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Trophic cascades: Top-down control determines ecosystem functioning?

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Abstract

The “Green World hypothesis” was proposed by Hairston et al in 1960. From that point on, a rigorous debate started on the importance of trophic cascades on ecosystem functioning. Aspects of this debate are where trophic cascades occur, what determines the strength of the cascade and which factors control the outcome. This literature study tries to give an overview of the evolution of literature about trophic cascades. Factors promoting trophic cascades are more often found in aquatic than terrestrial foodwebs. It will show that although most (and the strongest) trophic cascades are found in aquatic ecosystem, terrestrial cascades do occur.

Introduction

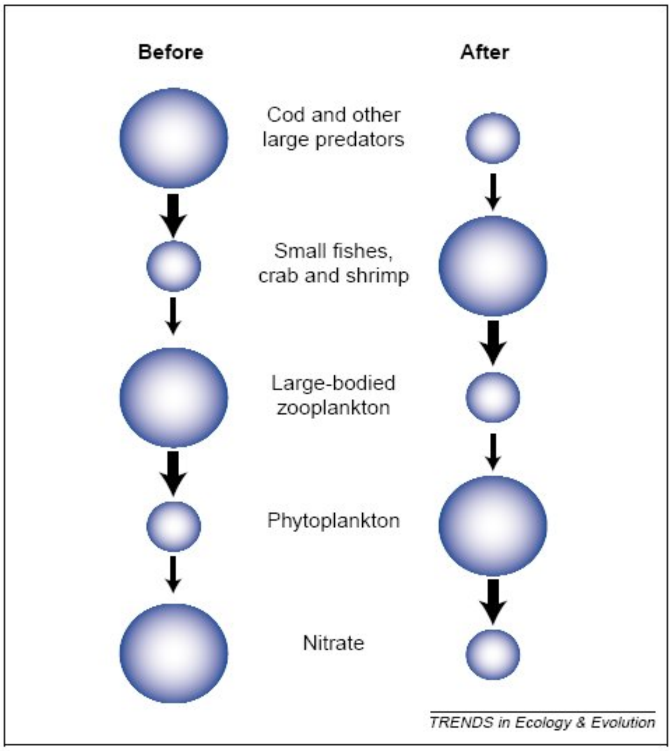

Figure 1: Conceptual model of a four level trophic cascade in a marine ecosystem before and after reduction of top-predators (Scheffer et al (2005))

With the process of photosynthesis, primary producers provide the energy that fuel food-webs. This energy is transferred when primary producers are grazed by herbivores or degraded by decomposers. If herbivores are only limited by their supply of primary producers, most parts of the world would be barren. Herbivores could potentially increase to numbers where the community of primary producers is not able to recover (runaway consumption) (Strong 1992), thus, since large parts of the world are green there are other factors than food availability that control herbivore populations (Polis 1999). One often proposed mechanism is predation (Hairston et al 1960). Haiston et al (1960) hypothesizes that since predators consume herbivores, they have direct control over herbivore population abundance. Thus, if a herbivore population grows in response to more primary producers, predator numbers increase as well, and may thereby reduce herbivore abundances to levels where they no longer can keep up with the increasing primary producers. The abundance of primary producers are then no longer controlled by the herbivore populations.
This implies, that top-predators essentially have indirect control over the population of primary producers, mediated through the herbivore community. This is known as a trophic cascade. Figure 1 demonstrates such a trophic cascade, where reduction of predators leads to an increase of herbivores, ultimately depleting primary producers. This has been demonstrated in numerous ecosystems (Pace et al 1999).
Predator removal is a tremendous problem in our ever expanding world, either by direct removal (due to hunting) or habitat destruction. Thus, changes in the intensity of trophic cascades could be an increasing problem that decreases ecosystem functioning, either by affecting the yield of primary producers or increasing the production of nuisance producers such as algal blooms (Eriksson et al 2009). However, there has been an ongoing debate in the literature on the importance of predator control for food-web structure and ecosystem functioning, where many authors have argued that trophic cascades are rare and generally more important in aquatic ecosystem. To understand how trophic cascades work could give us insight in ecosystem response to changing conditions, such as severe depletion of predator abundances, or even the response to reintroduced and invasive species.
My aim of this literature research is to explore what is known about trophic cascades, how common they are and how they affect our world. In this report I will examine 4

