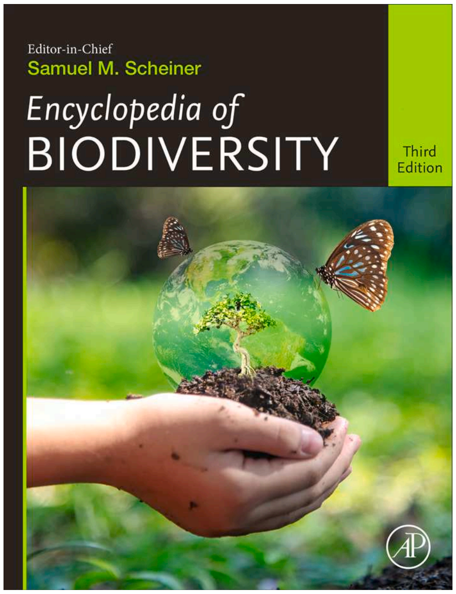

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Trophic Cascades

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Abstract

Trophic cascades are the effects of antagonists (e.g., predators and parasites) on victims (e.g., prey and hosts) that propagate down food webs. They cause inverse patterns of abundance and biomass among trophic groups. Complex interactions within food webs may limit trophic cascades, and researchers have debated where trophic cascades are most likely to occur and their relative strength. Nevertheless, trophic cascades are widely observed in aquatic and terrestrial ecosystems. Changes in trophic cascades may shift systems to alternate states, and trophic cascades influence many processes, including biogeochemical cycling, crosshabitat linkages, and ecosystem services. Restoration of top consumers and resulting trophic cascades are important targets for conservation that can contribute to sustaining biodiversity.

Glossary

Apex predators Predators that have no predators of their own and are at the top of the food web.
Ecosystem services Values to humans provided by ecosystems.
Indirect effects Effects on a third species or trophic group owing to a direct interaction between two species or trophic groups. Trophic cascades are the result of the indirect effect of predator–prey interactions on a third group.
Mesopredators Predators in the middle of the food web, usually small- to medium-sized animals that are preyed on by other predators and that often benefit when apex predators decline.
Meta-analysis Method of summarizing outcomes across numerous studies by compiling measures of the effect size of treatments as, for example, measures of the differences in biomass of primary producers in the absence versus presence of predators.
Natural experiments When a change occurs in a system due to natural or anthropogenic forces, and comparisons can be made with conditions before the change and with conditions in an environment where the change did not occur. For example, the recovery of a predator may provide a natural experiment in which conditions before and after recovery and conditions inside and outside the recovery area are compared.
Omnivory A consumer that feeds on many types of prey including, for example, a diet of plant and animal sources, therefore feeding on different trophic levels.
Regime shifts Dramatic changes in an ecosystem from one distinct state to another distinct state. Regime shifts are abrupt and often difficult to reverse.
Resource facilitation Activity of one species promoting the availability of resources for another species.
Trophic cascades The effects of predators or parasites on prey or hosts that propagate down more than one link in a food web. Trophic cascades cause inverse patterns in the abundance or biomass of trophic groups at successive levels of a food web.
Trophic downgrading Ecological and environmental consequences associated with losses of apex predators and other top consumers from ecosystems.

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Key Points

- Trophic cascades are indirect effects that propagate down the food web.
- Trophic cascades may shape patterns of abundance at different trophic levels, creating inverse changes in the abundances across different trophic groups.
- The effects of trophic cascades go beyond the changes in the species abundances, affecting ecosystem properties and services. Therefore, the loss of trophic cascades may have deep impacts to conservation biology.

