

The impact of the loss of top predators on terrestrial ecosystems

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Abstract

This report summarises some of the key research regarding the impacts of trophic cascades initiated by the loss of top, or apex, predators from ecosystems. Two primary case studies are first explored; the loss of top predators from islands on Lake Guri in Venezuela, followed by the loss and subsequent reintroduction of wolves in Yellowstone National Park in the United States. Following these two key examples, other possible implications are explored, including the impact on the carbon cycle and wildfires, though these require further academic inquiry. Overall, it is shown that the loss of top predators has a number of detrimental impacts on ecosystems including the reduction of biodiversity, decreased nutrient cycling and hence lesser soil fertility, and potentially the collapse of ecosystems entirely due to the lack of top-down control. This demonstrates a serious need for humans to reduce and potentially counteract the loss of top predators.

1. Introduction

We are currently in the midst of an age characterised by unprecedented rates of change to the environment driven by human activity (Gaffney and Steffen, 2017). In recent centuries, humans have become a force of nature (Steffen *et al.*, 2007), leading to the proposal of the 'Anthropocene' as a new geological epoch (Crutzen, 2002). In particular, humans have had a damaging impact on ecosystems, having already altered an estimated 75% of terrestrial environments (UN, 2019). This has caused a biodiversity crisis, with a 60% decline in vertebrate species population sizes from 1970-2014 (WWF, 2018) and approximately 27% of all species being threatened with extinction (IUCN, 2020). By some estimates, current extinction rates are already up to 1,000 times greater than the natural background rate (De Vos *et al.*, 2015), leading to speculation that we are in the midst of a sixth mass extinction (Kolbert, 2014). The issue of trophic cascades, which are species interactions originating at the top of the food chain (generally with predators) and spreading downwards often all the way to primary producers or further (Ripple *et al.*, 2016), is therefore of increasing concern. Trophic cascades are noteworthy, as they mean that relatively small changes to the populations of certain species have significant impacts on many other species. This report will focus on the loss of top predators from terrestrial (including freshwater) environments, as these species are the most threatened (WWF, 2018), and the consequences of the trophic cascades these losses can trigger. Top predators are species occupying the highest trophic levels within ecosystems (Pace, 2013; Wallach *et al.*, 2015) and therefore have the potential to initiate the greatest changes when their populations are altered. Two main case studies will be examined, those of Lake Guri and Yellowstone National Park, followed by other recent studies that investigate trophic cascades initiated by the loss of top predators to try and assess the impacts of these interactions.

2. Case Study 1: Lake Guri

The main difficulties surrounding the study of trophic cascades are first proving that they exist, and secondly in defining their impacts. With top predators, it is clear why this is difficult; in order to investigate the consequences, a top predator must be lost, and the ecosystem monitored for years to try and ascertain the impacts, making it a practically difficult phenomenon to study. The conditions of a fully functioning and complete ecosystem, are next to impossible to re-create, and even if it can be done, the impacts of such changes may not manifest for years (Estes *et al.*, 2011). Yet these difficulties were navigated in the Lake Guri experiment (Terborgh *et al.*, 2001). Lake Guri is a flooded valley in Venezuela, formed as the result of a hydroelectric project in the 1980s (showing the role of humans in altering terrestrial ecosystems), leading to the creation of various sized islands (Moore, 2006). Terborgh and his colleagues studied several of these islands, together with control areas on the mainland, and made a number of important findings. On the small islands (defined as less than two hectares in area) that they studied, the majority of invertebrates were lost within a few years (Moore, 2006), including predators such as pumas, jaguars and harpy eagles. This led to a rapid increase in the densities of herbivore species such as rodents, howler monkeys and leaf-cutter ants up to in the order of ten to one hundred times that of the mainland (Terborgh *et al.*, 2001), having a significant impact on the vegetation of the islands. Although all of the islands had started out with similar sapling densities, by 1997 the small islands had a sapling density that was just 37% that of the larger islands (areas greater than seventy-five hectares) which retained more vertebrate grazers and predators; by 2002 this had fallen to 25% (Moore, 2006; Terborgh *et al.*, 2001). The loss of top predators on the small islands led to increased herbivore populations, which in turn led to significant losses to native plant populations, and hence an overall loss of biodiversity (alongside that which represents the initial loss of the predator).

