Does predator presence affect stream hydrology via trophic cascades?

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The shrinking of historical ranges and extirpation of predators such as wolves and cougars throughout North America results in a trophic cascade, whereby changes reverberate down through the food chain from the loss of a top predator. This results in an altered ecosystem. Trophic cascade theory maintains that the extirpation of a top predator enables herbivores to increase grazing behaviors, which then depresses plant community recruitment, biomass and survivability of young plants and trees which are vulnerable to overbrowsing (represented in the schematic in Figure 1). In riparian ecosystems, this can lead to channel degradation through widening, bank failure, and disconnection from the floodplain.

Perhaps the most prominent example of trophic cascades and stream hydrology comes from the gray wolf (*Canis lupis*) population in Yellowstone National Park (YNP). The regional wolf populations were extirpated from the Yellowstone area in the early 1900's due to hunting, trapping, and poisoning. Wolves were reintroduced into Yellowstone in 1995, and the population has stabilized since 2009. Scientists have worked to understand how the restored wolf populations may check elk browsing intensity on willow communities and other woody stream side plants that serve to stabilize bank slopes. The reintroduction of the formerly extirpated top predator has provided a unique opportunity to examine removal and recovery impacts of a top predator on stream hydrology.

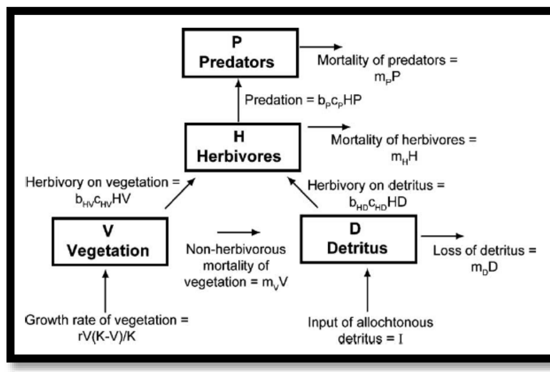

Figure 1: An example of a trophic food chain model. (Doyle, 2006).

There are several ways trophic cascades and stream hydrology may be linked. First, what is the connection between apex predator removal and channel morphology via riparian health? Second, would reintroduction of the predator reverse any channel degradation? Or will abiotic physical controls always outweigh any effects from trophic cascades? While there is broad and compelling evidence asserting that trophic cascades do result in damage to riparian plant communities, the literature is not in agreement on whether trophic cascades are the primary factor in stream channel degradation and whether reintroduction of the top predator is enough to initiate riparian and stream restoration.

Discussion

Trophic Cascades: Top-Down Controls

Certain studies have examined the link between lower riparian plant recruitment and over-browsing of herbivores as the result of a trophic cascade. Several of these studies have proceeded to link this impaired vegetation recruitment to increased bank erosion, increased channel width, floodplain erosion, loss of alluvium vegetation, channel incision, and an increased bankfull discharge return period (a key determinant in channel morphology). Averett et al. (2017) found that wild ungulate browsing impedes riparian restoration efforts in northeast Oregon. The study area was engaging in riparian restoration to add structure to Meadow Creek to regulate the stream temperature, attenuate peak summer flows, reinforce bank stability, influence channel evolution, and increase floodplain connectivity. Researchers protected areas of new plantings with a 1.2 m high fence to prevent browsing and left others unprotected. After two growing seasons, browsed plantings had decreased survivability by 30% and suppressed growth by 73% compared to protected, unbrowsed plantings, as shown in Figure 2. Critically, the survival rate for

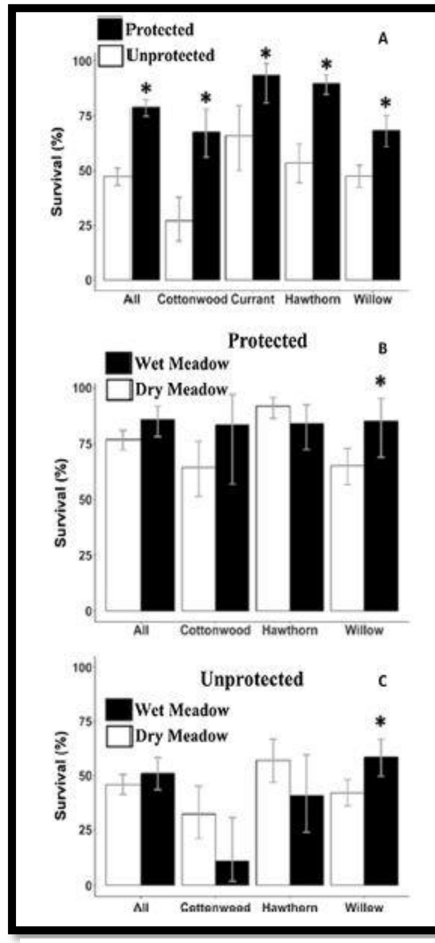

Figure 2: Survivability of protected and unprotected riparian plantings. Researchers also compared planting success in different soil moisture regimes. (Averett et al., 2017).

the browsed plantings was under 50%, which is the region's threshold for successful survival criteria in riparian restoration.