papers regarding this subject. In 1960, Hairston, Smith and Slobodkin started of the debate with a paper that hypothesizes about this matter. This hypothesis would later be known as the “Green world hypothesis”. From then on, numerous case- and literature studies have been performed. Strong (1992) theorized that trophic cascades are limited to aquatic systems. To test these hypothesis I’ve selected two papers combining over 100 field experiments in different types of ecosystems. The first of these two examines the conditions under which trophic cascades are present, and which conditions lead to what type of cascade. The second of these two looks at what determines the strength of cascades.

It will become clear that cascades are not present in all systems and differs in strength between systems. There are numerous factors controlling the strength and direction of trophic cascades, and it is therefore necessary to examine what these factors are.

Analysis

Community structure, population control, and competition.

N.G Hairston; F.E. Smith; L.B. Slobodkin (1960), *The American Naturalist*, Vol. 94, No. 879 pp 421-425

This article proposes a general model regarding population control and food-web dynamics, derived from a few observations. There are three mechanism for redistributing plant biomass; storage in the earth in the form of hydrocarbons, decomposition by microorganisms and herbivory. Almost no energy fixed is eventually stored as organic hydrocarbons. It can thus be concluded that a most of the organic carbon produced by primary producers is transported throughout the food web. This implies that the total group of organisms in the biosphere are limited by the amount of energy fixed (this means that the threshold-abundance of all organisms is determined by producers). This especially is the case for decomposing bacteria and fungi since the only trophic interaction decomposers have is with primary producers. However there are a lot more organism in the world than just primary producers and decomposers. So other trophic groups must consume the other parts of stored energy.

In most cases, there are no signs of plants being limited by either herbivore or catastrophe such as fire and weather. Hairston et al (1960) makes the assumption that primary producers are limited by abiotic factors. This can either be by light limitation or the amount of nutrients available.

When herbivores are unconstrained in their population growth, depletion of producers is imminent, but these are very rare cases. In natural communities herbivores are therefore not limited by the availability of food. Weather is sometimes proposed as a possible limitation for herbivore populations, but in the cases where extensive depletion of land plants occurred, this was mostly due to introduced species. It is therefore unlikely that weather is the limiting factor. Native species should have been able to adapt to the exposures brought on by weather conditions, or at least they should be able to survive better than introduced species.

Therefore Hairston et al (1960) concluded that herbivores are limited by predation. There are numerous examples of predator removal leading to depletion of primary producers.

From this the assumption Hairston et al (1960) derived that the predators and parasites are therefore food-limited. Although the article proposes that in some cases predators are also limited by territory, this can not hold true in all cases, because this would lead to rapid expansion of herbivore populations.
Why is this important? Hairston et al (1960) proposes (although not stated as such in this article) that predators control herbivore populations and therefore ultimately control the populations of producers. If predators would not limit herbivore populations, producer populations are bound to be depleted. There are a few examples of total depletion of producers, either due to predator removal, or the absence of a predator controlling an invasive herbivore.

