



Trophic cascade or trickle? Understanding the indirect effects of wolves on aspen

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Abstract A popular hypothesis in ecology and conservation is that large terrestrial carnivores have strong indirect effects on plants and abiotic processes by consuming and (or) scaring herbivores. However, a large body of ecological theory predicts that large carnivores have only weak indirect effects in terrestrial ecosystems. The purpose of this study was to assess the strength of the indirect effect of wolves (*Canis lupus*) on aspen (*Populus tremuloides*) in northern Yellowstone National Park, where regeneration of overstory aspen trees largely ceased during the latter half of the 20th century due in part to browsing by elk (*Cervus canadensis*). To the extent that increases in young aspen height and aspen canopy cover reflect the indirect effects of wolves, long-term data from 113 randomly selected stands and preliminary data from historic and contemporary aerial imagery support the prediction of a weak indirect effect of wolves on aspen. In 2022, 17% of plots did not regenerate any young aspen, and of those that did regenerate, 78% of young aspen were too short to reliably escape browsing and join the overstory. Remote sensing data suggest that these plot-level patterns may reflect an underappreciated level of stand deterioration and loss that has continued unabated since at least the mid-1950s.

Introduction

Understanding the ecological effects of large carnivores in terrestrial ecosystems is a central challenge in contemporary ecology and natural resource management. The trophic cascade hypothesis predicts that large carnivores have strong indirect effects on plants and abiotic processes by consuming and (or) scaring herbivores (Ripple et al., 2014). Some researchers have proposed that trophic cascades are “a universal property of ecosystem functioning, a law of nature as essential and fundamental to ecology as natural selection is to evolution” (Terborgh and Estes, 2013). However, theory predicts that large carnivores have weak indirect effects because terrestrial ecosystems are often (a) resource-limited such that carnivores have little regulatory effect on herbivores, and (b) ‘reticulated’ such that trophic levels include multiple species with similar resource requirements,

which weakens interactions among pairs of species (Strong, 1992; Schmitz, 2010). Despite the common assertion that large carnivores alter plant communities and other ecosystem properties, there is no scientific consensus about the strength of large carnivore indirect effects due in part to a lack of studies characterized by strong inference, quantification of underlying mechanisms, and multiple hypothesis testing (Ford and Goheen, 2015).

One popular example of a strong large carnivore indirect effect is the interaction between wolves (*Canis lupus*), elk (*Cervus canadensis*) and aspen (*Populus tremuloides*) in northern Yellowstone National Park. A large body of research argues that reintroduced wolves killed and (or) scared away enough elk to allow aspen stands to recover from decades of unchecked browsing (Ripple and Beschta, 2012; Beschta et al., 2018; Painter et al., 2018). However,