Introduction: The Far-Reaching Effects of Predation

When predators reduce prey populations, the effect can propagate, causing an increase in prey lower in the food web. This dynamic interaction is a trophic cascade. Trophic cascades cause inverse abundance or biomass patterns across more than one trophic link in a food web (Pace *et al.*, 1999). Consider a two-level food chain of primary producers and herbivores. A trophic cascade would occur if a predator were introduced that reduced the biomass of herbivores, resulting in an increased biomass of primary producers due to eased grazing (**Fig. 1**). However, not all predator–prey interactions propagate down food webs via trophic cascades. Extensive omnivory and multiple predators and prey embedded in complex food webs blunt trophic cascades (Polis and Strong, 1996). In addition, there are many behavioral, morphological, and chemical defenses that reduce the impacts of predators. Moreover, predators, parasites and other antagonists may have impact on lower trophic levels that are not based on changes in abundances but based on behavioral changes mediated by traits (Beckerman *et al.*, 1997; Gastreich, 1999; Werner and Peacor, 2003; Ohgushi, 2005; Schmitz *et al.*, 2004). Despite this complexity, trophic cascades are observed in terrestrial, marine, and freshwater systems and may cause transitory or permanent shifts in biomass of trophic groups within ecosystems.

The earliest studies of ecosystems provided a "bottom-up" perspective on the control of productivity. Physical–chemical forcing factors such as sunlight and nutrient availability controlled photosynthesis, and the resulting primary production determined production of secondary consumers via transfers of energy up the food web. Hairston *et al.* (1960), in a famous paper, challenged this perspective by arguing that predators limited herbivores, reducing herbivory, with the consequence of a "green" world of lightly grazed plants. Although the Hairston, Smith, and Slobodkin argument was controversial, their paper was among the first descriptions of predatory "top-down" regulation. Paine (1980) first described the propagating effects of predators in the marine intertidal zone as "cascading alterations in structure." Terrestrial researchers noted inverse patterns of biomass in some food chains of plants, rodents, and predators, especially those in high northern latitudes (e.g., Oksanen *et al.*, 1981). In freshwater systems, researchers observed that shifts in top fish predators caused strong cascading changes in prey fishes as well as in invertebrates, with consequences for primary producers (Hrbáček *et al.*, 1961; Power, 1990). Carpenter *et al.* (1985), drawing on examples from lakes, popularized the concept of trophic cascades and the impacts of apex predators that could transfer all the way down the food web.

Subsequent research has focused on the occurrence and relative importance of trophic cascades in a variety of ecosystems, with a particular interest in whether cascades influence primary producers. The term "trophic cascade" applies broadly across population, community, and ecosystem levels of organization. Hence, a species might be influenced by a trophic cascade with

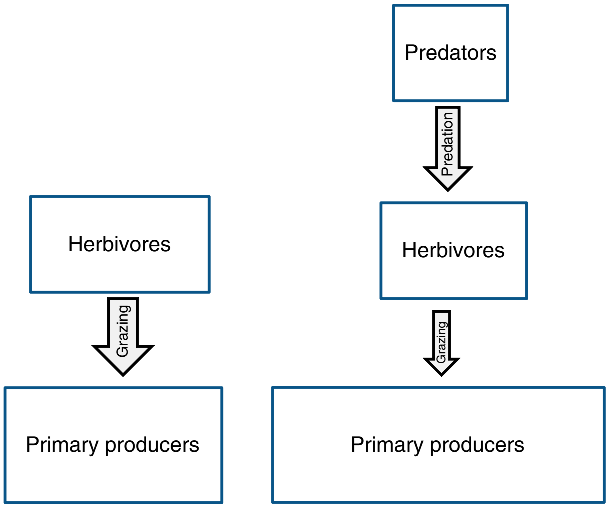

Fig. 1 Two simple food chains depicting the impact of a trophic cascade. In the two-level food chain, herbivore grazing limits primary producers. Adding a predator to create a three-level food chain causes a decline in herbivores, which leads to reduced grazing and an increase in primary producers.

consequent effects on its abundance. Because of elk grazing, aspen trees (*Populus tremuloides*) were rare when wolves (*Canis lupus*) were absent from Yellowstone National Park (USA) (Ripple *et al.*, 2010). When wolves were reintroduced, aspen increased to abundances similar to levels observed before the extirpation of wolves. The distribution and abundance of the aspen population are significantly driven by a trophic cascade. The term "trophic cascade" is also used in the context of communities. Trophic cascades may affect feeding groups or entire trophic levels. Some researchers have advocated labeling this pattern of top-down regulation as "community cascades," restricting the use of the term "trophic cascades" to specific cases in which the impact manifests as changes in primary production (Polis *et al.*, 2000). In this view, cascades are important only if they affect how "green" (i.e., productive) or "brown" (i.e., unproductive), in the case of terrestrial vegetation, an ecosystem appears (Polis *et al.*, 2000). In practice, the term carries a broader if more diffuse application (Ripple *et al.*, 2016).