Are all trophic cascades wet? Differentiation and donor-control in species rich ecosytems

D.R Strong (1992), Ecology, Vol. 73 No. 3 pp. 747-754

For a trophic cascade to occur, the potential for runaway consumption must be present. If herbivores are not limited, primary producers are grazed to the point where the population would be unable to recover. This implies the necessity of key-stone species with large top-down control (Paine 1980). But the potential for runaway consumption does not always lead to a trophic cascade.
Most trophic cascades occur in low-diversity ecosystems. Not only because few herbivore species are involved, but more important is the fact that for a cascade herbivores have to be non-selective (Hunter and Price 1992). If a herbivore is selective in the producers grazed (if for example only one species is removed) other species will take the place of the removed plant. It was demonstrated with an experiment by Lubchenco and Gaines (1981) that increased grazing by herbivores leads to a reduction of the abundance of ‘edible’ producers. But this means removal of competition for the other producers which thereby rapidly increasing in density. Thus, for a trophic cascade to occur, the entire producer community must consist of ‘edible’ species.
Producers in the aquatic systems tend to be more vulnerable to herbivory. In many pelagic systems there are less mechanisms that protect algae from herbivores compared to land plants. Furthermore, individuals are often completely removed. In terrestrial systems this is different. Although seedling are sometimes completely eaten, this is not necessarily the case in older individuals. Only a part of a plant is eaten, and the plant is able to recover.
Many trophic cascades are found in aquatic systems, but Strong only provides two examples of terrestrial cascade-like situations. The lesser snow geese is one of the few species that exhibit the strength of run-away consumption present in ecosystems with trophic cascades. Due to rapidly increasing density of these birds, plant communities are

completely destroyed to the point where they are unable to recover is short time (Kerbes et al 1990).
Another example is the giant tortoise on the island Aldabra. The tortoise is a extremely effective grazer. Evidence of this came from experiments where the tortoise was excluded from sections by fences (Gibson et al 1983). In these exclusions, species that were normally controlled by herbivory sprouted rapidly. Due to the fact that the island is extremely isolated from the main land, predators were not able to establish themselves on Aldabra. The tortoise would not probably be able to sustain in a main land system due to the presence of predators such as large cats (direct removal) or snakes (predation on tortoise eggs).

Strong (1992) proposes the idea that all trophic cascades are wet due to the fact that multiple conditions for trophic cascades to occur are found more often in aquatic systems. It is unlikely that predators have a significant effect on terrestrial primary producers mainly because effects of increasing herbivory on land has less effect than increasing herbivory in aquatic systems. However with the two examples of strong run-away consumption on land Strong doesn't entirely rules out trophic cascades on land.

Trophic cascades revealed in diverse ecosystems.

M.L .Pace et al (1999), *Trends in Ecology & Evolution*, Vol. 14, No. 12, pp 483-488

In recent years, trophic cascades have been studied in a wide variety of ecosystems. These have increased the knowledge of which conditions have effect on the trophic cascades. Pace et al (1999) comprised a list of these case studies and found that although trophic cascades have been demonstrated in terrestrial ecosystems, the most (and strongest) trophic cascades are found in aquatic systems. This is in concurrence to the assumption that most trophic cascades are found in simple aquatic ecosystems (Strong 1992). More diverse systems are less likely to have a trophic cascades due to the fact that diversity leads to more complex interactions (Polis and Strong 1996).

In contrast to Strong's (1992) assumptions that 'all trophic cascades are wet' (i.e. only in aquatic systems), an increasing number of cascades are found in terrestrial ecosystems. Recent studies show evidence that trophic cascades are also not entirely limited to low-diversity systems (Table 1) and that trophic cascades have large effects on ecosystem functioning (Paine 1980). A study performed on brown trout (*Salmo trutta*) in New Zealand shows that annual primary production is six times higher in streams where trout is present, opposed to streams that do not have this top-predator (McIntosh and Townsend 1996). This is a trophic cascade in a simple food web, but these effects have also been found in a more diverse topical forest on Costa Rica. This cascade includes four trophic levels, with plants, herbivorous insects, predatory ants and ant eating beetles When beetles density was increased, more ants were consumed. These ants 'protect' the plants against herbivorous insects, and accordingly, less ants led to an increase of plant consumptions (Letourneau and Dyer 1998).

