Title

Flawed analysis invalidates claim of a strong Yellowstone trophic cascade after wolf reintroduction: A comment on Ripple et al. (2025)

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Abstract

Ripple et al. (2025) recently argued that large carnivore recovery in Yellowstone National Park triggered one of the world's strongest trophic cascades, citing a ~1500% increase in willow crown volume derived from plant height data. In this comment, we show that their conclusion is invalid due to fundamental methodological flaws. These include use of a tautological volume model, violations of key modeling assumptions, comparisons across unmatched plots, and the misapplication of equilibrium-based metrics in a non-equilibrium system. Additionally, Ripple et al. rely on selectively framed photographic evidence and omit critical drivers such as human hunting in their causal attribution. These shortcomings explain the apparent conflict with Hobbs et al. (2024), who found evidence for a relatively weak trophic cascade based on the same height data and a long-term factorial field experiment. Our critique underscores the importance of analytical rigor and ecological context for understanding trophic cascade strength in complex ecosystems like Yellowstone.

Keywords

Crown volume, large carnivores, tautology, trophic cascade strength, Yellowstone National Park, willow

Main Text

Ripple et al. (2025; hereafter “Ripple et al.”) recently concluded that large carnivore recovery, including the reintroduction of wolves (*Canis lupus*), triggered a relatively strong trophic cascade in Yellowstone National Park, one they claim exceeds the strength of most cascades documented worldwide. Their analysis focused on changes in willow (*Salix* spp.) crown volume, a proxy for above-ground willow biomass, over a 20-year period (2001–2020), using willow height data originally collected and analyzed by Hobbs et al. (2024; dataset: Cooper and Hobbs 2023; hereafter “Hobbs et al.”). In contrast, Hobbs et al. concluded that carnivore recovery produced a relatively weak trophic cascade. Their interpretation was based on the same height data as well as a factorial field experiment that manipulated browsing pressure and stream hydrology. They attributed a limited willow response to reduced groundwater availability and continued browsing by elk (*Cervus canadensis*) and bison (*Bison bison*)—the latter, a relatively invulnerable prey species (MacNulty et al. 2020a). The purpose of this comment is to reconcile these conflicting conclusions.

To support their interpretation, Ripple et al. converted the willow heights reported by Hobbs et al. into crown volume estimates using an unpublished regression model that predicts crown volume from plant height (Kauffman and Cummings 2024). They used these modeled values to calculate average crown volume by year, aggregating measurements across marked plants and plots, and then computed $\log_{10}$ response ratios—a standardized indicator of trophic cascade strength—by comparing each year's average crown volume to that of 2001. On this basis, they reported a ~1500% increase in willow crown volume from 2001 to 2020, corresponding to a $\log_{10}$ response ratio of 1.21—stronger than approximately 98% of trophic cascade effects documented globally by Borer et al. (2005; see corrigendum to Ripple et al.). In the sections that follow, we explain why these findings are not valid.

Tautological model

A core problem is that the high explanatory power of the Kauffman and Cummings model is tautological, not empirically validated. This is because they did not independently measure the crown volume of each of the 53 willow plants from which they estimated the relationship between volume and height. Rather, they calculated the volume of each plant from its height and canopy dimensions using the equation:

$$Volume = \left(\frac{4}{3} \times \pi \times \frac{a}{2} \times \frac{b}{2} \times height\right) \times 0.5$$

where a and b are perpendicular canopy widths and $height$ is the plant's maximum vertical extent. They then regressed the natural log of these calculated volumes against the natural log of $height$:

$$\ln(Volume) = -1.1763 + [3.2511 \times \ln(height)]$$

Because height is used to calculate volume, it appears in both the predictor and the response. As a result, this regression does not test an independent relationship between variables—it recovers a mathematical identity. This is not a genuine empirical relationship but a predictable consequence of how the data were generated. The model yields a high $R^2 = 0.92$, but this is not evidence that height is a good predictor of crown volume—it simply reflects the fact that volume was partially constructed from height. A high R^2 in this context is meaningless from an inferential standpoint, because the regression is structurally guaranteed to be strong. Thus, the reported predictive power of the model reflects circular reasoning rather than empirical validation.