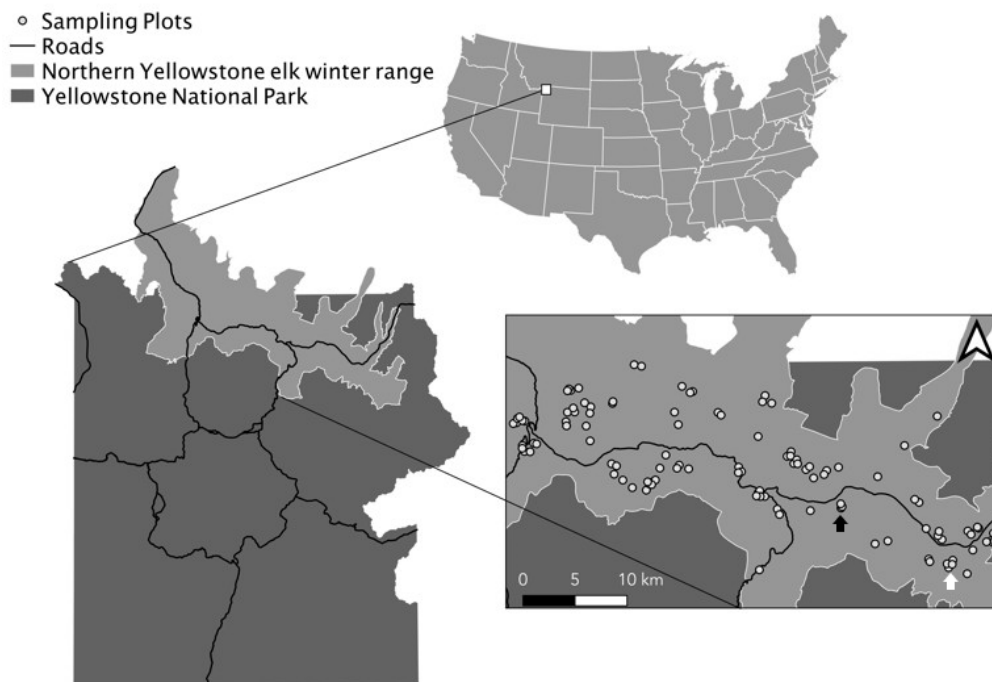


Figure 1. Locations of 113 randomly sampled aspen stands in northern Yellowstone National Park. The northern Yellowstone elk winter range is the maximum distribution of the northern Yellowstone elk population during winter when elk most often browse young aspen. Arrows point to aspen stands at Crystal Creek (black) and Lamar River (white) featured in Figure 5.

much of this research was based on a biased sampling method that measured the height of only the five tallest young aspen within a stand (reviewed in Brice et al., 2022).

Using a long-term dataset of randomly-sampled young aspen from 113 plots distributed randomly across northern Yellowstone (Figure 1), Brice et al. (2022) demonstrated that sampling the five tallest young aspen overestimated recruitment of overstory aspen by a factor of 4-7 compared to random sampling because it favored young aspen taller than the preferred browsing height of elk (120-130 cm) and overlooked non-regenerating aspen stands. This random sampling design, which included a more representative sample of aspen stands and saplings, suggested that wolves triggered a weak indirect effect that did not reverse the decline of all aspen stands (Figure 2; Brice et al., 2022).

The conclusion of a weak indirect effect is tentative because research to date has focused on height

growth of young aspen, which is possibly the least important aspect of aspen demography involved in the recovery of aspen stands. Growth, survival, and density of overstory trees in other size classes is also necessary to restore and maintain aspen canopy cover (Kulakowski et al., 2004). Historic landscape photographs suggest that aspen stands covered ~4–6% of northern Yellowstone during 1880–1900 (Houston, 1982; Meagher and Houston, 1999), and aerial photographs indicate that aspen coverage decreased to ~1% by 1992 (Larsen and Ripple, 2005). Surprisingly, the areal coverage of aspen stands has not been measured in the years since the 1995-1997 wolf reintroduction. As a result, the extent that a weak indirect effect of wolves on height growth of young aspen (Brice et al., 2022) reflects a correspondingly weak effect on aspen stand recovery per se is unknown.

The specific aims of this study were to (1) collect additional annual plot-level measurements of young



Figure 2. Previous research about the indirect effects of wolves on aspen in northern Yellowstone National Park mostly sampled aspen stands with robust regeneration of young aspen like the one at left, and overlooked aspen stands with little to no regeneration like the one at right. Long-term data from a random-sampling design indicate that many aspen stands have not regenerated despite wolf reintroduction (Brice et al., 2022). Credit: D. MacNulty

aspen height growth and overstory recruitment in the long-term sampling plots (Figure 1), and (2) assess the extent that plot-level variation in young aspen height growth and overstory recruitment is representative of remotely-sensed stand-level variation in canopy cover.

Methods

Measuring plots

Each plot was a 1 m × 20 m belt transect located randomly within an aspen stand that was itself randomly selected from an inventory of stands with respect to high and low wolf-use areas (Ripple et al., 2001). The inventory was a list of 992 grid cells (240 m × 360 m) that contained at least one stand. A ‘stand’ was a group of tree-size aspen (>10 cm diameter at breast height [dbh]) in which each tree was 30 m from every other tree. One hundred and thirteen grid cells were randomly selected from the inventory (~11% of 992 cells), one stand was randomly selected from each cell, and one plot was randomly established in each stand. Genetic testing suggests each plot is a genetically independent sample (Brice et al., 2022).