Trophic cascades are by definition dynamic. The outcomes of trophic cascades may result in a relatively permanent change in the structure of food webs and lead to distinct differences in the biomass of trophic levels, as indicated in **Fig. 1**. Ecosystems are complex, however, with temporal and spatial heterogeneity in population processes and trophic interactions. Trophic cascades may induce compensatory responses and result in variability in system components rather than permanent change. Consider a lake food web with four trophic levels: piscivorous fish, planktivorous fish and invertebrates, zooplankton herbivores, and phytoplankton. Variable recruitment of the top predators may lead to enhanced periods of predation pressure by planktivores on zooplankton. This occurs when dominant, older age classes of the piscivores die off, and planktivores (including young, planktivorous-feeding life stages of the piscivore) recruit in a pulse. These changes create a period of strong planktivory with cascading consequences that ameliorate as the piscivore population re-establishes (Post *et al.*, 1997). Thus, trophic cascades are one of many forces leading to variability in food webs. This dynamical aspect of trophic cascades is probably widespread and counters the simple view that cascades are significant regulatory forces only when effects cause community-level alterations in biomass or productivity that propagate to primary producers.

Trophic Cascade Examples: Wet and dry

Trophic cascades occur in terrestrial and aquatic ecosystems. The earliest examples of trophic cascades were found in coastal water and freshwater systems. Strong (1992) argued that cascades were "all wet" – meaning confined largely to aquatic systems – because of greater potential in aquatic ecosystems for "runaway" consumption of primary producers by herbivores. In contrast, terrestrial plants resist excess consumption through a variety of defenses. However, trophic cascades occur in a spectrum of ecosystems including many terrestrial environments (Pace *et al.*, 1999; Estes *et al.*, 2011). Further, many aquatic primary producers are also defended and resist herbivory. At this stage (*see* "Trophic Cascades: When, Where, How Much?") it is not clear whether trophic cascades are more common in aquatic systems than in terrestrial ones, but they are certainly not "all wet."

Some of the best evidence for the importance of trophic cascades comes from the recovery of apex predators. These recoveries have provided researchers with the opportunity to study and understand the impacts of cascades, as in the following two examples.

Sea otters (*Enhydra lutris*) drive a well-understood trophic cascade in the coastal waters of northwestern North America. Urchins (echinoderms) eat kelp, but otters eat urchins, and through predatory control of urchin populations, kelp forests can flourish. This cascade was first discovered when otters were protected from hunting, allowing their populations to recover from near-extinction (Estes and Palmisano, 1974). Subsequent site-specific reductions of otters due to disease or predation have led to a reversal of otter control on urchins. When otters decline to low levels, urchin populations increase unchecked and drive the loss of kelp beds, creating barren bottom areas. As a consequence, these coastal ecosystems exhibit alternate states of kelp forest and urchin barrens due to effects that emanate from otter predation. Regime shifts between alternate states as evidenced in the otter–urchin–kelp interaction are a significant outcome of changes in trophic cascades.

Like otters, wolves were driven to near-extinction throughout much of their range due to overhunting, but under protective laws, wolves are recovering in many areas. The return of wolves to the Banff region of the Canadian Rocky Mountains provides evidence of trophic cascades and other indirect effects of wolf predation (Hebblewhite *et al.*, 2005). Where wolves re-established, the population density, female survival, and recruitment of elk were all negatively impacted. In the absence of wolves, aspen and willow browsing by elk was greater and recruitment of these trees was near zero (**Fig. 2**). This effect on tree recruitment is the same as described for Yellowstone Park. Interestingly, the higher elk populations in areas of Banff not used by wolves were also associated with lower populations of beavers and song birds due to reductions in riparian vegetation caused by elk grazing (**Fig. 2**). This is a case of an indirect effect of predators on other animal populations through a trophic cascade that changes habitat suitability and biodiversity.