Diamond (2001) argues that the study by Terborgh *et al.* (2001) was too focussed on proving the existence of terrestrial trophic cascades, meaning it overlooked other more nuanced impacts of the loss of top predators. Diamond argued that the Lake Guri experiment resulted in the loss of palatable plant species and rising dominance of unpalatable species due to selective consumption by growing herbivore populations (Diamond, 2001). This again demonstrates how the loss of top predators had an adverse effect on biodiversity. It also shows potential longer term impacts, whereby bottom-up control begins to kick in. If palatable plant species disappear due to increased consumption, food scarcity will begin to act as a control on herbivore populations, creating a new ecosystem dynamic. Diamond also goes into greater depth regarding behavioural changes in some species as a result of the trophic cascade that occurred. Leaf-cutter ants are generally night-time foragers, but due to the loss of their top predators, armadillos, army ants and phorid flies, they increasingly began to forage during the day due to a lack of fear of predation (Diamond, 2001). This represents a major behavioural shift in the ecosystem, and this lack of fear regarding predation led to increased foraging, contributing to the loss of plant biodiversity. Behavioural changes mark a potential indirect, or at least non-consumptive, impact of the loss of top predators, which Ripple *et al.* (2016) consider at least as significant as direct impacts, but this is a contested notion.

3. Case Study 2: Yellowstone National Park

One ecosystem that demonstrates both direct and indirect impacts of the loss of top predators is Yellowstone. Wolves were extirpated from Yellowstone in the mid-1920s (Ripple *et al.*, 2015) but this had a number of perceived negative impacts on the ecosystem. These concerns combined with growing public sentiment regarding the loss of the wolves led to their reintroduction in 1995-96 (Marris, 2014). This reintroduction had a number of impacts that highlighted the magnitude of the effects of their initial loss. The most salient was on elk populations, which grew steadily following the extirpation of wolves, and which were reduced dramatically when they were re-introduced, falling from about 19,000 in 1994 to only about 6,300 by 2008 (Ripple *et al.*, 2015). It has been suggested that there were other factors involved in this drop in elk populations, such as other carnivores, including grizzly bears (Marris, 2014), hunting and drought (Ripple *et al.*, 2015). However, the fact that there was a steady increase following the loss of wolves, and then a marked decrease following the re-introduction of wolves provides compelling evidence that wolves act as the major control on elk populations. The loss of wolves and subsequent rise in elk populations in Yellowstone had a profound effect on vegetation, particularly aspen trees (*Populus tremula*), with aspen coverage of the winter range of the northern Yellowstone elk herd dropping from 4-6% to about 1% by 2000 (Ripple *et al.*, 2001). Since the re-introduction of wolves, aspen populations have recovered slightly, likely both as a direct impact of decreased elk populations and as a result of behavioural changes in elk. Ripple *et al.* (2001) developed the behavioural-cascade hypothesis following examination of aspen growth patterns. They found that aspen growth was greatest in narrow stream-side locations where the wolves hunted regularly, suggesting the elk had become less likely to browse in such environs due to risk of predation (Ripple *et al.*, 2001). This demonstrates how through both a combination of direct predation and the risk of predation leading to behavioural changes, a trophic cascade occurred whereby the loss of a top predator, wolves, lead to increased elk populations and decreasing aspen populations. The reintroduction of wolves had the inverse effect. Greater aspen densities are thought to have a positive impact on the environment, particularly where they grow along river banks as riparian trees help to stabilise banks, and thus prevent erosion, and provide shade for aquatic life (Beschta and Ripple, 2006), showing how the loss of top predators has extensive negative consequences on ecosystems.