Aspen were measured at the end of the growing season (late July–early August), focusing on plants >1 year old, which were termed ‘young aspen’. The browsing status (browsed or unbrowsed) and height of the leader (tallest) stem of each young aspen in

each plot was measured. A leader was ‘browsed’ if its growth from the previous growing season had been eaten, which was identified by a sharp, pruned edge at the base of the current year’s growth. Diameter at breast height was used to estimate the height of young aspen >350–400 cm based on a regression model of the relationship between height and dbh for aspen in the study area (MacNulty, unpublished data). Previous research indicates that elk were likely the primary ungulate species browsing young aspen in plots during the study (Brice et al., 2022).

Measuring stands

The study focused on the 113 stands encompassing the sampling plots. Baseline information about the areal extent of these stands was obtained from the earliest available remote sensing data for the study area. This consisted of 24 black and white aerial photographs taken on 16 August 1954 (Larsen and Ripple, 2005), approximately 28 years after wolves were extirpated, and 41 years before they were reintroduced. Project collaborators with the NASA DEVELOP Program downloaded scanned copies of these aerial photos from the U.S. Geological Survey Earth Resources Observation and Science Center and georeferenced them in ArcGIS Pro 3.0.2. The scale of the imagery was 1:37400 and scanned at 1000 dots per inch, resulting in a ~1 m pixel size. The team georeferenced each image to control points that changed little since 1954 (e.g., ridges and rock forma-

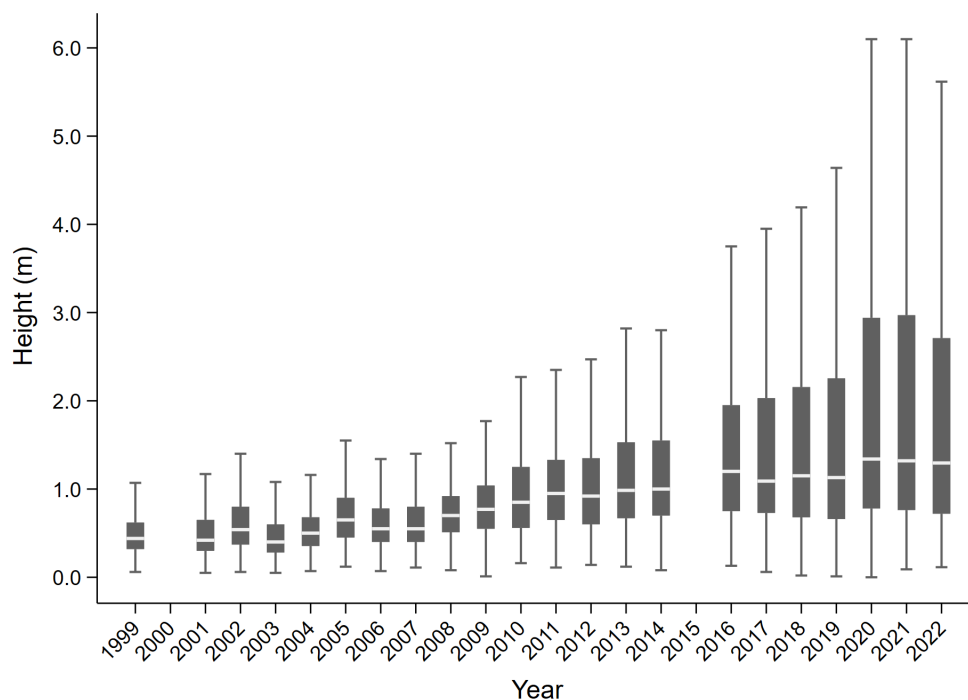


Figure 3. Annual height distributions (m) of young aspen in northern Yellowstone National Park, 1999-2022. Data are from 1 m × 20 m plots in 113 randomly selected aspen stands, which yielded 29,142 stem measurements. The midline of each box plot indicates the median height, and the bottom and top of the box indicate the 25th and 75th percentile (first and third quartile), respectively. The whisker lines extend to the lowest and highest datum within 1.5 times the interquartile range. No plots were measured in 2000 or 2015.

tions). Orthorectification was impractical because the images included insufficient metadata (Bailey et al., 2022).