The wolf and sea otter recoveries also illustrate the difficulty of studying trophic cascades that originate from top predators. Natural experiments as opposed to controlled manipulations provide the evidence supporting conclusions about trophic cascades in these cases. Research to establish these impacts was carried out over large areas, took many years, and required comparison among systems. To encompass and evaluate large consumers with extensive ranges, researchers must often consider large spatial areas and long time scales. Many consumers are also difficult to manipulate and do not fit within typical experimental units (e.g., cage enclosures). The study and understanding of predator impacts has lagged partly because of these difficulties and partly because top predators are absent and, unlike otters and wolves, have not recovered in their native ecosystems.

Shifts caused by predator introductions do not always result in a return to a previous state as in the wolf and otter cases. Novel predators may cause trophic cascades that move an ecosystem far from the "native" condition. On Christmas Island south of Java,

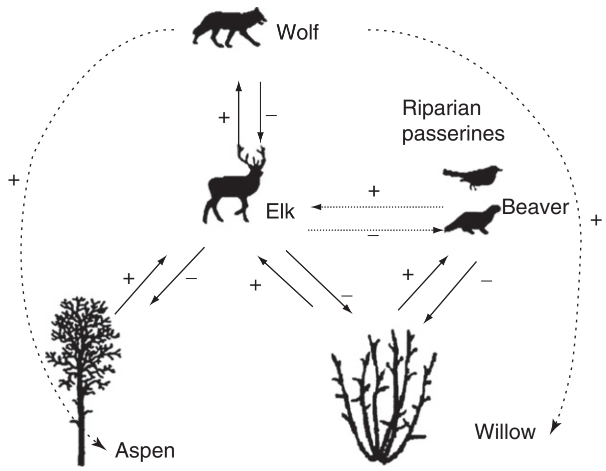

Fig. 2 Trophic interactions for the Banff National Park area of Canada depicting the trophic cascade of wolves–elk–aspen/willow. Solid lines are direct predator–prey interactions, with + / − indicating the direction of the effect. Dashed lines represent indirect effects; for example, wolves have a positive indirect effect on aspen and willows, whereas elk have negative indirect effects on birds and beavers. Reproduced from Hebblewhite, M., White, C. A., Nielvelt, C. G. *et al.* (2005). Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135–2144, with permission from ESA.

red land crab (*Gecarcoidea natalis*) was an extremely abundant herbivore that suppressed forest understory plants. Explosive population growth of an invasive ant species (*Anoplolepis gracilipes*) wiped out the crabs over much of the island, allowing plant recruitment and the development of a lush forest understory (O'Dowd *et al.*, 2003). In locales where crabs remain abundant the forest floor is open with few saplings and little leaf litter, but where the island is dominated by ants, there is much higher plant biomass and richer plant diversity. Ants also altered the canopy by developing associations with scale insects collectively promoting the growth of molds, leading to canopy dieback. The ecosystem under ant dominance is now completely different (O'Dowd *et al.*, 2003).

Trophic Cascades: When, Where, how Much?

