



Short communication

The strength of the Yellowstone trophic cascade after wolf reintroduction

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ABSTRACT

Trophic cascades, the indirect effects of predators propagating downward through food webs, play a critical role in shaping ecosystems. We evaluated the strength of a large carnivore-induced trophic cascade in northern Yellowstone National Park, focusing on riparian willows (*Salix* spp.) as primary producers. Using the $\log_{10}$ response ratio, a standardized indicator of trophic cascade strength, we quantified changes in willow crown volume following the 1995–96 reintroduction of gray wolves (*Canis lupus*), which completed the large carnivore guild. Reduced herbivory pressure from Rocky Mountain elk (*Cervus canadensis*) followed their reintroduction, leading to increased growth in willows. Crown volume, a proxy for above-ground biomass, was calculated using a predictive model based on willow height and was used to index primary producer response. Data from a 20-year study (2001–2020) revealed a relatively strong trophic cascade, with a ~1500 % increase in average willow crown volume and a $\log_{10}$ ratio of 1.21. This ratio surpassed 82 % of those reported in a global meta-analysis of trophic cascades. These results emphasize the importance of long-term monitoring to capture gradual and nonlinear ecosystem responses following predator reintroductions. They also underscore the substantial effect restored large carnivores can have on riparian vegetation and highlight the utility of crown volume as a metric for assessing trophic cascade strength.

1. Introduction

Trophic cascades are indirect effects of predators extending downward through food webs. These cascades can influence biodiversity, primary productivity, and nutrient cycling and are therefore key to understanding the structure and function of ecosystems (Estes et al., 2011). Impacts of these cascades are shaped by ecosystem type, productivity, environmental conditions, biological traits, and the plant response variables considered (Strong, 1992; Borer et al., 2005; Jia et al., 2018). Thus, determining the strength of a trophic cascade and whether a particular predator is influencing herbivores and plants in any given system requires measurement of plant traits that are reliably responsive to changing patterns of herbivory and comparable across ecosystems. Here, we use the $\log_{10}$

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response ratio to quantify the strength of a large carnivore trophic cascade in northern Yellowstone National Park, USA. The plant response $\log_{10}$ ratio is a widely-used, standardized indicator of trophic cascade strength that compares plant variables such as primary producer biomass in the presence or absence of predators, as mediated by herbivores (Shurin et al., 2002; Borer et al., 2005).

By the 1920s, gray wolves (*Canis lupus*) were locally extirpated and cougars (*Puma concolor*) were greatly reduced in Yellowstone National Park, leading to increased herbivory by Rocky Mountain elk (*Cervus canadensis*) on the park's northern elk winter range (Peterson et al., 2020). This increase in elk herbivory resulted in long-term suppression of palatable woody plants in riparian areas due to browsing, despite human hunting of elk along the park's northern boundary and a government elk culling program inside the park (Kay, 1990). Cougar numbers started increasing in the 1980s (Ripple et al., 2022), and the reintroduction of wolves in 1995 and 1996 completed the park's large carnivore guild, creating a natural experiment for evaluating the ecological effects of large predator restoration through a trophic cascade.

Researchers largely concur that the decline in woody plant communities in northern Yellowstone can be attributed primarily to the loss of wolves and the suppression of other large predators, which led to increased browsing by elk (Peterson et al., 2020). Similar results have also been found in Banff and Jasper National Parks following the loss of wolves (Hebblewhite et al., 2005; Beschta and Ripple, 2007a). The science appears relatively settled on the ecological effects of wolf extirpation, but questions remain in the Yellowstone ecosystem about the strength of the trophic cascade triggered by the restoration of wolves and other large carnivores. More broadly, there has been little work, worldwide, quantifying the strength of trophic cascades on plants after large carnivore restoration (Terborgh and Estes, 2010).

In northern Rocky Mountain locations, such as Yellowstone National Park, riparian areas normally occupy a small portion of the landscape. However, these areas are nevertheless important due to their high biodiversity and productivity. Here, our objectives were to 1) quantify the strength of trophic cascades in Yellowstone's northern range using the $\log_{10}$ ratio of change in riparian willows (*Salix* sp.) as primary producers, and 2) put this finding into context using a meta-analysis of other studies quantifying trophic cascade strength. Our purpose was to quantify trophic cascade strength only, not to characterize the stage of ecological restoration on the northern range.

