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Calibrating Carnivore Chronicles: Trophic Cascades and Mesopredator Release

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For most of my research career, I have worked with people primarily working on carnivores. Adding to that, my PhD on the Himalayan wolf severely exposed me to a worldview of the carnivores. Which is that by holding the top of the trophic pyramid, carnivores are the main drivers of ecosystems, shaping the structure of life beneath them through what we call the top-down effect or the *trophic cascade* (Ripple *et al*. 2016). As carnivore ecologists, we develop a notion that the outsized effect of the carnivores on the ecosystems they live in raises their status compared to other species, giving them some sort of ecological supremacy. In fact, I've often opened my talks on wolves by invoking these very theories, sometimes as scientific grounding, sometimes as reverence. But lately, I've felt compelled to step back to have an ecologically wide view and examine this fascination for carnivores as ecosystem engineers.

If you haven't come across once viral short film *How Wolves Change Rivers* (2014) yet, I urge you to stop reading this article and go on YouTube to watch it. This four and half minutes long video perfectly captures the essence of the trophic cascade – how wolves, reintroduced into Yellowstone National Park after decades of absence, reshaped the entire ecosystem as top predators. The story goes that wolves regulated elk numbers, which in turn allowed vegetation to recover, stabilising riverbanks and even altering water courses (Ripple & Beschta 2012).

The idea originated with Hairston *et al*. (1960) arguing that the abundance of herbivores is generally limited by their predators and not by the food (plants). The term '*trophic cascade*' was later coined by Robert T. Paine, who further conducted experimental work by studying the effect of a top predator removal, sea star *Pisaster ochraceus,* on the marine community of the intertidal zone (Paine, 1980). Incidentally, Paine also coined the term 'keystone species'. The cascading interactions do not play out only by changing population numbers but also through fear. Apex predators can alter the behaviour of their prey; the presence of a predator's scent or sight alone can shift foraging patterns and space use (Palacios *et al*., 2016). The core of the trophic cascade theory is that predators can exert a controlling influence over entire ecosystems, not just by what they eat, but by how they make other species behave.

Ripple *et al*. (2016) noted about a decade ago that "the term [trophic cascade] has been a central or major theme of more than 2000 scientific articles", suggesting strong evidence for trophic cascades. For example, Terborgh *et al*. (2001) described how predator loss in island forest systems leads to over-browsing and collapse of vegetation regeneration, while Myers *et al*. (2007) found that the decline of sharks on the U.S. Atlantic coast allowed cownose rays to boom, devastating scallop populations. The pattern that removal of the top predator changes the structure of the ecosystem, sometimes to the point of breaking, repeats across continents and biomes.

But what happens when the apex predator disappears in a multi-predator system? The predators that functioned under the top carnivore so far try to fill the void. Enter the *mesopredator release hypothesis*, another quite influential and debated idea in modern ecology.

We need to first clarify another question before we dive into the mesopredator release hypothesis - what a mesopredator actually is? Researchers have used a couple of different ways to define a meso-predator. Relative body size is one of the approaches, e.g., 1 to 15 kg in the case of terrestrial carnivores (Gehrt & Clark 2003). Inability to hunt down the large prey can also be used as a predatory-efficiency based criterion. However, the ecological definition is a mid-ranking predator in a given food web. A species can be an apex predator in one ecosystem and a mesopredator in another. Wolves are a good example of functioning as top predators as well as second-order predators in areas with bears and tigers.

The term 'mesopredator release' first appeared in Soulé *et al.* (1988), later popularised by Crooks & Soulé (1999), who described how the decline of coyotes in fragmented Californian landscapes allowed smaller predators, particularly domestic cats, to proliferate, devastating local bird populations. The concept caught on quickly. It offered a simple, compelling narrative – remove the apex predator, and the mesopredators' numbers will rise, leading to a collapse of smaller prey and a loss of biodiversity. The framework has since been applied across ecosystems, from sharks and rays in the oceans (Myers *et al.*, 2007) to dingoes, foxes, and feral cats in Australia (Johnson *et al.*, 2006), and wolves and coyotes in Yellowstone (Berger *et al.*, 2008). In each case, the arc of the story is that the top falls, the middle rises, and the bottom breaks.