Information about the current areal extent of sampled stands was derived from orthorectified aerial imagery collected by the National Agricultural Imagery Program (NAIP) on 17 July 2022, approximately 27 years after wolves were reintroduced. The spatial resolution of the NAIP imagery was 0.6 m. Digitization of stand extent and estimation of stand area for the 113 stands in 1954 and 2022 remains a work in progress. Reported below is a qualitative assessment of aspen cover change from 1954 to 2022 in two focal areas that exhibit contrasting stand dynamics. The Crystal Creek and Lamar River areas are located ~11 km apart in the eastern portion of the study area (Figure 5), where elk numbers were very high in the 1980s and 1990s before dropping to current numbers, which are substantially less than numbers in 1954 (Hous-

ton, 1982; Painter et al., 2015; MacNulty et al., 2020). Predation from wolves and other predators, especially hunters that killed adult female elk that migrated across the park's northern boundary in winter (Figure 1), contributed to the drop in elk numbers (Vucetich et al., 2005; Peterson et al., 2014; MacNulty et al., 2020).

Preliminary results

Plot-level dynamics

Eighty-four (74%) of 113 plots were measured during the 2022 field season (30 July to 6 August). Twenty-nine plots were not measured because they were inaccessible due to historic flooding in the study area during mid-June. Most of the unmeasured plots (27 of 29) were in the Lamar Valley area, which was closed to the public, including most researchers. During the preceding 21 field seasons (1999, 2001-2014, 2016-

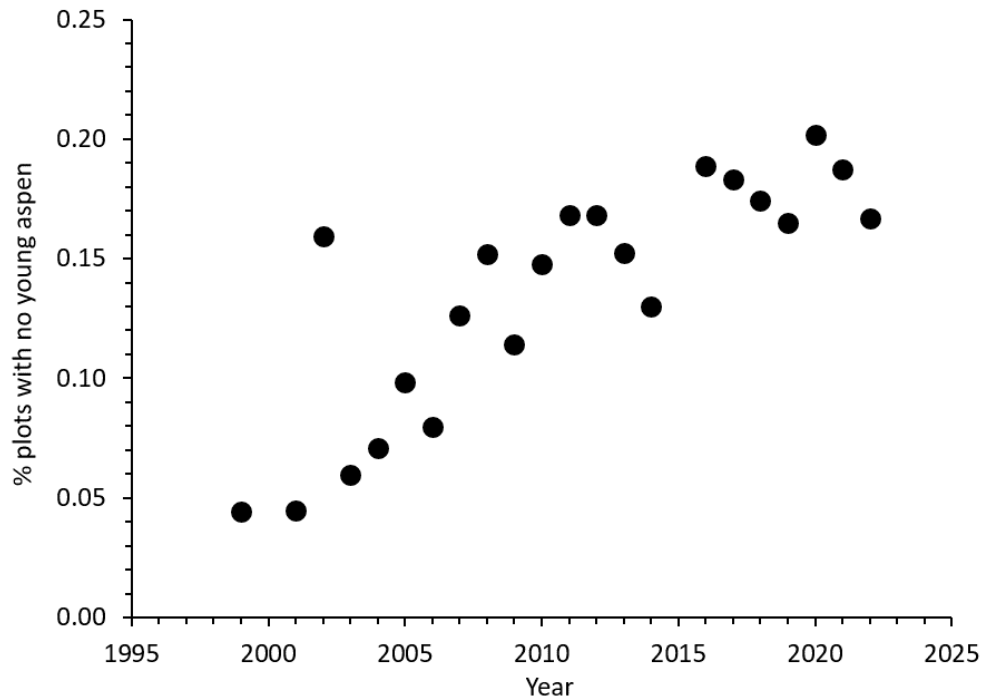


Figure 4. Annual percentage of plots in randomly selected aspen stands in northern Yellowstone National Park that produced no young aspen, 1999–2022. The number of plots measured each year ranged from 61 to 113 (mean \pm SE = 98 \pm 4). No plots were measured in 2000 or 2015.

2021), the average number of plots measured per season was 99 (range = 61–113 plots). The 2022 field season ranked sixth in terms of fewest plots measured per season. Despite the smaller sample of plots in 2022 compared to most other years of the study, results from 2022 were consistent with those from previous years in two important respects.