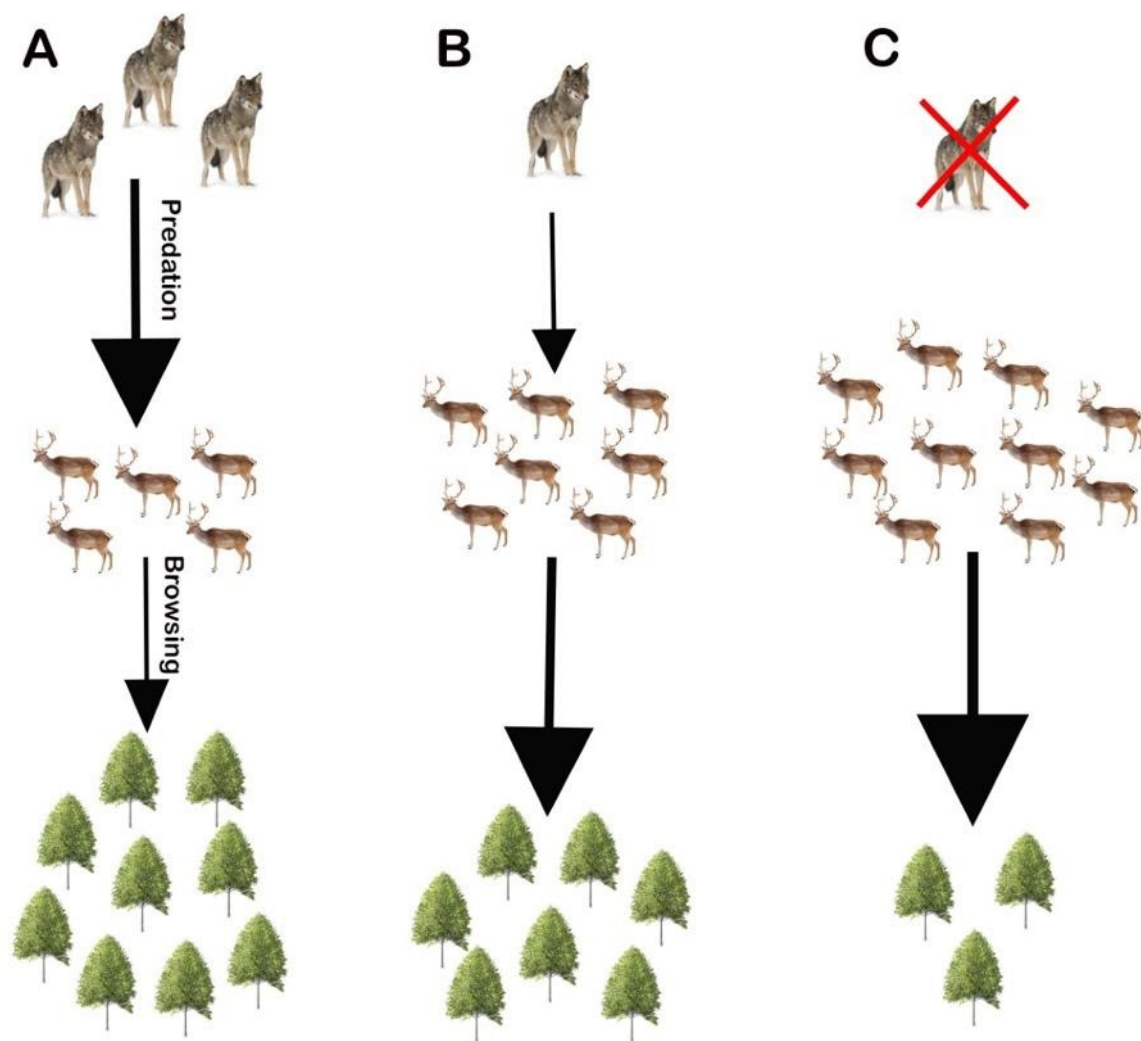


Figure 1. A diagram illustrating the behavioural cascade hypothesis. Scenario 1.A shows a 'natural' ecosystem, such as Yellowstone prior to extirpation of wolves. In 1.A, predators (in this case wolves) control herbivore (in this case elk) populations due to direct predation and this plus the risk of predation limits herbivore browsing of vegetation such as aspen. 1.B shows how a decrease in predator population means a greater herbivore population, but still limited browsing due to the risk of predation and hence allows vegetation populations to remain fairly strong. Scenario 1.C shows how extirpation of predators removes the risk of predation, meaning greater herbivore populations that do not fear predation, and hence greater browsing and grazing of vegetation leading to a decrease in the population of species such as aspen. (Source: author original)

Reintroduction cannot solve all problems. Another consequence of the loss of wolves from Yellowstone and resulting increase in elk populations was a decrease in willow densities, which subsequently led to a decline in beaver numbers, who rely on willow. Marshall *et al.* (2014), demonstrate that beaver numbers are not recovering in spite of the reintroduction of wolves, showing how trophic cascades can have long-lasting negative impacts. There is also evidence that counters Ripple *et al.*'s behavioural cascade hypothesis.

