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Non-random sampling measures the occurrence but not strength of a textbook trophic cascade

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Title: Non-random sampling measures the occurrence but not strength of a textbook trophic cascade

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Abstract

Although sampling the five tallest young aspen in a stand is useful for detecting the occurrence of any aspen recruitment, this technique overestimates the population response of aspen to wolf reintroduction. Our original conclusion that random sampling described a trophic cascade that was weaker than the one described by non-random sampling is unchanged.

Main Text

Understanding trophic cascades (indirect effects of predators on plants and abiotic processes) requires information about their occurrence and strength. A basic metric of trophic cascade strength in the study of wolves, elk, and aspen in northern Yellowstone National Park has been the annual change in browsing and height of young aspen following wolf reintroduction. Knowledge about these annual changes has been based mainly on three time series that were built from one or two years of sampling the three or five tallest young aspen within a stand and retrospectively inferring past browsing and height using potentially inaccurate plant architecture techniques (reviewed in Brice *et al.* 2022).

Ripple & Beschta (2007) pioneered the 'five tallest' technique (hereafter, 5T sampling), and they described it as a "limitation" because "data are only representative of the first recovering aspen (5 tallest per [stand]) and not an estimate of the aspen population response across Yellowstone's northern winter range" (Ripple & Beschta 2007:518). Kauffman et al. (2013) further elaborated that "choosing the five tallest individuals for an evaluation of stand-level height and growth is…inherently biased." Our study quantified the extent of this bias, revealing, for example, that 5T sampling overestimated regeneration of overstory aspen by a factor of 4-7 compared to random sampling (Brice *et al.* 2022: Figure 5). We concluded that 5T sampling overestimated the aspen population response to wolf reintroduction, confirming previous concerns about its limitations.

In their Comment, Painter et al. (2023) (hereafter Painter et al.) do not challenge our conclusion, acknowledging that our results demonstrate that the height of the typical young aspen has increased "more slowly than the tallest" young aspen. Instead, Painter et al. describe the utility of 5T sampling for detecting the *occurrence* of a wolf-elk-aspen trophic cascade. They emphasize that "[t]he 5T method efficiently detected increases in heights of young aspen in stands that historically had been suppressed by elk browsing." While we agree that 5T sampling allowed Ripple & Beschta (2007) to document "the first significant growth of young aspen in over half century," the occurrence of a height increase says little about the strength of the wolf-elk-aspen trophic cascade, which was the central focus of Brice et al. (2022).

Painter et al. conflate the use of the 5T method for detecting trophic cascade *occurrence* (changes in browsing and height of young aspen) with measuring trophic cascade *strength* (rate of those changes across the aspen population). Painter et al. focus on previous work that used the 5T method to detect change, whereas we focused on previous work that used the 5T method to describe the rate of change (Brice et al. 2022: Table 1). Our results suggest that these published trends overestimate trends in the aspen population at large, affirming Ripple & Beschta's (2007) early acknowledgement that the 5T method does not provide a representative estimate of the aspen population response. Therefore, Painter et al.'s statement that "the results of Brice et al. actually supported the previous work they characterized as 'biased' and 'exaggerated'" is not an accurate description of our results or their implications. We emphasize that our study characterized the 5T method as biased because it exaggerated estimates of population-level changes in browsing and height of young aspen compared to random sampling.

Painter et al. also rely on the traditional assumption that a negative correlation between browsing and height of young aspen is an exclusive indicator of browsing suppressing height of young aspen. We found that height of young aspen is both a cause and an effect of reduced browsing. It is a cause of reduced browsing because elk consume aspen at a 'preferred browsing height' beyond which browsing pressure decreases as height increases (Brice et al. 2022: Figure 4a). Thus, a negative correlation between browsing and young aspen height is not reliable evidence of a wolf-elk-aspen trophic cascade because it does not represent an unambiguous causal link between reduced browsing and increased height of young aspen.

Furthermore, Painter et al.'s argument that leader length (an index of growth rate and site productivity) does not contribute to variation in height of young aspen is contradicted by their data (Painter *et al.* 2015: Appendix A, Table A1) and our own (Figure 1). Together, these data support the hypothesis that site productivity has an ecologically meaningful influence on young aspen height in the northern Yellowstone study area.

In summary, we agree with Painter et al. that 5T sampling can efficiently detect the occurrence of recruitment. However, understanding the full scope and outcome of the wolf-elk-aspen trophic cascade requires more than knowing that it occurs. Knowledge about the strength of the cascade is also vital, and this requires a random sampling design that provides a representative estimate of the aspen population response to wolf-caused reductions in elk browsing pressure.

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Figure 1. Effect of leader length (an index of growth rate and site productivity) on height of randomly sampled, unbrowsed young aspen in northern Yellowstone National Park, 2007-2017 ($\beta = 0.013$, SE = 0.0003, $p < 0.001$). Results are population-averaged fitted values and associated 95% confidence intervals from a generalized linear mixed model (GLMM) of height of unbrowsed young aspen (*N* = 5,581 leader stems, excluding 7 outliers with leader length > 100-cm) as a function of leader length with crossed random intercepts for stand identity (*N* = 113 stands) and year to account for (i) correlation between measurements taken on the same stand in multiple years and on multiple stands in the same year, and (ii) unmeasured stand- and year-related effects. Leader length equals the current annual growth of the leader stem. We treated the leader stem as the unit of analysis and used a GLMM with a gamma distribution and a log link to analyze total height of the leader stem, which took only non-negative values that were strongly right skewed. The sample of young aspen included in this analysis is a subset of the sample analyzed in Brice et al. (2022). The rug on the x-axis illustrates the distribution of the data.