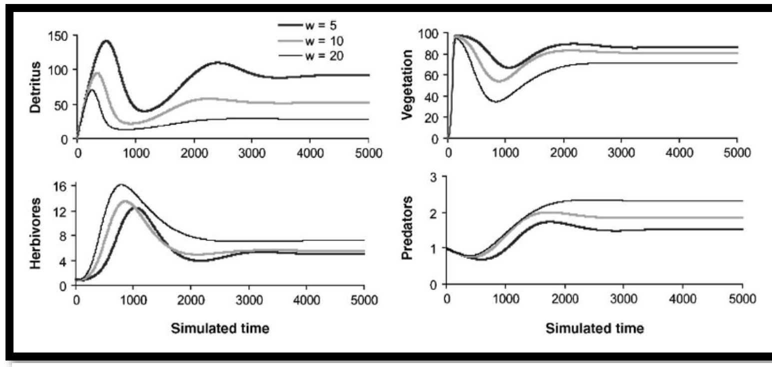

Figure 3: Simulation results of trophic level populations with varying channel width. (Doyle, 2006).

Other studies directly link woody plant success and channel planform to predator health. Callan (2010) found a significant, positive correlation ($y = 0.0934x + 0.798$, $R^2 = 0.379$, $p<0.0001$) between wolfpack presence and density of palatable, woody stems 50-100 cm tall. This correlation did not hold for unpalatable species and taller size classes, which supports the author's conclusion that the wolves have triggered a top-down trophic cascade. Unpalatable woody plants are not linked to wolf presence because deer (the study's herbivore of interest) do not graze these species, and taller plants are outside of herbivore grazing reach. Unlike research that studies trophic cascade influence on stream morphology, Doyle (2006) developed a computational model to examine geomorphic influences on trophic interactions. This research studied the effects of varying stream velocity and geometry on trophic food chain interactions and found that the modeled food chain is sensitive to changes in channel geometry, particularly around threshold conditions. Threshold conditions are based on previous research that shows a decline in hunting efficiency in predators below a certain channel depth, and a decline in grazing efficiency of herbivores above a certain velocity. It should be noted that the author referred to this model as "fast-and-frugal", emphasizing that the heuristic model was not calibrated and validated by empirical data, and therefore should not be used for specific predictions but to show general trends that may guide future research. Figure 3 shows example results of trophic effects from varying channel width.

Figure 5: Photos of reaches studied. Reach A was outside of elk range, while B and C were within elk range. (Beschta and Ripple, 2006).

Beschta and Ripple (2006) took transect data at three reaches in the Gallatin River in YNP—one outside of local elk range (Reach A), and two within the elk range (Reach B and C) (see Figure 4 for photos of the reaches). Reach A had 85% willow cover, and an average bankfull return period of 3.1 years, while B and C had 26% and 5% willow cover and 32.4 year and 10.6 year bankfull return periods, respectively (return periods were calculated using regional intensity-duration-frequency (IDF) curves). Beschta and Ripple (2012) also studied orthophotos of the Hoh, Queets, and Quinault Rivers in Olympic National Park (ONP) and took channel measurements in North Creek and Virgin River in Zion National Park (ZNP) to study possible trophic effects in these habitats. Wolves, extirpated from ONP since the early 20th Century, are unable to check elk grazing. Cougars, common in some parts of ZNP and rare in others, act as a check on mule deer. The researchers attributed altered channel morphology (such as bank erosion and higher width-to-depth ratios) to overgrazing of wild ungulates in all three parks. Figure 5 shows sample results from varying cougar presence on a common riparian tree species, the cottonwood, in ZNP.

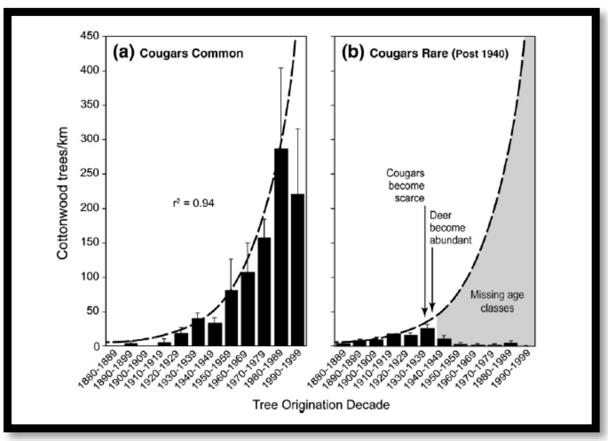

Figure 4: Cottonwood tree density in areas of Zion National Park were cougars are common and can check deer grazing and where cougars are rare. (Ripple and Beschta, 2006).

