Biological Conservation 145 (2012) 205–213

Contents lists available at SciVerse ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

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

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ARTICLE INFO

Article history:
Received 14 August 2011
Received in revised form 27 October 2011
Accepted 3 November 2011
Available online 15 December 2011

Keywords:
Wolves
Elk
Aspen
Yellowstone
Trophic cascades

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.

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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doi:10.1016/j.biocon.2011.11.005

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://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