The tautological structure of the Kauffman and Cummings model invalidates Ripple et al.'s analysis because applying it violates the scientific principle that conclusions must be supported by evidence that is independent of the data used to generate them (Hurlbert 1984; Nakagawa & Parker 2015). Ripple et al. used the model to transform willow height data into crown volume estimates and then interpreted the resulting increases in volume as evidence of a strong trophic cascade. However, since the volume estimates are mathematically derived from height, they do not constitute an independent line of evidence. In this case, the conclusion (a strong trophic cascade), the evidence (increasing volume), and the data (plant height) are not empirically separable. Consequently, Ripple et al.'s conclusions are not based on new empirical information and are therefore flawed. This helps explain the conflicting conclusions: the strong cascade inferred by Ripple et al. does not reflect different empirical patterns, but rather a circular reinterpretation of the same height data that underpinned Hobbs et al.'s finding of a relatively weak trophic cascade.

Unmet assumption about willow crown shape

Even if the Kauffman and Cummings model were empirically valid, it would overestimate the crown volume of willow plants in the Hobbs et al. plots (unfenced) because it was parameterized for unbrowsed or lightly browsed willows, assuming a dome-like, half-ellipsoidal crown structure. In contrast, annual browsing intensity in the Hobbs et al. plots, defined as the proportion of shoots browsed, was rarely below 0.25 on average, and frequently exceeded 0.50 for individual plants (see Fig. 12 and 13 in Hobbs et al. 2024). Although Hobbs et al. did not measure crown shape per se, photographic evidence suggests that browsing intensities were high enough to alter plant architecture, producing crown forms that deviated substantially from the half-ellipsoid structure assumed by the model (Fig. 1 A and B). As Kauffman and Cummings (2024) noted, their model "would not likely accurately predict" the crown volume of "moderately to heavily grazed willows", and that it is "only suitable for those willows with half-ellipsoidal/spherical structure."

Ripple et al., however, asserted that willows in the Hobbs et al. plots "generally were consistent with the assumption of half-ellipsoid shape," citing photographs from two sites taken in 2005 and 2021 as support. They acknowledged that crown shape might differ in "other areas where crown shape has been altered by intensive herbivory," but did not address the sustained browsing pressure in the Hobbs et al. plots or the clear guidance from Kauffman and Cummings against applying the model to such plants.

The consequences of violating the model's shape assumption are not trivial. In 2001, willows in the Hobbs plots were short, heavily browsed, and structurally deformed—conditions clearly inconsistent with the half-ellipsoidal crown architecture assumed by the model. Although browsing intensity declined through 2010, it increased again in later years, even as some willows grew taller. Some of these taller plants may not have regained—or may never have developed—the dome-like shape required for accurate volume estimation. Because the model calculates crown volume by multiplying height with canopy widths under the assumption of ellipsoidal symmetry, it likely overestimated volume more severely in later years, when applied to tall willows that retained distorted crown shapes (e.g., Fig. 1 D and E). Used under these conditions, the model exaggerates apparent change over time, especially when used to calculate proportional change via log response ratios. This structural bias, amplified by increasing height but persistent asymmetry, likely contributed to Ripple et al.’s inference of a strong trophic cascade, despite underlying trends in willow height and browsing that align more closely with Hobbs et al.’s conclusion of a relatively weak one.

These shape-related issues are compounded by concerns about the model’s ecological relevance. Thirty-eight percent of the 53 willows used to construct the model were *Salix lutea*, a species absent from the Hobbs et al. dataset, and 11% were sampled outside northern Yellowstone. These mismatches raise concerns about applying the model to different species and environments, where canopy form and responses to browsing may differ. Such extrapolation increases the risk of systematic bias and further weakens the inference of a strong trophic cascade.