The preponderance of evidence in the literature directly linking the trophic cascade effect on channel morphology comes from Beschta and Ripple (2006a, 2006b, 2012a, 2012b, Painter et al., 2017). These researchers have examined the role predators' presence and absence play in river morphology. They posit that wolves check elk grazing through direct predation and behaviorally mediated patterns of herbivory, and ultimately trophic cascades are a primary control on stream morphology. However, consistently in their papers, they did not discuss alternative hypotheses thoroughly. For example, in Ripple and Beschta (2006), they briefly discuss alternative hypotheses of climate fluctuations, in-channel human interventions, and preexisting site conditions as factors in ZNP channel forms. They dismiss the first two altnerative hypotheses quickly based on observations and only took measurements to study the third. As another researcher pointed out, “Some of the studies emphasizing a top-down explanation for the reported willow recovery in Yellowstone are based on measurements that did not have the power to detect the influence of abiotic factors on plant productivity,” (Tercek et al., 2010). This methodology was common in their research and perhaps underlies the disgreements in conclusions other researchers make in concluding bottom-hydrological controls overwhelm top-down trophic controls.

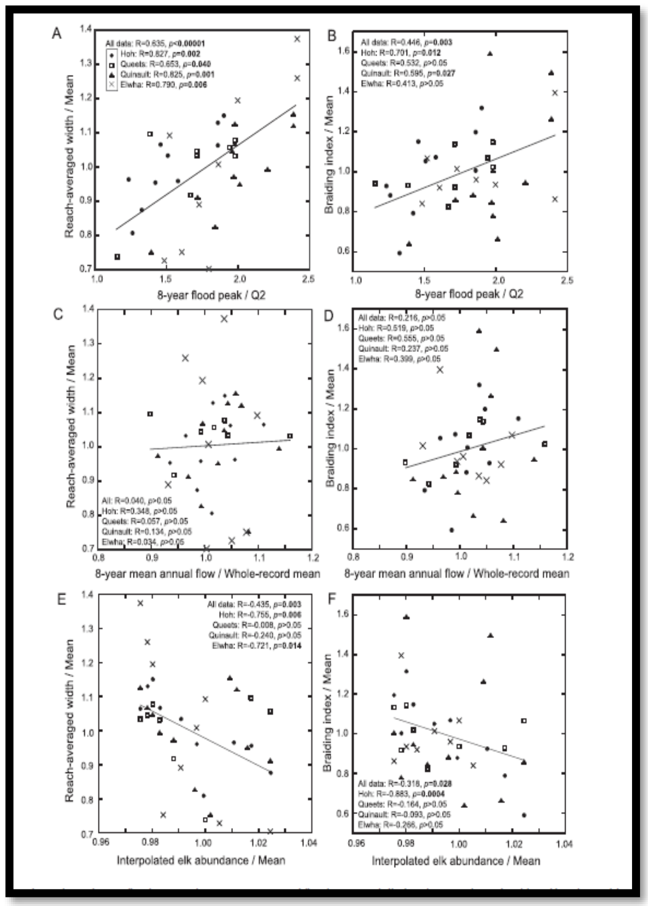

Figure 6: The effect of (A) peak flows, (B) average flows, and (C) elk abundance on channel width and braiding in Olympic National Park. (East et al., 2017).

Physical Controls: Bottom-Up Factors

Other studies have found evidence that changes in stream channel are due to abiotic, bottom-up factors in hydrology, such as increased peak stream flows, snow depth, water tables levels, and increased rates of sediment accretion. These studies conclude that top-down trophic cascades may be correlated with these stream channel changes, but are not causing them. East et al. (2017) studied channel planform evolution on the Hoh, Queets, Quinault, and Elwha Rivers in ONP using a 74-year aerial photographic record to investigate whether trophic-driven cascading factors or physical controls are the dominant drivers of channel planform. The researchers found that annual peak flows were the strongest predictor of channel width and braiding (see Figure 6), and that elk abundance did not correspond temporally to channel morphology. The researchers do not dismiss Ripple and Beschta (2012), pointing out the YNP rivers would likely have different geomorphic evolutions due to annual precipitation differences and wood availability. East et al. (2017) conclude that any influence elk may have on channel morphology is overwhelmed by "physical forcing" and hydrological factors.