Are trophic cascades an ecological curiosity or a phenomenon of widespread importance, common in many systems? When and where do trophic cascades occur, and what factors are related to the strength of trophic cascades? These questions address the generality and significance of trophic cascades. Ecologists have posed many ideas about characteristics of food webs, diversity of producers and consumers, metabolic attributes, key traits of consumers, and other features that could influence the propensity and strength of cascades. One way to address these questions is by synthesizing the results of many studies through the techniques of meta-analysis. A common metric for assessing trophic cascades is the biomass of autotrophs (primary producers) with and without top predators. The log of the ratio of autotrophic biomass in the presence to absence of predators was compared for over 100 studies that included a wide diversity of methodologies and ecological characteristics (Shurin *et al.*, 2002; Borer *et al.*, 2005). Trophic cascades as measured by the log ratio are stronger in some types of systems (e.g., the marine benthos) and the strength of cascades is related to the metabolic efficiency of herbivores and predators. For example, trophic cascades are stronger when herbivores have a high metabolic efficiency (e.g., ectothermic organisms), allowing enhanced conversion of the autotrophic food to growth. Many other factors such as diversity of consumers or producers within a trophic group or rates of primary production had little influence when considered across a large suite of studies (Borer *et al.*, 2005). These types of synthetic studies also indicate limitations in the data available for meta-analysis. For example, there are relatively few studies from terrestrial systems and even fewer studies that have manipulated terrestrial endothermic predators (Borer *et al.*, 2005).

The generalities drawn from meta-analyses need cautious consideration because, in part, results are analyzed for studies that use a variety of methodologies and experimental scales (Whittaker, 2010). In lakes, for example, the patterns of trophic cascades across gradients of nutrient enrichment and primary production differ from the results of meta-analysis based on many different types of systems. Whole lake manipulations done with consistent methods over the same temporal scale illustrate that trophic cascades are stronger when nutrient loading (additions of nitrogen and phosphorus) and hence potential primary production is greater (Carpenter *et al.*, 2001). Lakes responded to increased nutrient loading with large increases in phytoplankton biomass when plantivores and small grazers were the dominant food web constituents (**Fig. 3**). In contrast, in lakes dominated by piscivores and large zooplankton grazers, there was a limited increase in phytoplankton primary production and biomass across a range of nutrient loads (**Fig. 3**). This result contrasts with the lack of any effect of primary production on the strength of trophic cascades found in meta-analyses (Borer *et al.*, 2005). Stronger trophic cascades in more productive ecosystems may be particular to

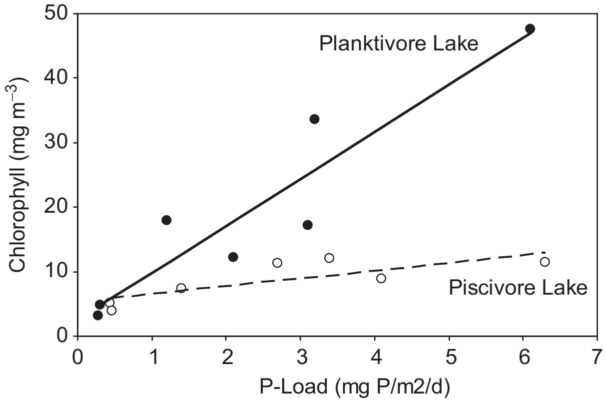

Fig. 3 Trophic cascades in lakes affect the response of phytoplankton biomass measured as chlorophyll to increased nutrient loading measured as phosphorus input. Each point represents a different year for the two lakes – one with planktivorous fish as top predators and one with piscivorous fish as top predators. In the planktivore lake, herbivores were smaller, less effective grazers and phytoplankton biomass was greater at the given nutrient load. In the piscivore lake, herbivores were larger, more effective grazers and phytoplankton biomass was lower. Reproduced with permission from Terborgh J., Estes J. A. (eds.) (2010). Trophic cascades: Predators, prey and the changing dynamics of nature. Washington, DC: Island Press.

lakes, or alternatively, data across many types of ecosystems may be too limited to have strong confidence in the results of meta-analyses.

The ecological features that promote or inhibit cascades remain an open question because: (1) methods in ecological research are variable among studies, making comparisons difficult; (2) trophic cascade studies typically require large spatial and temporal scales and studies at these scales are less common; and (3) the number of case studies is limited, especially those that consider trophic cascades under varying ecological conditions, such as differences in nutrient loading. Ecologists can still profitably argue about whether trophic cascades are more likely in terrestrial versus aquatic systems, whether predator-induced switches to efficient herbivores are critical for driving cascades to primary producers, and how the characteristics and diversity of plant communities influence cascades. Simple answers may not emerge but instead may depend on the organisms and the context of particular ecosystems. Nevertheless, a recent volume that includes many case studies points to the importance of predators and cascading trophic interactions in ecosystems throughout the biosphere (Terborgh and Estes, 2010).