Inappropriate comparison across unmatched plots

The log response ratio is a reliable measure of ecological change only when its numerator and denominator refer to the same or equivalent observational units across time, ensuring that observed differences reflect real change rather than differences in sample composition (Hedges et al. 1999; Lajeunesse 2015). Ripple et al.’s analysis deviates from this principle by comparing crown volume in 2001 and 2020 using largely different sets of plots. Although they describe this as a 20-year trend across 25 plots, only 22 plots were sampled in 2020, and just three of those had corresponding measurements from 2001—meaning the baseline crown volumes for the remaining 19 plots are unknown (Fig. 2).

If any of these 19 plots had larger crown volumes in 2001 than the three plots measured that year—and remained large or grew larger by 2020—their inclusion in the 2020 average would exaggerate the apparent increase in crown volume and artificially inflate the log response ratio. This inflation plausibly contributed to Ripple et al.'s conclusion of a strong trophic cascade. More fundamentally, the estimated effect size conflates ecological change with sampling bias, undermining its validity as measure of trophic cascade strength.

Unmet assumption about equilibrium

Ripple et al. emphasized the relative strength of the Yellowstone trophic cascade by comparing willow crown volume changes to the global meta-analysis by Borer et al. (2005). However, this interpretation neglects a key assumption of the Borer analysis—that plant communities have reached equilibrium by the end of each study, an assumption justified by temporal stability criteria from time-series data. In contrast, Yellowstone's willow recovery is ongoing, nonlinear, and shaped by complex biotic interactions such as persistent browsing from a reorganizing ungulate community, as well as abiotic factors including altered hydrological regimes due to lost beaver activity and stream incision (Hobbs et al. 2024). Thus, Yellowstone clearly reflects transient rather than equilibrium dynamics.

Equilibrium matters because it ensures observed biomass changes reflect stable trophic interactions rather than ongoing ecological transitions or disturbances. Under equilibrium, biomass changes can be reliably attributed to predator-driven control of herbivores, enabling unbiased assessments of trophic cascade strength. Conversely, ignoring this assumption in non-equilibrium environments like Yellowstone can lead to misinterpretations. Biomass changes (or lack thereof) in such contexts may reflect ecological adjustments, legacy effects, or persistent environmental constraints rather than current predator-herbivore interactions. Thus, applying equilibrium assumptions in non-equilibrium contexts undermines comparisons and risks misleading conclusions about trophic cascade strength.

Selective photographic evidence and attribution bias

Figure 1 of Ripple et al. presents chronosequence photographs from 2004–2005 and 2021 showing substantial increases in willow growth at select sites along Blacktail Deer Creek in northern Yellowstone. Although the authors describe these images as “examples only,” their presentation introduces a risk of visual confirmation bias—the tendency to overgeneralize from visually striking but unrepresentative examples. Notably, two of the three photo-pairs (panels B and C) depict nearly the same location, calling into question the spatial representativeness of the imagery. Moreover, Ripple et al. do not explain how these sites were selected or whether they reflect typical conditions. In a landscape where willow recovery is highly variable (e.g., Hobbs et al. 2024), omitting such context allows isolated successes to stand in for more complex and uneven outcomes.

Photographs from other locations tell a different story. As shown in Figure 3, many areas of the northern range—such as Yancey’s Hole and other sites along Blacktail Deer Creek—continue to show minimal willow regrowth decades after wolf reintroduction. These counterexamples underscore the spatial heterogeneity of willow responses and highlight how Ripple et al.’s imagery selectively emphasizes recovery, potentially overstating the generality and strength of the trophic cascade.

