The Big Scientific Debate: Trophic Cascades

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Wolves generate controversy. Usually it's of a cultural kind, like how they should be managed or should we have them at all. Scientific debates tend to take the back seat. Probably the most intense of these is the impact of wolves on their prey because the answer may influence wildlife management. In Yellowstone, a somewhat unique controversy, largely centered within scientific circles, has cropped up and questions how wolves impact ecosystems–if at all (Peterson et al. 2014). This is interesting because wolves and other carnivores (not bears) have been functionally absent for most of the 20th century; and now with their return, a comparison can be made. Sounds straightforward, but it's not. Nature is complex.

The debate has centered on the phenomena called "trophic cascades" or how species interact within a food web (i.e., how nature is organized, if one can characterize the near impossible complexity!). Specifically, a trophic cascade refers to a predator's impact "trickling down one more feeding level to affect the density and/or behavior of the prey's prey" (Silliman and Angelini 2012). The question then, simply put, is: Have wolves impacted plants? Here we are referring to just woody plants–primarily willow and aspen. For most of the 20th century these woody plants have been suppressed, or not growing tall due to elk browsing (which led to National Park Service reductions in elk); then coinciding with wolf recovery, some plants showed signs of "release" from the suppression of browsing (Painter et al. 2015). Most studies agrees with this scenario (with some exceptions), and the debate is about why the sudden growth.

Theoretically the argument is framed as "top-down" vs. "bottom-up." Top-down is predators eating prey, reducing their number (or changing behavior), and causing fewer plants to be eaten. Bottom- up is sunlight causing growth in plants, and plants providing food to a certain number of prey which then determines the number of predators. So which is more important? Because Yellowstone had few predators for decades, and now that they're back, we can compare the system before and after predator recovery. Because this was not a properly run experiment, there are many uncontrolled variables, which has led to disagreement. The first problem to be solved is to determine how this works. Early on the idea of a "landscape of fear" was presented: without wolves, elk were unconstrained to roam the landscape (Brown et al. 1999). With wolves this changed and some places made elk vulnerable to attack, so elk avoided these "risky" places. In short, this change in elk behavior explained why willows exhibited signs of release before elk populations became really low (Beyer et al. 2007). This is a behaviorally mediated trophic cascade. Others disagreed (Marshall et al. 2013). It was just fewer elk or a numeric effect (Kauffman et al. 2010). Which is it? Or is it both?

Yet another argument was site and water availability; fewer elk was not enough (Marshall et al. 2014, Marshall et al. 2014). Alternatively, it was attributed to weather or climate change (Despain 2005). When conditions were right or the climate was favorable, woody plants grew despite elk. Also beavers had been lost about the same time elk increased in the early 20th century, and the loss of beavers changed streams in a way that reduced willow and aspen (Wolf et al. 2007, Bilyeu et al. 2008). Beavers were a linchpin. Determining the cause of changes in willow growth was complicated–too many factors varied simultaneously.

In short, we have competing and very complex arguments. Is there any way to resolve this debate? Some say we need to design the right experiment, despite the vast size and cost of such an undertaking. Importantly, and other than the climate hypothesis, no one is arguing that top-down effects are not important, or that natural predation has no impact on the lower trophic layers. What is being debated is the extent that changes in woody plants are due to the effects of wolves (and other carnivores) on elk and how these top-down influences ripple through the food web. Part of the disagreement comes from crediting wolves as the only agent, ignoring cougar recovery and increases in bear numbers, and of course elk management outside of the park (which also reduced elk and kept them in the park). Another criticism is that too much impact has been attributed to elk, that other factors like water availability need inclusion in any explanation. In dry areas with reduced elk herbivory no willow response was observed.

Another question is the distribution of willows. There has been no increase in the area of willow and aspen, only a height increase in existing stands, which may be dependent on beaver occupation. Maybe the changes to Yellowstone mid-20th century were so significant that a couple decades of fewer elk is not enough to erase the long-term damage on woody plants (Wolf et al. 2007).

Lastly, and most recently discovered, is an important elucidation of how wolves and elk really interact across the varied landscape of Yellowstone. Possibly the most intense debate centers on what wolves do to elk. This is the behavioral vs. numeric argument typically framed as one or the other. But what happens if that's not how wolves and elk really interact? After years of painstakingly collaring wolves and elk, an answer may be emerging. Elk do respond behaviorally to the risk of wolf predation, but not all the time; they avoid risky areas only when wolves are active. This is a fascinating discovery and suggests the increase in woody vegetation is potentially attributable to a combination of fewer elk responding to wolf activity. Elk are not avoiding risky areas but are aware of wolves. These factors together may have allowed some woody plants to show signs of release on appropriate sites (enough water) after decades of suppression. So many factors are involved, including the possible impact of a changing climate. But it would also be difficult to say it's only weather. Surely, we've made progress, but we're not there yet.

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