Kauffman *et al.* (2010) also studied aspen populations in Yellowstone, but argued that the decline in aspen recruitment following the loss of wolves was due to gradually increasing elk populations, not due to a change in their behaviour (Kauffman *et al.*, 2010). While this does undermine the idea of behaviourally mediated trophic cascades, it still shows the consequences of the loss of a predator on populations of herbivores and subsequent impacts on vegetation, and does not really address the issue of behavioural changes due to the reintroduction of predators.

4. Wider Implications of the loss of top predators

The loss of top predators also has the potential to alter carbon storage, which can have global ramifications. Wilmers and Schmitz (2016) investigated the role of wolves in ecosystem carbon cycling, finding that the loss of wolves can lead to a decrease in net ecosystem productivity (NEP) of 24.0-52.0g C/m²/year in boreal forests and a 30.03-102.88g C/m²/year increase in NEP in grasslands. The loss of wolves in grasslands leads to more grazing by herbivores, stimulating root growth and thus increased productivity. In contrast, in boreal forests, fewer wolves leads to greater browsing of deciduous trees by moose and thus an increase in the proportion of conifers and a decreased litter nitrogen return to the soil, hence lower productivity (Wilmers and Schmitz, 2016). In a similar vein, Schindler *et al.* (1997) found that the loss of apex predatory fish lead to higher populations of planktivorous minnows, thus decreased zooplankton populations and therefore increasing phytoplankton density, allowing lakes to transition from net sources of atmospheric carbon dioxide to net sinks (Estes *et al.*, 2011). These examples demonstrate how the loss of top predators can cause changes to ecosystem carbon fluxes and storage, with the potential to lead to global changes in atmospheric carbon concentrations, though the exact scale of this is as yet unknown. The comparison between grassland and boreal forests also shows how the effects of the loss of top predators can vary widely between different locations, hence it is dangerous to extrapolate the results of studies of these impacts and apply them to different scenarios.

Finally, there are other proposed indirect effects of the loss of apex predators. Holdo *et al.* (2009) found that increased populations of ungulates in the Serengeti, which could occur due to the loss of top predators, leads to a decrease in total plant biomass, meaning less common or extreme wildfires (Estes *et al.*, 2011). This suggests a positive effect of trophic cascades, but some large herbivores, such as elephants and rhinoceros, are effectively too large to be readily preyed upon by top predators (Sinclair *et al.*, 2003), reducing the control exerted by top predators, and making the link between loss of predators and wildfires tenuous.

5. Conclusions

Until the late twentieth century the extent to which top-down processes operated in ecosystems, especially terrestrial ones, was not fully understood, in part due to difficulties in studying them. However, the work of Terborgh *et al.* (2001) provides compelling evidence that top-down models operate, and that the loss of top predators has profound impacts on ecosystems. Several studies have now documented that loss of top terrestrial predators

causes herbivore populations to increase, leading to increased selective consumption of palatable vegetation, losses in biodiversity, new behavioural patterns, changes in soil fertility and changes to primary production. Top predator loss restructures the populations of lower trophic levels, with the potential to alter carbon storage and have further impacts relating to wildfires. Overall, there is vast variation in these impacts depending on the ecosystem and the species present, so it is difficult to generalise, particularly due to an incomplete understanding of all components and processes of ecosystems. This demonstrates the need for continued further research into ecosystem dynamics and the changes initiated by loss of species. In general, however, the loss of top predators has a detrimental impact on ecosystems, and the ecological benefits of top predators are now better understood and appreciated. As humans continue forward through the Anthropocene, there is a need to try and limit our impact on the natural world, and perhaps greater protection of top predators offers one starting point in doing so.

6. References

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Acknowledgements

This essay is based off of one that I completed for my Director of Studies, Dr. Harriet Allen, who provided me with useful feedback on the original. The University of Cambridge Department of Geography has been responsible for my teaching this past year, and without the skills and knowledge that this has taught me, this essay would not have been possible.