Finally, Ripple et al. attribute ecological changes primarily to large carnivores—particularly wolves—without adequately acknowledging the well-documented role of human hunting in reducing elk populations (Vucetich et al. 2005; Wright et al. 2006; Eberhardt et al. 2007; MacNulty et al. 2020b). Omitting this key factor skews causal inference and contributes to attribution bias by overstating the singular role of large carnivores in driving observed willow changes.

Conclusion

Taken together, the flaws in Ripple et al.'s analysis—including a tautological volume model, violations of key assumptions, comparisons across unmatched plots, and the misapplication of equilibrium-based metrics to a non-equilibrium system—render their estimate of trophic cascade strength untenable. Rather than offering new empirical insight, their findings rest on a circular reinterpretation of existing data, selectively presented and narrowly contextualized. These methodological shortcomings reconcile the apparent conflict with Hobbs et al., whose experimental design and explicit attention to hydrological and ungulate dynamics yield a better-supported conclusion: that the effects of large carnivore recovery on willow vegetation in northern Yellowstone have been modest and spatially variable. This conclusion is consistent with numerous other studies documenting weak and inconsistent indirect effects of large carnivores on deciduous woody plants in northern Yellowstone and elsewhere in the Greater Yellowstone Ecosystem (Creel and Christianson 2009; Kauffman et al. 2010, 2013; Kimball et al.

2011; Winnie 2012, 2014; Peterson et al. 2020; Brice et al. 2022, 2024; MacNulty et al. 2024). Far from indicating a strong, system-wide cascade, the current evidence points to a more complex and constrained outcome—one that underscores the importance of analytical rigor and ecological context in evaluating the consequences of large carnivore recovery.

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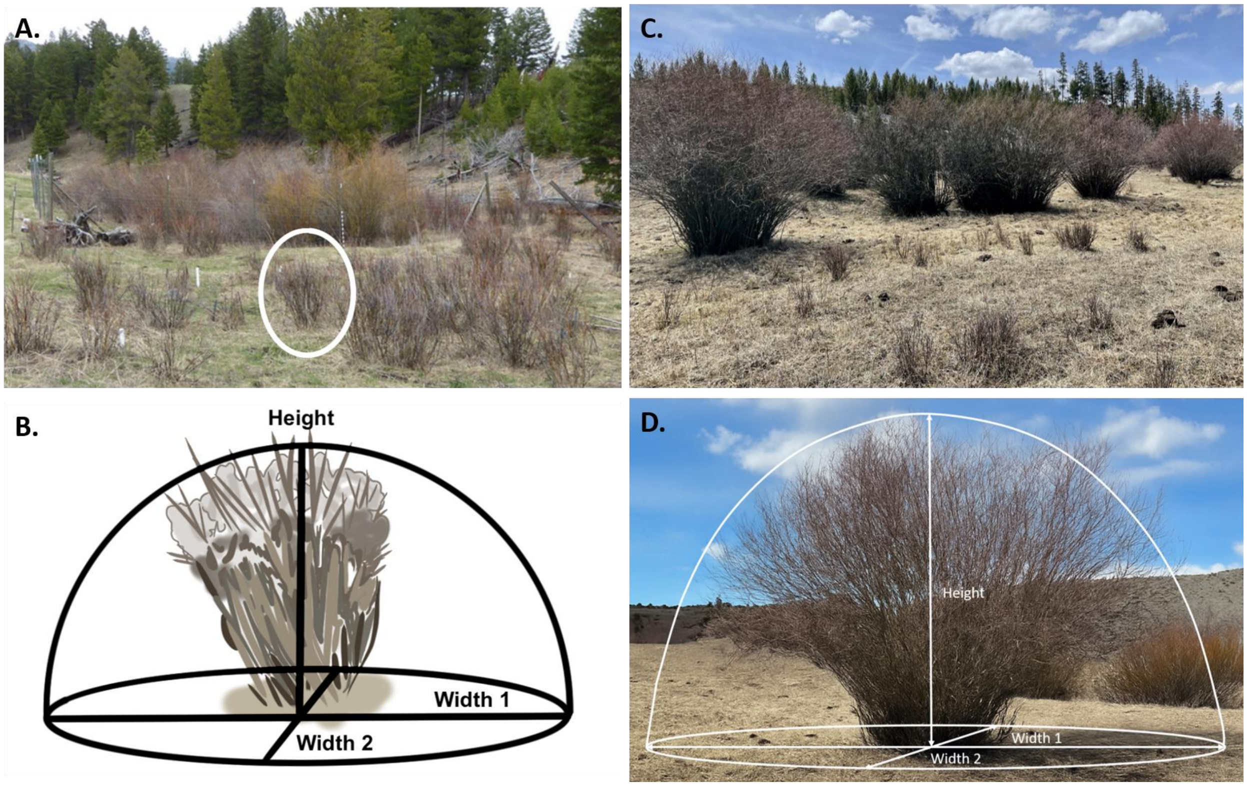