Consequences of Trophic Cascades

The cascading impacts of predators are not just about whether ecosystems have more or less primary production but include many other effects. Here a distinction is needed between direct predatory effects and the indirect effects inherent in trophic cascades. Recall that, by definition, beyond the direct effect of predator on prey, trophic cascades require an indirect effect at lower levels of the food web. Other indirect consequences result from the shifts in biomass and organism abundances induced by trophic cascades. These include consequences for processes related to biogeochemical cycling, crosshabitat linkages, and ecosystem services. Indeed, given the impacts of predators on phenomena such as fire frequency and disease (Estes *et al.*, 2011), it is likely that there are many other collateral consequences of trophic cascades yet to be discovered.

Biogeochemical processes are largely driven by the unique metabolic capabilities of microorganisms in concert with primary producers that utilize nutrients and generate the organic matter fueling elemental cycles. Trophic cascades driven by predatory animals can determine patterns of nutrient recycling and even the net direction of biogeochemical fluxes. For example, the presence or absence of piscivorous, largemouth bass (*Micropterus salmoides*) in experimental lakes fertilized with nutrients was the key to whether lakes were net sources or sinks of CO_2 (Schindler *et al.*, 1997). How did bass influence a physical–chemical process such as the flux of a gas between the atmosphere and a lake? In the absence of bass, planktivorous fish dominated, suppressing large-bodied zooplankton grazers and promoting greater phytoplankton production and hence uptake of CO_2. Under these conditions, lakes became undersaturated in CO_2 with a resultant movement of CO_2 from the atmosphere to the lake. In other experimental lakes with bass, zooplankton exerted greater control of phytoplankton production. Phytoplankton took up less CO_2 and in combination with the microbial respiration of terrestrial organic matter more CO_2 was produced than consumed. The bass-dominated lakes were net sources of CO_2 to the atmosphere.

Trophic cascades can spill across habitat boundaries via the movement, life histories, and predatory impacts of organisms. Dragonflies deposit their eggs in water and the larvae grow in the aquatic system, where they are a favored prey item of fish. Knight *et al.* (2005) compared ponds with and without fish and found many more dragonfly larvae in fishless ponds. This predator–prey interaction caused a trophic cascade that affected the pollination of riparian plants (**Fig. 4**). Around the fishless ponds, dragonfly adults were more abundant, they preyed on pollinator insects, and as a consequence, there were fewer pollinator visits to plants

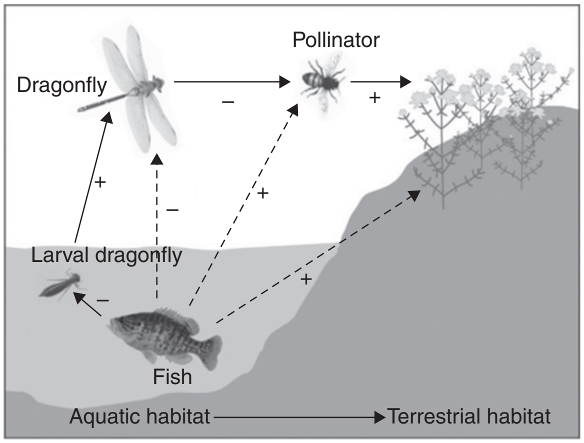

Fig. 4 A crosshabitat trophic cascade of fish–dragonflies–insects that affects the pollination of riparian plants. Solid lines indicate the direct effects of trophic interactions. Dashed lines indicate the indirect effects of fish. Modified from Knight, T. M., McCoy, M. W., Chase, J. M., McCoy, K. A. and Holt, R. D. (2005). Trophic cascades across ecosystems. Nature 437, 880–884, with permission from nature Publishing Group.

such as St John's wort (*Hypericum fasciculatum*). The opposite conditions prevailed in and around ponds with fish – dragonfly larvae and adults were fewer, flies and bees were more abundant, and pollinator visits to *Hypericum* plants were more frequent. The trophic cascade in this case was crosshabitat with pollination influenced by dragonflies as both prey and predators.