2. Materials and methods

We used data from a 20-year study (2001–2020) of established willows growing on riparian floodplains and stream terraces in the park's northern range (Cooper and Hobbs, 2023; Hobbs et al., 2024). Willow height has typically been used in Yellowstone's riparian areas to help understand the ecosystem effects of large carnivore restoration following the reintroduction of wolves (Beschta and Ripple, 2016; Painter and Tercek, 2020; Hobbs et al., 2024). However, height may not be the most robust indicator of a trophic cascade's strength for willows because it does not fully capture the magnitude of the plants' overall growth or productivity. Willow crown volume encompasses the total three-dimensional space occupied by the willow's stems, branches and leaves, which correlates highly with above-ground willow biomass (Yao et al., 2021). Biomass is a popular variable for assessing the strength of a trophic cascade because it provides a measure of the amount of organic material available at the primary producer level (Shurin et al., 2002; Borer et al., 2005). See Fig. 1 as an example illustrating dramatic change in willow crown volume and biomass over time for several stream reaches in northern Yellowstone.

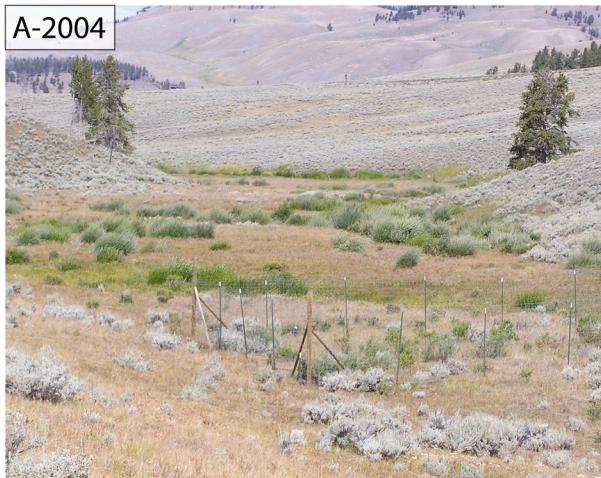
Recently, Kauffman and Cummings (2024) developed a model for predicting willow crown volume (m^3) from plant height using field data from various sites in northern Yellowstone National Park. Their dataset consists of 52 randomly selected willows exhibiting a wide range of heights and crown sizes, with heights ranging from 26 cm to 459 cm. They measured willow heights and horizontal crown dimensions and used these measurements to estimate crown volume, assuming a half-ellipsoid shape, and then fit a model to predict crown volume (m^3) from willow height (m). This model, which has $r^2 = 0.92$, estimates the natural log of willow volume (m^3) to be equal to $[3.2511 \times \ln(\text{height})] - 1.1763$.

Based on the annual fall willow heights presented in Cooper and Hobbs (2023), we utilized the Kauffman and Cummings (2024) model to estimate the crown volume of each of their plants. We used these individual volume estimates to calculate the average crown volume by year along with the associated 95 % one-sample t-confidence intervals. We then calculated $\log_{10}$ ratios of average crown volume for each year relative to the first year, 2001, using the formula $\log_{10} \left(\frac{\bar{V}_i}{\bar{V}_{2001}} \right)$ where $\bar{V}_i$ and $\bar{V}_{2001}$ are the average volume in year i and year 2001 respectively. Similarly, we also calculated $\log_{10}$ ratios using the average height in each year. We considered northern range sites from the Cooper and Hobbs (2023) dataset where willows were fully accessible to ungulates (i.e., 4 control sites and 21 additional observational sites). Willows on their sites generally were consistent with the assumption of half-ellipsoid shape (Fig. 1), but this may not be the case in other areas where crown shape has been altered by intensive herbivory.

3. Results and discussion

Results indicated an average willow height of 92 cm in 2001, compared to 192 cm in 2020. This more than doubling of average willow height results in a $\log_{10}$ ratio of 0.32 from the beginning to the end of the study. Willow release from browsing actually began soon after wolf reintroduction in the late 1990s (Beschta and Ripple, 2007b; Beyer et al., 2007)—a few years before Cooper and Hobbs (2023) started collecting data in 2001. Thus, a $\log_{10}$ ratio of 0.32 for willow height may represent a conservative estimate of trophic cascade strength as some time had already passed since willows began growing taller (Painter and Tercek, 2020).