Marshall et al. (2013) takes care to point out that while there is much evidence showing the effect of predator removal on the impoverishment of riparian and other plant communities, that far less is understood about the effect of the reintroduction of predators on plant restoration. These researchers study how browsing has affected riparian plant growth in YNP and takes a closer look at how declining beaver numbers may play a larger role than wolf populations in riparian health. Through damming, beavers raise the water table which may help riparian trees like willows grow. These researchers measured how willow growth and biomass varied in (1) browsed and unbrowsed areas and (2) dammed and undammed sites. The researchers concluded that willow productivity was more heavily controlled by water table depth (bottom-up hydrological factors) than by top-down control of herbivory. As Figure 7 shows, dammed sites had higher biomass and growth, and only unbrowsed and dammed sites surpassed the two-meter threshold recovery height (where willows are out of grazing reach). Researchers further assert that the 70-year absence of wolves altered the disturbance regime so much that it cannot be reversed by wolf reintroduction.

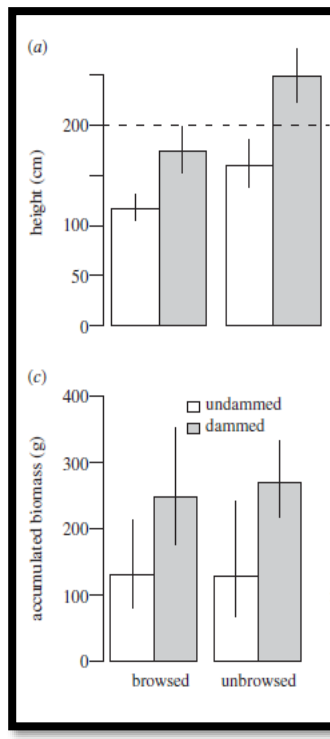

Figure 7: Willow height and biomass in sites that were fenced, unfenced, dammed and undammed. (Marshall et al. 2013).

Tercek et al. (2010) investigated how abiotic soil and water table characteristics effect woody riparian plant communities. This study concludes that recovery of willows throughout YNP has not been uniform. The researchers determined that abiotic limiting factors are the main contol on the variability in willow recovery. The abiotic factors interact with trophic cascade factors, which *are not* primary controls. Researchers found that taller (>250 cm) willow sites had greater soil moisture, higher water table depths (shown in Figure 8), cooler soil temperatures in the growing season and warmer soil temperatures in the winter, deeper snow pack and snow water equivalent and higher nutrient cycling than short (<250 cm) willow sites.

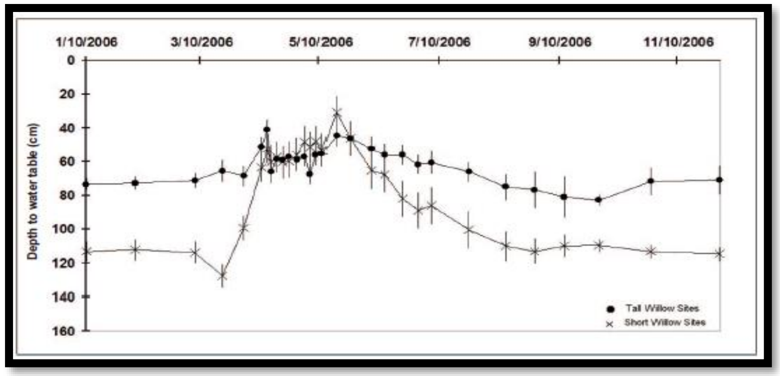

Figure 8: Depth to water table in tall and short willow study sites in Yellowstone National Park. (Tercek et al. 2010).

Conclusion

The literature is largely in agreement that the removal of top predators allows herbivores to increase grazing behavior, which in turn depresses riparian communities. This then can trigger a feedback loop that leads to channel widening, loss of floodplain connectivity, and drier soil moisture regimes which are unable to support the native riparian communities. However, when it comes to concluding the primary control on channel evolution, researchers fall into two camps: (1) that top-down trophic cascades control channel evolution and therefore predator reintroduction can help passively restore streams, or (2) bottom-up abiotic, physical, and hydrological controls interact with trophic cascades, but ultimately are the overwhelming primary control on channel evolution. Regardless of which camp may be correct, researchers asserting trophic cascades are the primary control need to study alternative hypotheses more thoroughly, perhaps by actively taking data, instead of dismissing them through observations which may not take into all abiotic, contributing factors. It would also be beneficial to understand trophic effects on stream health in other areas of North America (or even internationally) as nearly all of the research is set in the western United States. Furthermore, some studies emphasize spatial differences in channel evolution and while others emphasize temporal differences, making it difficult to compare conclusions. More research is needed to understand the interactions of a predator mediated food chain and stream morphology.

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