Humans harvest natural resources and receive many benefits from ecosystems. Resources and benefits that result from the operation of ecosystems are known as ecosystem services. Alterations of trophic cascades can change the services provided by ecosystems with important impacts on human welfare. For several centuries, the continental shelf off Nova Scotia, Canada, supported a highly productive cod (*Gadus morhua*) fishery. The cod population collapsed due to overfishing in the early 1990 s. The loss of cod altered the system via a shift in cascading trophic interactions (Frank *et al.*, 2005). When cod collapsed, small pelagic fishes, crabs, and shrimp increased, zooplankton declined, and phytoplankton increased. Interestingly, this shift was observed despite the physical dynamics and the large food web complexity of the marine environment, which might be expected to obscure strong trophic cascades.

The collapse of cod had great economic impact, but the rise of the pelagic fishes and crustaceans led to a new fishery that currently produces a higher economic value than the prior cod fishery (Frank *et al.*, 2005). In this case, cascading trophic interactions changed with the resulting impact that the former ecosystem service was lost but a new service of greater value emerged. Although this may seem a positive outcome, the decline of cod had devastating social effects that extended beyond fishing. In most cases where ecosystem services are lost, they are expensive or in some cases impossible to replace. For example, in an agricultural region of south central Texas, USA, Brazilian free-tailed bats (*Tadarida brasiliensis*) prey on agricultural pests of cotton, reducing crop damage – a trophic cascade (Cleveland *et al.*, 2006). Brazilian free-tailed bats have a positive effect on both conventional and genetically modified cotton, reducing the number of sprayings of pesticides and hence costs to growers (Federico *et al.*, 2008). Other species of bats with similar impacts on agricultural systems are currently in decline in North America due to emerging diseases (e.g., a fungal infection of hibernating bats) and other factors (e.g., mortality from the growing use of wind turbines). The estimated value of bats in the US as agents of pest control may be over a billion of dollars (Boyles *et al.*, 2011). Loss of trophic cascades involving bats, insect pests, and crop plants would invoke significant costs due to lost production and increased expenses of treatment with pesticides.

Conserving not Only the big and Fierce but Also the Small and Timid

Colinvaux (1978) wrote a book explaining the general concepts of ecology including a problem posed in the book's title, "Why big fierce animals are rare (..)." The answer to this problem relates to the efficiencies of ecological food chains. You are more likely to encounter a squirrel in your backyard than a lion because squirrels feed lower on the food chain, mainly on a variety of plentiful plant items. Lions feed on vertebrate prey, which they must hunt, attack, and kill. Lions must pay a large cost in acquiring food, and there is a greater limitation of prey (fewer wildebeest than nuts). Energy limitation explains the rarity of large predators.

But predators are also rare because they have been persecuted by humans. In every ecosystem of the earth, apex predators have been killed because they either compete with or are a danger to humans. Apex predators are also targeted for food, for fur, and as trophies. Consequently, there is a second, more insidious answer to Colinvaux's problem. Large, fierce predators are rare because humans have diminished or totally eliminated their populations. The nexus of effects of this loss of top or apex predators has been dubbed "trophic downgrading" (Estes *et al.*, 2011). Generally, trophic downgrading of ecological systems has led to a loss of top-down regulation with changes in the abundance of consumers susceptible to predation as well as many consequences related to a lack of predators. For example, in the absence of wolves, abundant deer populations impact riparian vegetation, causing erosion and loss of shoreline integrity on stream banks (Ripple *et al.*, 2010). The global diminishment of the "big and fierce" has led to impoverished ecological interactions, some of which are now lost forever due to permanent predator extinctions.