Based on the Cooper and Hobbs (2023) willow height data and the Kauffman and Cummings (2024) model, average willow crown

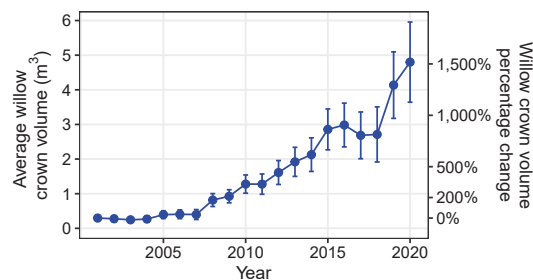


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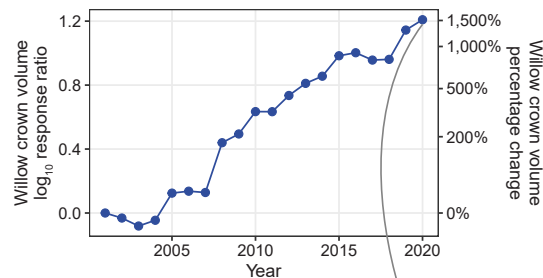
Fig. 1. (A) Downstream view of the East Fork of Blacktail Deer Creek in August 2004 and September 2021, northern range of Yellowstone National Park, USA. Note the 2.4 m tall fenced ungulate enclosure near the bottom right of the 2004 photo with willows alongside sagebrush, which was part of a [Cooper and Hobbs \(2023\)](#) experimental site. In 2002, willow heights outside the newly constructed fence averaged 68 cm whereas willows inside the fence averaged 85 cm in height (25 % taller). In 2020, willow heights outside the fence averaged 165 cm while willows fully protected from ungulate herbivory inside the fence were 195 cm in height (18 % taller). The fence was constructed in 2001 and removed by the spring of 2021. The similarity, in this example, between inside and outside the enclosure in 2021 is consistent with the strong trophic cascade quantified in the full time-series dataset. (B) Upstream view of Blacktail Deer Creek in 2005 and 2021 and (C) an across channel view in 2005 and 2021 of another reach farther downstream. These chronosequence photographs should be considered examples only, but they do indicate that tall willows, with greatly increased crown volumes, had become relatively common along the valley bottom and floodplains of Blacktail Creek. Photo credits; R.L. Beschta, photo point location for (A) Lat. N 44°57'01" Long. W110°34'03" for (B) Lat. N44°57'58" Long. W110°35'30" and for (C) Lat. N44°57'58" Long. W110°35'28". See [Figs. S1-S3](#) for high resolution versions of the photos.

volume increased approximately $\sim 1500\%$ ($0.3\text{--}4.8\text{ m}^3$) from the start to the end of the 20-year willow study ([Fig. 2A](#)). This increase in crown volume indicates considerably more nesting habitat for birds, greater shading of streams, as well as other ecological benefits. Using willow crown volume as our basis, the plant $\log_{10}$ ratio from the start to the end of the dataset by [Cooper and Hobbs \(2023\)](#) was

A. Yellowstone willows 2001–2020



B. Yellowstone willows log ratio 2001–2020



C. Trophic cascade meta-analysis

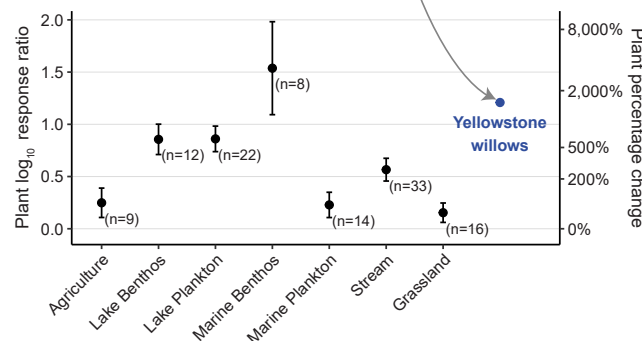


Fig. 2. The Yellowstone trophic cascade in context. Wolves were introduced into Yellowstone in 1995 and 1996. Between 2001 and 2020, estimated average willow crown volume in northern Yellowstone rose from approximately 0.30 m^3 to 4.80 m^3 (A; error bars indicate 95 % confidence intervals). This change corresponds to a $\log_{10}$ response ratio of 1.21 (B), which is substantially greater than the response ratios observed in many other studies (C). Willow crown volume was calculated using height data from [Cooper and Hobbs \(2023\)](#) and the crown volume model from [Kauffman and Cummings \(2024\)](#). Except for Yellowstone willows, average $\log_{10}$ ratios by system type were obtained from a trophic cascade meta-analysis of plant biomass studies ([Borer et al., 2005](#)); sample sizes are shown in parentheses; error bars represent one standard error of the mean (C).