		Table 1: Overview of case studies	
Study by	Trophic levels	Trophic cascade studied	Results
McIntosh and Townsend (1996)	3	Trout (*Salmo trutta*) in New Zealand	Seven-fold increase in annual PP in streams with trout compared to streams without trout
Letourneau and Dyer (1998)	4	Herbivorous insects, predatory ants and ant-eating beetles	More beetles present led to increase ant consumption resulting in higher plant consumption due to increased herbivore abundance
Carpenter et al. (1995)	4	Removing top-predator and increasing meso-predator in one lake (another lake unaltered) and increasing nutrient imput	Without extra nutrients: Increased grazing efficiency by herbivores but no change in PP With extra nutrients: Two fold lower PP in lake with toppredator present
Schriver et al. (1995)	3	Lake system where the most important planktivorous fish species is removed, refuges for zooplankton present (to escape predation by other planktivores)	Succesfull suppression of algual blooms
Pringle and Hamazaki (1998)	3	Enclosures eliminating access of omnivorous fish (system where omnivore is top-predator)	Increase of herbivores in enclosure, no reduction of primary production
Stein, Devries and Dettmers (1995)	4	System with omnivorous fish, but top-predator is piscivorous	Increase in omnivorous fish leads to a reduction of piscivores and herbivores, thereby dampening the effects of the trophic cascade
Estes et al. (1998)	4	Introduction of a new top-predator	New top-predator preys on the mid-level predator. This leads to depletion of primary producers

Top-down control is not the only factor controlling a cascade. In a recent nutrient enrichment experiments in lakes, two food-webs were created by removing the top-predator (piscivorous) and adding meso-predators (planktivorous) in one lake, while the other lake was not altered (and was dominated by the top-predators). Although the herbivorous zooplankton community differed significantly in size and grazing efficiency, primary production did not. Some time after these observations, the lakes were enriched with nutrients. In the lake that was dominated by the top-predators, primary production was more than two-fold lower than in the lake without the top-predator. It became evident that despite the absence of an obvious trophic cascade in the natural system, when nutrient input in the lakes were increased, the top-predator had a significant dampening effect on the grazer community, thereby controlling primary production (Carpenter et al 1995).

Another important factor to consider is the presence of refuges. In a lake system where planktivorous fish were reduced, large zooplankton populations began to flourish (Schriver et al 1995). These were able to escape predation by other species due to the presence of refuges, where they were protected during daytime. At night the zooplankton migrated to open waters, where they grazed on phytoplankton. Such cascades are often used to successfully control phytoplankton blooms in shallow lakes.

There are also compensatory mechanisms that reduce the strength of cascades. A key factor is omnivory. In an experiment that used enclosures to eliminate access of omnivorous fish, herbivore insects did increase, but this did not lead to a reduction of primary production. (In this case the top-predator was an omnivore. Even though herbivore abundance increased, this only compensated for the reduced grazing by the top-predator. In another example, a mid-level omnivore has an effect on the abundance of herbivore grazers, planktivorous and piscivorous fish, thereby reducing the effects of the cascades (Stein, Devries and Dettmers 1995). In case of the fish, omnivores compete on the preferred prey with other species, thereby limiting the numbers of planktivores and piscivores. It is important to consider the effects human-induced alteration of food-web structures has on trophic cascades. Studies show that the historical extinction of large bodied fauna are associated with the migration of early humans (Alroy 1999). These extinction must have led to a shift in the balance of trophic cascades. But human induced food-web alteration is not a problem of the past. A good example is the effect that the sea otter has on the production of kelp (Estes et al 1998). The sea otter prays on urchins, which in turn consume the kelp. The otter was extensively hunted in past times, which almost led to their extinction. When the sea otter populations increased, new kelp forests were formed. However, in the 1990s, kelp forest decreased again when killer whales shifted their diet in some area's and began preying heavily on sea otters, which decimated the kelp forests (Figure 2). This shift in killer whale is