First, the height distribution of young aspen in 2022 was consistent with the observed pattern of height increase since 1999, which is characterized by slow increase in median height and fast increase in variance of height (Figure 3). During the 24-year period from 1999 to 2022, median height of young aspen (\sim 0.4 m in 1999) increased 3 times and its variance increased by a factor of 51, as a minority of young aspen exceeded 3 m, while a majority had less to no height increase. Median height has leveled off in recent years, peaking at 1.4 m in 2020 and dipping to 1.3 in 2022. The preferred browsing height of elk in the study area is \sim 1.2–1.3 m, and the height at which

young aspen generally escape browsing is \sim 3.0 m (Brice et al. 2022). In 2022, 22% of 966 young aspen exceeded 3.0 m.

Second, the total absence of young aspen in some plots in 2022 was consistent with a long-term increase in the frequency of plots not regenerating any young aspen (Figure 4). During the 24-year period from 1999 to 2022, the annual percentage of plots with no young aspen increased from 4% (of 113 plots) to 17%. In 2022, this percentage was down from its peak in 2020 (20% of 109 plots).

Stand-level dynamics

Preliminary analysis suggests that remotely-sensed stand-level variation in aspen canopy cover tracks plot-level variation in young aspen height growth and overstory recruitment. This is exemplified in a comparison of aspen cover change between stands in the Crystal Creek and Lamar River areas from August 16, 1954 to July 17, 2022 (Figure 5).

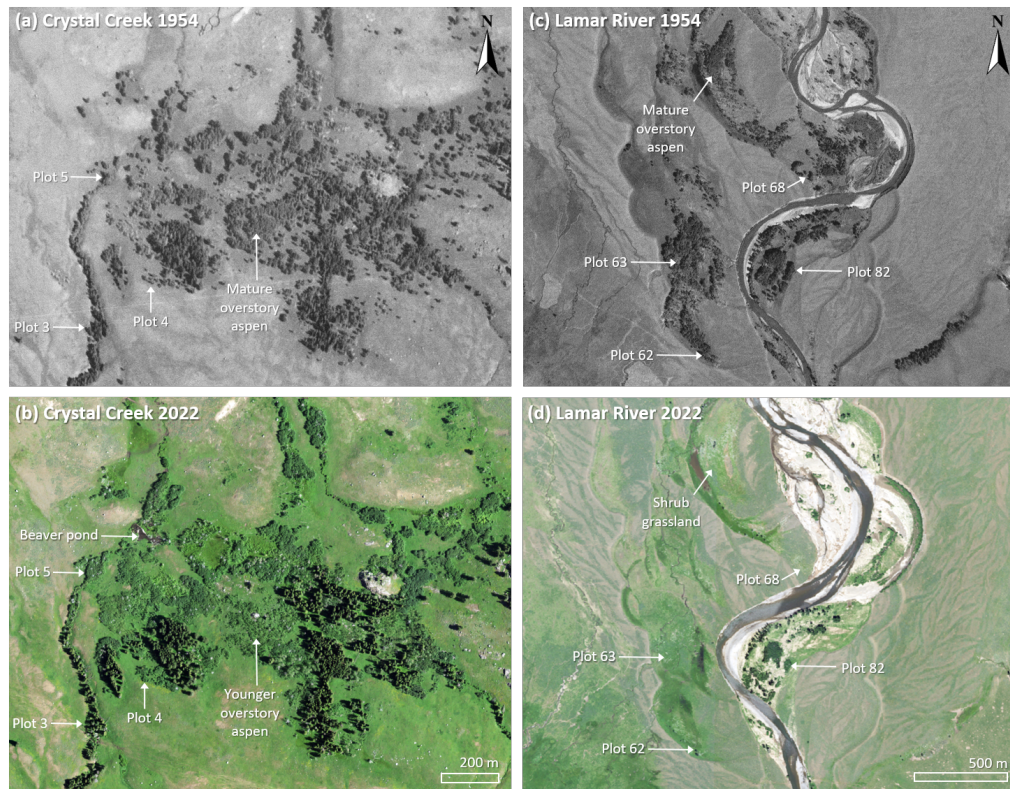


Figure 5. Contrasting patterns of aspen regeneration and overstory recruitment in stands adjacent to Crystal Creek (a, b) and Lamar River (c, d) in northern Yellowstone National Park between 16 August 1954 (a, c) and 17 July 2022 (b, d). Imagery acquired from aircraft using film (a, c) or digital (b, d) cameras. Each plot number corresponds to a 1 m × 20 m belt transect established in 1999 in a randomly selected aspen stand. Between 1954 and 2022, most aspen stands in the Crystal Creek area regenerated and some increased in areal extent (a, b), whereas most aspen stands in the Lamar River area converted to shrub-grassland vegetation (c, d).