1.21 (Fig. 2B). This value was greater than 93 (~82 %) of the 114 unique plant $\log_{10}$ ratios reported in a meta-analysis by Borer et al. (2005) of trophic cascades that included a variety of freshwater, marine, and terrestrial systems around the world (Fig. 2C).

The crown volume $\log_{10}$ ratios generally increased year over year (Fig. 2B). Thus, considering the length of time since predator reintroduction can be essential when assessing trophic cascades' effects on plant communities. The return of predators may trigger immediate changes in ecosystem processes, such as decreased browsing due to influences on prey populations or behavior. However, their effect on plant community dynamics may unfold more gradually and non-linearly across a larger landscape (Newbold et al., 2020). Accordingly, early assessments may not capture the full impact of a restored predator, as plants with a long regeneration time often respond slowly to altered herbivore pressures and ecosystem dynamics. By contrast, long-term studies help to reveal trends in plant biomass, reflecting sustained predator-prey-plant interactions (Figs. 2A and 2B). Thus, accurately measuring trophic cascade effects on woody plants requires monitoring ecosystems over extended periods post-predator reintroduction. The magnification of the trophic cascade effects may continue through time, but at some point may become asymptotic or tempered as willows reach their maximum heights or other biotic or abiotic factors dampen the response.

Synthesis work has shown strong evidence of trophic cascades following wolf reintroduction in Yellowstone, including 24 studies that examined willows and other deciduous woody plants in riparian areas (Beschta and Ripple, 2016). All but two of these 24 studies reported increases in plant height, stem diameter, stem establishment, canopy cover, or recruitment. Over half of the studies assessed ungulate browsing, consistently finding that increased woody plant growth and cover followed reduced browsing pressure. Nearly half also investigated the influence of climatic and hydrologic variables on plant community changes and generally found that they were unlikely to have driven the observed changes to riparian plant communities. Thus, the trophic cascade in Yellowstone has been well documented and our goal here was to quantify the strength of the trophic cascade, which has not clearly been done to date.

The reintroduction of wolves into Yellowstone reveals how recovering ecosystems may diverge from their original states. For example, prior to the return of wolves, elk overbrowsing severely reduced riparian vegetation across the landscape and, in doing so, contributed to the loss of beavers (*Castor canadensis*), a keystone species essential for maintaining wetland habitats and stabilizing stream hydrology along some reaches. Subsequent increases in channel erosion caused significant downcutting of streams and lowering of water tables, thus inhibiting the recovery of riparian willows away from the streams. This situation represents an example of ecological hysteresis, where the system's trajectory of recovery does not exactly follow its path of degradation and highlights the emergence of alternative states, in which the ecosystem can attain an alternative configuration for an unknown length of time, despite the restoration of apex predators. As a result, the recovery trajectory is shaped by the interplay of trophic dynamics, altered abiotic conditions, and the long-term absence of keystone species like wolves and beavers, whereby recovering ecosystems may not yet have the full array of structural and functional attributes that were present historically (Peterson et al., 2020; Hobbs et al., 2024).

Though a before-after control-impact (BACI) experimental design would have allowed for the strongest inference, the data we used for this project are similar to most other trophic cascade studies that focus on the reintroduction of extirpated large predators into parts of their native range. This approach utilizes a "natural experiment," a form of observational study that examines the effects of naturally occurring events without deliberate manipulation. In this framework, temporal changes serve as the primary basis for comparison. This method is particularly useful with large landscapes and wide-ranging predators, especially within a national park setting where experimental manipulations are typically prohibited. Here, the first year of the time series (2001) represents the "before" data and since this measurement occurred several years after wolf reintroduction, any results should be viewed as conservative. Willow heights before the 1995–96 reintroduction of wolves were typically shorter than the "year 1" willow heights in 2001 (Singer et al., 1998; Barmore, 2003). In addition to yearly means of crown volume, we report the associated 95 % t-confidence intervals as a measure of variability to make these data more suitable for future meta-analysis on trophic cascades (see Table S1).