Across the world, management practices and conservation planning have drawn heavily on these two theories. Reintroduction programs, from wolves in Yellowstone and lynx in Europe to tigers and cheetahs in India, often cite trophic cascades as justification. The mesopredator release concept has shaped predator control policies, arguing that maintaining apex predators helps keep smaller carnivores in check and protects biodiversity. For example, protecting dingoes in Australia was proposed as a natural control mechanism for invasive cats and foxes (Johnson *et al.*, 2006). In practice, though, the results are far from expected. Field results often show that apex predator recovery doesn't always suppress mesopredators as neatly as theory predicts.

Let's take the case of wolves and coyotes in Wisconsin. Despite wolf recovery, coyote numbers did not decline significantly, suggesting that top-down control is not universal and may depend on landscape features and prey abundance (Crimmins & Deelen, 2019). In Norway, mesopredator increases were linked not to predator absence but to bottom-up effects, getting benefitted by carrion from high densities of reindeer (Henden *et al.*, 2014). In some systems, mesopredators may even stabilise ecosystems by partially taking on the roles of missing apex predators (Suraci *et al.*, 2017). Jachowski *et al.* (2020), investigating mesopredator release in terrestrial North American mammalian predators, found no support or mixed support in 46% cases. The more we study, the more we realise that these patterns are not always generalizable but context dependent.

The reason is that it is fundamentally difficult to prove that mesopredator populations increase only because of the loss of apex predators, and not because of other factors, like habitat changes, that often happen at the same time. The fragmented landscapes provide an ideal setting for explosive mesopredator population growth because both the top-down control by predators and bottom-up constraints (like resource scarcity) are relaxed. "Uncertainty surrounding the causal mechanisms that underlie mesopredator outbreaks muddies prescriptions for management" (Prugh *et al.* 2009).

The global rise of free-ranging domestic dogs is another interesting story about the effect of carnivores on ecosystems. Currently, the most abundant carnivore on earth, dogs have become dominant competitors in the mesocarnivore guild in India and many parts of the developing world, thriving on human subsidies and outcompeting native species like foxes and jungle cats (Vanak & Gompper, 2009; Carricondo-Sanchez *et al.*, 2019). Native carnivores often shift their diets, activity patterns and habitats to avoid dogs (e.g. Reshamwala *et al.* 2018). In this case, dogs act as 'mesocarnivore suppressors', causing declines in smaller species through direct competition and indirectly via transmitting diseases like rabies and distemper. Here, human influence blurs the trophic hierarchy of the carnivore guild around the wilderness areas.

Mesopredators may increase in response to the disappearance of the top predator but are less likely to reduce once the top predator is back, which questions the strength of the top-down effect itself. Our favourite ecological success story and example of a trophic cascade, the Yellowstone wolves, has also sparked debate in recent years. Studies suggest that vegetation recovery in Yellowstone's valleys owes as much to climate variation, the historical loss of beavers affecting stream conditions and human management as to wolves themselves (Smith *et al.* 2016). While wolves contributed to shaping ecosystems, they are just one factor among many. Some studies have further questioned the sampling and cascade strength calculation as well (Brice *et al*. 2021).

It reminds us that ecological systems are rarely governed by a single driver. Bottom-up forces, like nutrient availability and productivity, often shape ecosystems just like top-down predation. Add to that the pervasive influence of humans, such as land modification, hunting, overextraction of resources, global warming, pollution, etc. In today's Anthropocene (Crutzen & Stoermer, 2000), ecosystem dynamics are controlled by three major processes – top-down control, bottom-up constraints, and human interference. Human activity doesn't just disrupt; it often creates new forms of ecological order. Resource subsidies, altered fire regimes, and conservation interventions like plantations and species recovery can all produce their own kinds of cascades.

However, this is not to suggest that the theories matter any less. Theories give us the scaffolding to think about complexity, to see hidden connections, to predict, and to ask questions. They remind us that ecology is not chaos but a pattern, even if that pattern is sometimes fuzzy or incomprehensible.

Scientific communication classes will tell you that storytelling is a key skill. I don't doubt them. Good stories turn heads, make headlines and let films like *How Wolves Change Rivers* go viral. But stories demand simplicity while science is often complex. Newer facts are discovered, and older understanding is updated. In due course, the scientific process disregards storytelling over fact-telling. The Yellowstone story was powerful, until it wasn't. Nonetheless, carnivores continue to fascinate us, and as Prugh *et al*. (2009) put it that perhaps the most important motivator is simply that they compete with us for food and space.

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