Another consequence of the loss of large, apex predators is that smaller predators lower in the food web have become more abundant and have assumed in many systems the role of apex predators, a phenomenon known as mesopredator release. These mesopredators include a variety of species. In terrestrial environments they are often small- to medium-sized vertebrates. In aquatic systems they are either the younger and smaller age classes of the apex predator fishes or medium-sized fish species that were previously in the middle of the food web. Mesopredator release appears responsible for many ongoing changes in ecological systems. For example, the loss of large predators, including lions and panthers, has released olive baboons (*Papio anubis*) in Ghana, West Africa (Brashares *et al.*, 2010). In many locales, baboons are now hyperabundant. Baboons may shift to a more carnivorous diet when released, and there are correlations between increases in baboons and declines in numbers of small primates, in numbers of small ungulates, and in bird nesting success (Brashares *et al.*, 2010). In addition, marauding troops of baboons increasingly invade homes and destroy crops. This is one of many examples where mesopredator release has resulted in some species becoming abundant with attendant losses of biodiversity and negative impacts on humans (Prugh *et al.*, 2009).

In species-rich, complex food webs the removal of top consumers may have multiple outcomes. For example, Pires and Galetti (2022) suggest that, depending on the type of anthropogenic impact, neotropical communities may be driven to three different defaunation syndromes: (1) herbivore-dominated, (2) seed predator-dominated, or (3) mesopredator-dominated systems. The effects of top consumers as apex predators and megafaunal herbivores on complex ecosystems, include shifts in the network structure of food webs (Baskerville *et al.*, 2011). Top consumers are often highly connected species that link food chains based on distinct producers in food webs (Baskerville *et al.*, 2011). The extinction of top consumers may lead to disconnected food chains with consequences to network stability. Similarly, highly connected species generate a myriad of weak interactions across the food web, which in turn may promote stability by dissipating strong demographic feedbacks (Neutel *et al.*, 2002).

Sustaining predators and restoring trophic cascades are important goals for conservation and restoration. Apex predators are a key target as conserving these species may also contribute to sustaining many attributes of the ecosystems that support them. For example, apex predators may promote species richness through trophic cascades and a variety of other mechanisms such as resource facilitation as when predators make carrion available for scavengers (Sergio *et al.*, 2008). Apex predators are also indicators. Where present, they are often associated with high biodiversity and greater ecosystem complexity. The absence of predators can indicate anthropogenic disturbance associated with lower diversity. Finally, because apex predators require large areas, their effective conservation can lead to the creation of large reserves and promote the establishment of corridors between conserved areas for predator movement (Sergio *et al.*, 2008).

With the perspective of trophic cascades, it is also clear that some intermediate species in the food web are necessary targets for conservation and restoration. An example is the European wild rabbit (*Oryctolagus cuniculus*). Within its native range, European rabbits are an important grazer and a key prey for many vertebrate predators, including two endangered species: the Iberian lynx (*Lynx pardinus*) and the Spanish imperial eagle (*Aquila adalberti*; Lees and Bell, 2008). Although the European rabbit is quite fecund and capable of rapid growth, populations are diminished in Iberia because of habitat loss, human hunting pressure, diseases, and predation. Hence, conservation of apex predators such as lynx depends, at least in part, on rabbit conservation, and rabbits are being restocked in areas of Spain and Portugal to promote predators and reestablish native trophic cascades. Maintaining the big and fierce also requires the small and timid.

Conclusion and Prospects

Trophic cascades are a feature of many ecological systems. Although cascades are now documented for many locales, the ecological rules that promote cascades are incompletely understood. This means, as in many areas of ecology, there is a need for theory that can better explain trophic cascades. The addition or removal of predators particularly as the result of human activity often makes trophic cascades apparent. A frontier research area is to gain a greater appreciation for the many consequences of trophic cascades, particularly those that impact ecosystem services. Another frontier is the restoration of lost trophic cascades. Trophic cascades should be partially restorable with the return of large apex predators to systems where they have been extirpated, reorganizing the network structure of food webs (Pires, 2017). Restoring and conserving these predators in a world of changing climate, growing human populations, and increased pressure on natural systems will require new knowledge about ecological systems, better surveillance of predator populations, and a willingness to manage ecosystems to promote predator survival. The alternative is a world of trophic downgrading and cascades lost.

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Further Reading

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