Figure 1. Field photographs and geometric reference diagrams illustrating the mismatch between the half-ellipsoid crown geometry assumed by the Kauffman and Cummings (2024) predictive model and the actual structure of willow (*Salix* spp.) plants in northern Yellowstone National Park. (A) A control (unfenced) plot at the Elk Creek experimental site in 2016, with the fenced plot visible in the background. The circled shrub is a marked individual from the Hobbs et al. study, exhibiting a heavily browsed, asymmetrical crown structure. (B) A half-ellipsoid superimposed on the same shrub shown in panel A, defined by the plant's measured maximum height and two perpendicular canopy widths. The actual crown clearly falls short of occupying the full theoretical volume. (C) A cluster of tall *Salix* shrubs photographed in April 2025 along the East Fork of Blacktail Deer Creek. Despite their height, the crowns are distorted and asymmetrical, lacking the regular, dome-like form assumed by the volume model. These examples show that crown deformation can persist even in taller individuals. (D) A single tall *Salix* shrub from the same site as panel C, overlaid with a schematic half-ellipsoid reference volume. The crown's uneven lateral spread and schematic internal voids demonstrate a poor fit to the assumed geometric form. These deviations illustrate how applying the predictive model to structurally deformed plants can lead to systematic overestimation of crown volume. Photo sources: (A) David Cooper, (B) Michael Procko, (C-D) Daniel MacNulty.