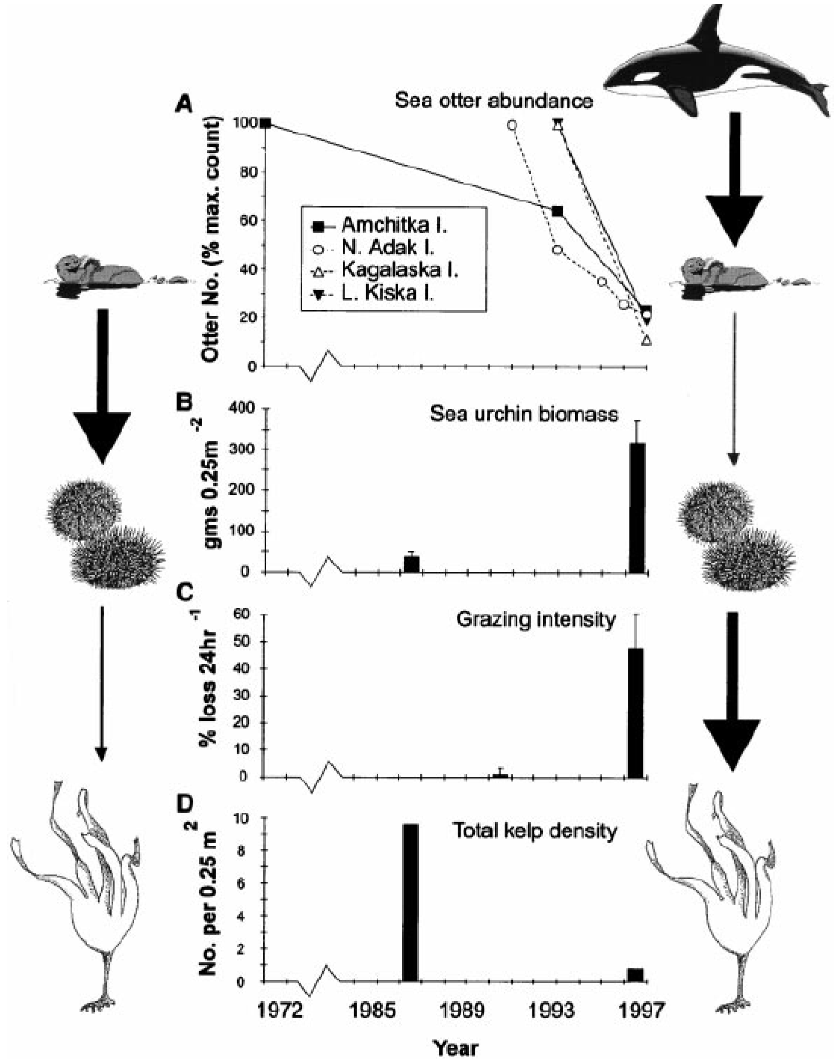

Figure 2: Results of case study by Estes et al (1998). Introduction of a new top-predator ultimately leads to depletion of the primary producer community

presumed to be caused by the decline of the killer whales preferred prey, sea lions and seals. The hypothesis is that the decline of sea lions and seals are caused by overfishing on their prey species. (Steneck 1998)

A cross-ecosystem comparison of the strength of trophic cascades.

J.B. Shurin et al (2002), *Ecology Letters*, Vol 5, pp785-791

I demonstrated the theory behind trophic cascades and which factors are likely to have an effect on the strength of trophic cascades. Now it is important to consider which systems propagate the strongest cascades. As stated earlier, several authors have claimed that cascade strength is largest in aquatic systems. Shurin et al (2002) performed a meta-analyses of 102 field experiments across 6 different ecosystems; lentic plankton and benthos, stream benthos, marine plankton and benthos, and terrestrial grassland. The strength of the cascades are described as the plant and herbivore biomass log-ratio of the system with predator divided by the biomass in the system without the predator. This makes it possible to compare the strength of the cascades between the different ecosystems.