At the Crystal Creek site, aspen cover increased from 1954 to 2022, including in three stands where plots were established in 1999 (plots 3-5; Figure 5a,b). The increase in cover included increases in the density of overstory trees within stands (e.g., plot 4) as well as increases in the areal extent of stands (e.g., plot 5). In addition, some mature overstory trees in 1954 were replaced by younger overstory trees by 2022. Another notable change was the development of a beaver colony including several dams and lodges constructed from aspen trees in the immediate vicinity (Fig. 5b). Increases in overstory recruitment in plots 3, 4, and 5 were consistent with the stand-level increase in canopy cover documented in the remote sensing data.

At the Lamar River site, nearly all the overstory as-

pen cover that was present in 1954 (Figure 5c) had vanished by 2022 (Figure 5d). Dead and down aspen trees, which are visible on the ground as white lines in Figure 5d, mark the presence of these formerly extensive stands. Four plots were established at this site in 1999 (Figure 5d), and regeneration of young aspen ceased in two of these plots, one (plot 63) after 2002 and another (plot 68) after 2013. Regeneration in the third plot (62) has been declining since 2008, with no young aspen having ever grown taller than 1.55 m. Regeneration in the fourth plot (82) has been robust, with the median height of young aspen exceeding 3.0 m every year since 2014. These inter-plot differences in regeneration and overstory recruitment are consistent with remotely-sensed variation in canopy cover across the corresponding stands (Fig. 5c,d).

Conclusions

To the extent that increases in young aspen height (Figure 3) and aspen canopy cover (Figure 5a, b) reflect the indirect effects of reintroduced wolves (Beschta and Ripple, 2016; Beschta et al., 2018) versus those of other predators (MacNulty et al., 2020), results from this study support the prediction that large carnivores in terrestrial ecosystems have weak indirect effects (Strong, 1992; Schmitz, 2010; Ford and Goheen, 2015). Twenty-seven years after the wolf reintroduction, the latest plot data indicate that less than 25% of young aspen grow tall enough to reliably escape browsing and join the overstory (Figure 3). Moreover, regeneration of young aspen has ceased in many plots (Figure 4), and preliminary analysis of remote sensing data suggests that this plot-level pattern is indicative of stand deterioration and loss that has continued unabated since at least the mid-1950s (Figure 5c, d; Bailey et al., 2022; Steen et al., 2022). Moisture stress may ultimately limit the indirect effect of wolves on aspen stand regeneration and maintenance in northern Yellowstone because this area is near the minimum annual precipitation limit of aspen (≥ 38 cm; DeByle and Winokur, 1985) and much of it is projected to become unsuitable for aspen within the next 60 years due to climate warming and drying consistent with increases in atmospheric greenhouse gases at rates similar to present (Piekielek et al., 2015; Brice et al., 2022).

Future work

The regeneration of at least some aspen stands in northern Yellowstone National Park following wolf reintroduction is a significant ecological outcome given previous concerns about the persistence of aspen in the area (Romme et al., 1995; Huff and Varley, 1999). Future work will focus on two key questions. First, how many aspen stands relative to the number occurring in 1954 have actually regenerated since wolf reintroduction? This question seeks to determine which of the two patterns in Figure 5 is the more common one. The long-term plot data (Figure 3 and Figure 4) suggest that the pattern of regeneration exemplified at Crystal Creek (Figure 5a, b) is less widespread than the pattern of stand loss ex-

emplified at Lamar River (Figure 5c, d). Second, how stable is the pattern of regeneration? Here, the aim is to understand the persistence of regenerated stands. Conceivably, future environmental disturbances (e.g., drought, pathogens, beaver foraging, elk population increase, etc.) could act independently or synergistically to reverse recent increases in aspen canopy cover. Answers to both questions are vital to understanding the ecological effects of wolves and other predators in terrestrial ecosystems.

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