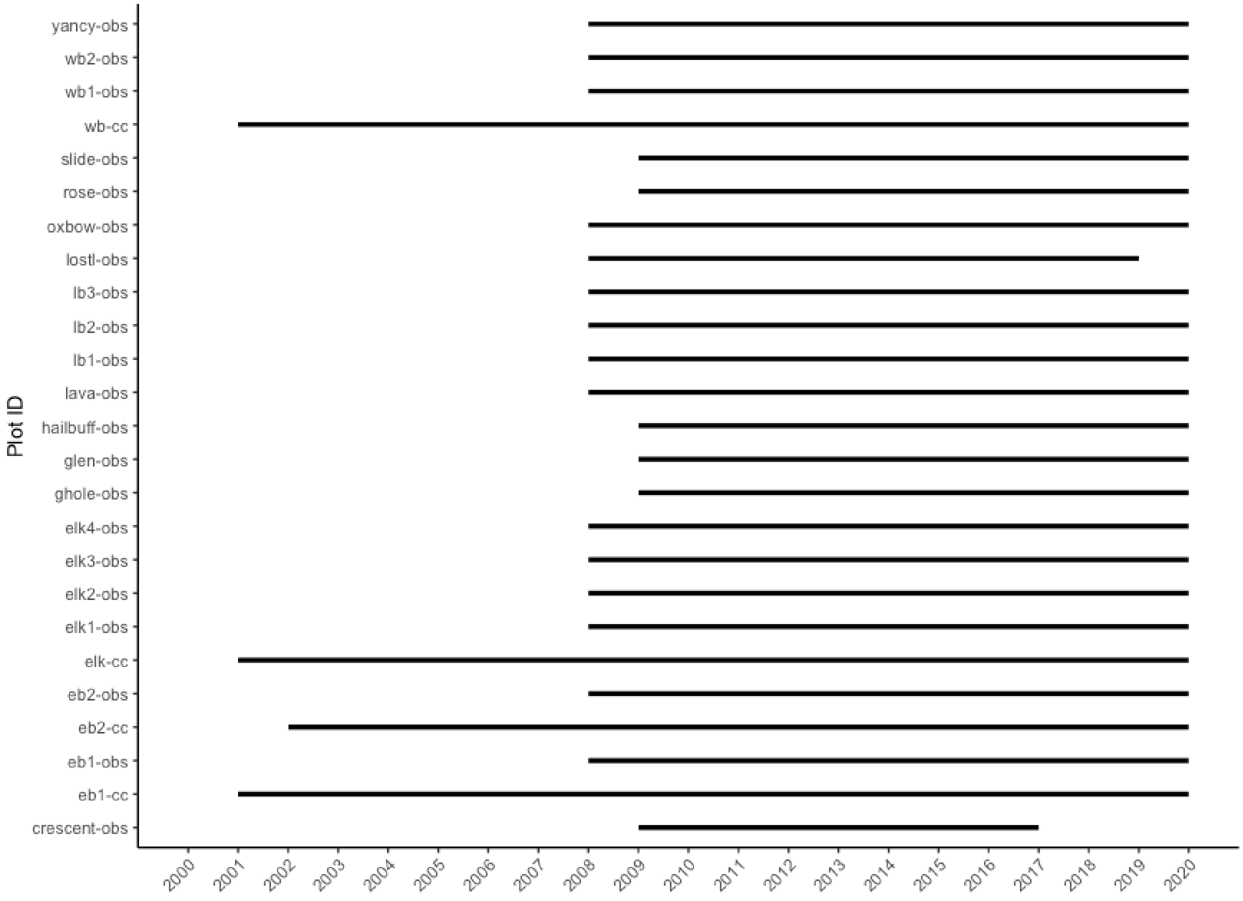

Figure 2. Monitoring history for the 25 plots included in Ripple et al.'s (2025) analysis, based on data originally collected by Hobbs et al. (2024). Each horizontal line indicates the years during which a specific plot was sampled. Plot identifiers on the y-axis follow Hobbs et al.'s naming convention: "obs" indicates an observational plot and "cc" indicates a control plot at one of four experimental sites. The x-axis spans the full duration of the study period (2001–2020). Although Ripple et al. describe their analysis as a 20-year trend across 25 plots, only 22 plots were sampled in 2020, and just 3 of those had corresponding measurements from 2001. The lack of plot-level continuity undermines the validity of log response ratio estimates that assume matched or equivalent sampling units over time.

Figure 3. Historical and contemporary photographs illustrating the long-term absence of willow (*Salix* spp.) recovery in parts of northern Yellowstone National Park. (A) A view of Yancey's Hole in 1890 showing extensive willow cover along the riparian corridor and around historic structures and trails. (B) The same location photographed in 2017, showing a persistent lack of willow regeneration despite more than two decades of large carnivore recovery, including wolf reintroduction. (C) A 2025 downstream view of the East Fork of Blacktail Deer Creek, where multiple riparian areas similarly show minimal to no visible willow crown development. These counterexamples contrast with the selectively framed photographic evidence in Ripple et al. (2025), which emphasized sites with vigorous willow recovery while omitting locations like these, where recovery remains limited or absent. The persistent absence of regeneration highlights the spatial heterogeneity of willow responses and challenges claims of a strong, system-wide trophic cascade across the northern range. Photo credits: (A) Montana Historical Society Research Center, Helena, Montana; (B) Dan Kotter; (C) Dan MacNulty.