4. Conclusions

Because crown biomass and crown volume are highly correlated (Yao et al., 2021), we conclude that crown volume was a reasonable surrogate for assessing the strength of the trophic cascade in northern Yellowstone. Hence, as a proxy for the biomass of riparian willows, researchers investigating trophic cascades might consider methods to determine crown volume, rather than just using willow height. We also conclude that the large carnivore trophic cascade on Yellowstone willows was relatively strong as quantified by the $\log_{10}$ ratio of willow crown volume, compared to a variety of other published trophic cascade studies that used biomass as a response variable. Quantifying trophic cascade strength in Yellowstone's willow populations highlights not only the substantial impact of large carnivores on plants but also the importance of long-term monitoring to capture gradual ecological responses following predator reintroductions. This knowledge can inform future conservation efforts and adaptive management strategies, especially in ecosystems undergoing restoration, where accurate assessment of trophic cascade dynamics is essential for evaluating recovery progress and biodiversity outcomes.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03428](https://doi.org/10.1016/j.gecco.2025.e03428).

Data availability

All data used in our analysis are available in the public repositories that we have cited.

References

- Barmore, W.J., 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis, pp. 1962–1970. Yellowstone Center for Resources, Yellowstone National Park: Mammoth, WY.
- Beschta, R.L., Ripple, W., 2007a. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Can. J. For. Res.* 37, 1873–1885.
- Beschta, R.L., Ripple, W.J., 2007b. Increased willow heights along northern Yellowstone's Blacktail Deer Creek following wolf reintroduction. *West. North Am. Nat.* 67, 613–617.
- Beschta, R.L., Ripple, W.J., 2016. Riparian vegetation recovery in Yellowstone: the first two decades after wolf reintroduction. *Biol. Conserv.* 198, 93–103.
- Beyer, H.L., Merrill, E.H., Varley, N., Boyce, M.S., 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade? *Ecol. Appl.* 17, 1563–1571.
- Borer, E.T., Seabloom, E.W., Shurin, J.B., Anderson, K.E., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2005. What determines the strength of a trophic cascade? *Ecology* 86, 528–537.
- Cooper, D., Hobbs, N.T., 2023. Twenty years of *Salix* height in response to experimental manipulation of browsing and water table, northern range of Yellowstone National Park [Dataset]. <http://doi.org/10.5061/dryad.sqv9s4n7n>.
- 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.
- 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.
- Hobbs, N.T., Johnston, D.B., Marshall, K.N., Wolf, E.C., Cooper, D.J., 2024. Does restoring apex predators to food webs restore ecosystems? Large carnivores in Yellowstone as a model system. *Ecol. Monogr.* 94, e1598.
- Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., Luskin, M.S., 2018. Global signal of top-down control of terrestrial plant communities by herbivores. *Proc. Natl. Acad. Sci.* 115, 6237–6242.
- Kauffman, J.B., Cummings, D., 2024. Predictive Equations for Determining Crown Area and Crown Volume of Recovering and Intact Willows Based upon Height at Yellowstone National Park. <http://doi.org/10.6084/m9.figshare.27905172.v2>.
- Kay, C., 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm [PhD dissertation]. Utah State University: Logan, UT. USA.
- Newbold, T., Tittensor, D.P., Harfoot, M.B., Scharlemann, J.P., Purves, D.W., 2020. Non-linear changes in modelled terrestrial ecosystems subjected to perturbations. *Sci. Rep.* 10, 14051.
- Painter, L.E., Tercek, M.T., 2020. Tall willow thickets return to northern Yellowstone. *Ecosphere* 11, e03115.
- Peterson, R., Beschta, R., Cooper, D., Hobbs, N., Johnston, D., Larsen, E., Marshall, K., Painter, L., Ripple, W., Rose, J., 2020. Indirect effects of carnivore restoration on vegetation. *Yellowstone wolves: Science and discovery in the world's first national park* 204–222.
- Ripple, W.J., Beschta, R.L., Painter, L.E., 2022. The history of cougars in Yellowstone National Park. *West. North Am. Nat.* 82, 752–759.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* 5, 785–791.
- Singer, F.J., Zeigenfuss, L.C., Cates, R.G., Barnett, D.T., 1998. Elk, multiple factors, and persistence of willows in national parks. *Wildl. Soc. Bull.* 26, 419–428.
- Strong, D.R., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73, 747.
- Terborgh, J., Estes, D.J.A. (Eds.), 2010. *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*, first ed. Island Press.
- Yao, X., Yang, G., Wu, B., Jiang, L., Wang, F., 2021. Biomass estimation models for six shrub species in Hunshandake Sandy Land in Inner Mongolia, Northern China. *Forests* 12.