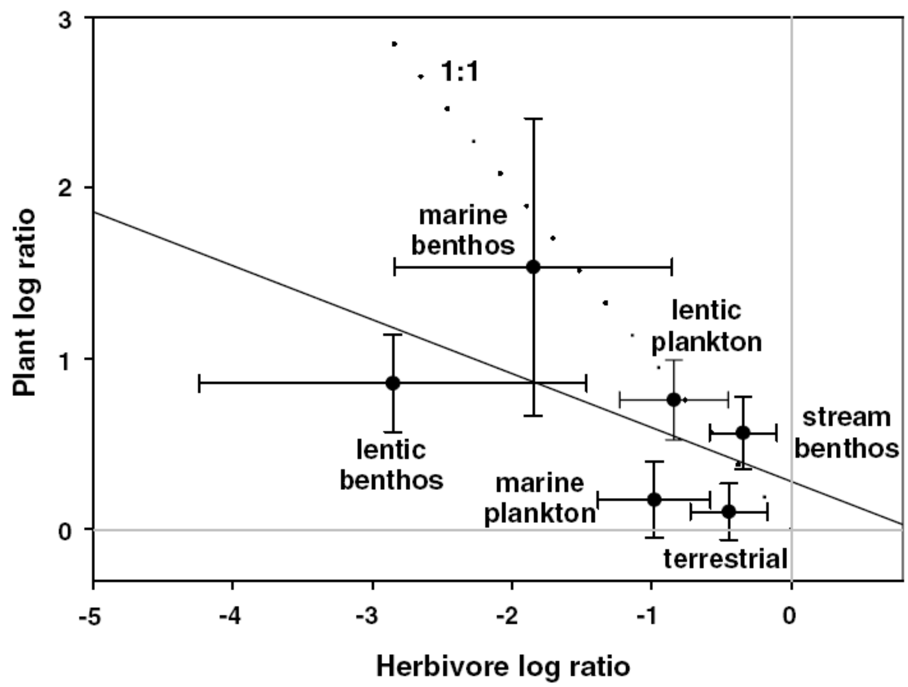

Figure 3: Comparison between herbivore- and plant abundance with absence of predators in different ecosystems (compared to the same systems with predators present) (Shurin et al 2002)

In every system herbivore density was significantly decreased in the presence of a predator (Figure 3). Strongest effects were observed in lentic systems (17.3 fold reduction) opposed to a 1.4-fold reduction of herbivore abundance in streams. Although this demonstrates a huge effect of presence of predators on the herbivore community, the effects on primary producer biomass was not as large (4.7-fold increase in marine benthos, to a mere 1.1-fold increase (non-significant) increase of plant biomass in terrestrial systems). The systems that had the largest effect of predators on herbivore abundance also had the largest increase in plant biomass. Combined the aquatic system showed a stronger response to predators than terrestrial systems. System type explained 28.6% of the variation is plant biomass compared to 35.0% of variation on herbivore abundance. Predator type also affected the outcome of the plant responses. Systems with vertebrate predators shown larger effects of predator on plant biomass, than systems with invertebrate predators (such as the terrestrial systems). Vertebrate predators also have a larger effect on herbivore abundance. However, the difference among ecosystem type was more important than predator type. There were no studies performed in terrestrial ecosystem with vertebrate predators.

This confirms the hypothesis that top-down control is larger in aquatic systems than in terrestrial systems. However, the variation among aquatic systems was as large as the variation between ‘wet’ and ‘dry’ systems. Strongest cascades were found in benthic systems. This is presumably due to the larger response of herbivores from predation and larger impact of herbivores on the primary producers. Although herbivore response on predator removal was significant in terrestrial systems, this did not lead to a reduction in plant biomass. This is presumed to be a consequence of a weaker link between herbivore and primary producers, opposed to herbivore predator interaction.

Although there are some methodological differences among the experiments, none are shown to affect the outcome of the field studies. A key difference is duration of the experiment. In some studies, duration lasted longer then one generation time of the primary producers (mostly in systems with unicellular producers). But the most pronounced plant response (marine benthos) and the least (terrestrial system) both have producers with a long generation time. None of the experiments showed a relationship between experimental duration and plant response.

