocene megafaunal extinctions. *BioScience* 60, 516–526.
- Ripple, W.J., Painter, L.E., Beschta, R.L., Gates, C.C., 2010a. Wolves, elk, bison, and secondary trophic cascades in Yellowstone National Park. *Open Ecology Journal* 3, 31–37.
- Ripple, W.J., Rooney, T.C., Beschta, R.L., 2010b. Large predators, deer, and trophic cascades in boreal and temperate ecosystems. In: Terborgh, J., Estes, J.A. (Eds.), *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press, Washington, DC, pp. 141–161.
- Ripple, W.J., Wirsing, A.J., Beschta, R.L., Buskirk, S.W., 2011. Can restoring wolves aid in lynx recovery. *Wildlife Society Bulletin*, in press. doi: 10.1002/wsb.59.
- Smith, D.W., Tyers, D.B., 2008. The beavers of Yellowstone. *Yellowstone Science* 16, 4–14.
- Smith, D.W., Peterson, R.O., Houston, D.B., 2003. Yellowstone after wolves. *BioScience* 53, 330–340.
- Smith, D., Stahler, D., Albers, E., McIntyre, R., Metz, M., Irving, J., Raymond, R., Anton, C., Cassidy-Quimby, K., Bowersock, N., 2011. Yellowstone Wolf Project: Annual Report, 2010. YCR-2011-06. National Park Service, Yellowstone National Park, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.
- Soulé, M.E., Estes, J.A., Berger, J., Martinez Del Rio, C., 2003. Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* 17, 1238–1250.
- Strong, D.R., Frank, K.T., 2010. Human involvement in food webs. *Annual Review of Environment and Resources* 35, 1–23.
- Terborgh, J., Estes, J.A. (Eds.), 2010. *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press, Washington, DC.
- Tercek, M.T., Stottlemeyer, R., Renkin, R., 2010. Bottom-up factors influencing riparian willow recovery in Yellowstone National Park. *Western North American Naturalist* 70, 387–399.
- Turner, M.G., Romme, W.H., Reed, R.A., Tuskan, G.A., 2003. Postfire aspen seedling recruitment across the Yellowstone (USA). *Landscape Ecology* 18, 127–140.
- White, P.J., Garrott, R.A., 2005. Yellowstone's ungulates after wolves – expectations, realizations, and predictions. *Biological Conservation* 125, 141–152.
- White, C.A., Feller, M.C., Bayley, S., 2003. Predation risk and the functional response of elk-aspen herbivory. *Forest Ecology and Management* 181, 77–97.
- White, P.J., Proffitt, K.M., Mech, L.D., Evans, S.B., Cunningham, J.A., Hamlin, K.L., 2010. Migration of northern Yellowstone elk: implications of spatial structuring. *Journal of Mammalogy* 91, 827–837.
- White, P.J., Proffitt, K.M., Lemke, T.O., in press. Changes in elk distribution and group sizes after wolf restoration. *American Midland Naturalist*.
- Wilmers, C.C., Crabtree, R.L., Smith, D.W., Murphy, K.M., Getz, W.M., 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. *Journal of Animal Ecology* 72, 909–916.
- Wolff, J.O., Van Horn, T., 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* 81, 266–271.