There are some important differences between aquatic and terrestrial ecosystems that may provide an answer to the apparent variation is cascade strength. The elemental composition of aquatic primary producers is more cognate to the composition of their herbivores and are therefore more nutritious than terrestrial producers (Polis & Strong 1996; Cebrian 1999; Elser et al 2000). This results in less recycling of nutrients and thus more effective grazing. Also the production of mass-specific biomass is far more effective in aquatic producers (Cebrian 1999). Terrestrial plants produce more inedible biomass (such as wood) and may therefore be protected against intense herbivory. Parts of the plant remain intact so the potential for recovery is higher. The fraction of primary producers consumed is also three-fold higher in aquatic systems compared to terrestrial systems (Cyr & Pace 1993)

The overall conclusion of this article is that indeed aquatic systems are more likely to have stronger cascading effects than terrestrial systems. Key differences between aquatic and terrestrial systems led to a stronger top-down control in aquatic systems. It is therefore a logical assumption that alteration of the food web, such as extensive hunting of the top-predator are more likely to have stronger effects in aquatic systems than on land.

Conclusion and Discussion

It is clear that Hairston et al (1992) 'Green world hypothesis' still holds, but it is not as clear whether trophic cascades are limited to aquatic systems. Although evidently not all trophic cascade 'are wet', the most dominant plant response are indeed found in aquatic systems. There are numerous possibilities that may have a cause for this significant variation among systems. One of the most compelling arguments comes from Polis (1999) who claims that in aquatic systems, herbivores consume an average of 51% of annual netto primary production, compared to only 18% in terrestrial systems. Furthermore, in terrestrial systems, the ratio of standing biomass (of plants) compared to the annual netto primary production is 17 times greater, in favour of standing biomass. In aquatic systems this is only 3-7 %. This implies that herbivores in aquatic system are tremendously more effective grazers than herbivores in terrestrial systems. As stated earlier in the analysis, plant response to herbivore density is very important in controlling the strength of a trophic cascade. So more effective grazers could lead to a significantly larger strength of the cascade.

But this does not imply that all trophic cascades that will be found in terrestrial systems will be significantly weaker than in aquatic systems. Shurin et al (2002) for example investigated 86 aquatic communities, compared to only 18 terrestrial systems. So only 17.5% of the sample size was terrestrial. A significant portion of aquatic systems did not have a strong plant biomass response. Even though this group (stream benthos) is half the sample size of the terrestrial group, plant biomass response to increased herbivore density was not significantly larger than the terrestrial group.

Another issue to address is generation time of primary producers. In aquatic systems this is much less than terrestrial systems (compare for example the generation time of algae to generation time trees). A studies in Yellowstone National park used enclosures to fence of wolves and their prey to investigate aspen recruitment. Inside the enclosures, recruitment was very successful, but outside the enclosures recruitment started to drop in 1920 due to extirpation of grey wolves which led to increasing elk populations (dominant herbivore in this ecosystem) (Halofsky and Ripple (2008)). After 1950 recruitment of Aspen completely ceased. This shows that when examining terrestrial cascades, longer research duration is required. Interesting to note is that now grey wolf populations are recovering in Yellowstone, it seems recruitment of trees is recovering (Beyer et al (2007)). This is important because it is evidence that once ecosystems are in an alternative state due to changes in the normal trophic interactions, changes are not irreversible and it might be fairly easy to restore natural balance. Time will tell if this is truly the case.

Evidence provided by all the papers is in my opinion not compelling enough to assume that aquatic systems will always posses stronger trophic cascades compared to terrestrial systems. Important to consider is the fact that 5 different aquatic ecosystems were investigated, to only 1 terrestrial. This obviously limits the variation in terrestrial systems.

Advice for further research logically is to increase the efforts in investigating terrestrial cascades, not only to increase the sample size, but also to be able to compare different terrestrial ecosystems. Optimum would be a comparison of 50-50 between aquatic systems and terrestrial systems.

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