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Opinion

What is a Trophic Cascade?

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Few concepts in ecology have been so influential as that of the trophic cascade. Since the 1980s, the term has been a central or major theme of more than 2000 scientific articles. Despite this importance and widespread usage, basic questions remain about what constitutes a trophic cascade. Inconsistent usage of language impedes scientific progress and the utility of scientific concepts in management and conservation. Herein, we offer a definition of trophic cascade that is designed to be both widely applicable yet explicit enough to exclude extraneous interactions. We discuss our proposed definition and its implications, and define important related terms, thereby providing a common language for scientists, policy makers, conservationists, and other stakeholders with an interest in trophic cascades.

Trends

The notion of trophic cascades has evolved from a foundational concept in ecology to one that helps define modern goals for conserving and managing ecosystems.

The term 'trophic cascade' has grown into a modern lexicon of inconsistent definitions that obscures clear meaning.

We propose that trophic cascades specify the effects of predators that propagate downward thorough food webs across multiple trophic levels.

Trophic cascades can be triggered by consumptive interactions between predators and prey and nonconsumptive effects due to perceived predation risk by prey.

Various 'knock-on effects', initiated by trophic cascades and propagating laterally or upward from the main interaction chain, should not be thought of as part of the trophic cascade.

Opening Remarks

Emergence of the 'trophic cascade' concept was an important step toward the ways in which ecologists have come to view and understand the structure and dynamics of populations, communities, and ecosystems. The term has since resonated strongly with scientists, managers, and even the general public because of its relevance to a range of topics in theoretical and applied ecology, ecosystem management, and biological conservation [1,2]. Yet, the term has also been variously defined (Box 1), thus resulting in an increasingly inconsistent usage, much as terms such as 'habitat' [3] and 'keystone species' [4] were loosely used in the past. Accordingly, the study of trophic cascades has come to an important juncture. The thrust to resolve mechanisms, to expand the spatial and temporal scales of analysis, and to broaden the number of studied systems and species considered, creates the need for a clear definition, from which testable criteria for trophic cascades follow. Our objective here is to advance a historically grounded definition that offers easy and consistent interpretation, thereby leading to more coherent conclusions from research and a broader utility of published research for scientists, managers, and the general public.

A Brief History of Trophic Cascades

The term 'trophic cascade' first entered the scientific vernacular in 1980 with R.T. Paine's Tansley Lecture [5], which described how predators can structure entire communities through interactions with their prey. However, the concept itself pre-dates this publication. Perhaps one of the earliest written descriptions of a trophic cascade was in 1859 from *The Origin of Species* [6], in which Darwin described the way in which domestic cats controlled populations of mice that were otherwise free to devour the honey combs of 'Humble bees', in turn affecting plant–pollinator mutualisms. In villages where cats were more abundant, the number of mice was reduced, freeing bees to pollinate red clover. Darwin concluded '. . .that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district' ([6] pp. 77–78). Nearly a century later, Aldo Leopold [7] famously described a wolf–deer–shrub cascade that resulted in 'every

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Box 1. Historical Trophic Cascade Descriptions

Cascades to Lower Trophic Levels (top down)

1994: 'Trophic cascades are indirect effects mediated through consumer-resource interactions' ([32], p.448).

1994: 'The top-down (trophic cascade) model predicts that changes in density at one trophic level are caused by opposite changes in the next higher trophic level and that such inverse correlations cascade down a food chain' ([19], p.1555).

1997: '.. the indirect interaction between predators and the resources consumed by the predators' prey..' ([44], p. 10735).

1999: '[Trophic] Cascades are defined as reciprocal predator–prey effects that alter the abundance, biomass or productivity of a population community or trophic level across more than one link in a food web..' ([17], p. 483).

2001: 'A trophic cascade is the progression of indirect effects by predators across successively lower trophic levels' ([45], p. 859).

Cascades to Primary Producers (top down)

2000: 'Species-level cascades' occur within a subset of the community or compartment of a food web, such that changes in predator numbers affect the success of a subset (one or a few) of the plant species. 'Community-level cascades' substantially alter the distribution of plant biomass' ([16], p. 473).

2004: 'Trophic cascades–the indirect effects of carnivores on plants mediated by herbivores..' ([23], p. 153).

2005: '..indirect positive effects of predators on plant biomass..' ([29], p. 528).

2010: 'The trophic cascade is the simplest top-down interaction: (i) predators suppress herbivores and allow plants to thrive, and (ii) apex predators suppress smaller mesopredators, releasing herbivores to suppress plants' ([46], p.3).

Bidirectional Cascades (bottom up and top down)

2006: 'A trophic cascade is the process by which a perturbation propagates either up or down a food web with alternating negative and positive effects at successive levels..' ([47], p. 253).

edible bush and seedling browsed, first to anemic desuetude, and then to death', an outcome he credited to the effects of unimpeded browsing by deer in a 'wolfless' America ([7] pp. 131).

In these examples, emergence of the trophic cascade was apparent because the respective systems had been perturbed by either the addition or removal of predators. Both cases implied the effects of changing top-predator abundance that propagated down food chains, ultimately having strong effects on plants. The idea that plant abundance was often regulated by such top-down effects of predators was formalized in 1960 as the 'Green World Hypothesis' [8]. This hypothesis was extended by Fretwell and Barach's recognition that the influence of predators on plants will vary with food-chain length [8] and Oksanen *et al.*'s 'Exploitation Ecosystems Hypothesis' [9], which described how food-chain length varied with net primary productivity. However, this theoretical work was just the beginning of what would develop empirically with a continuous series of discoveries of trophic cascades in diverse ecosystems.

Discovering Trophic Cascades

During the 1960s, limnologists were the first to describe the indirect effects of predators on plankton in lake food webs (e.g., [10,11]). By the 1970s, Estes and Palmisano discovered that sea otters (*Enhydra lutris*) regulated urchin (*Strongylocentrotus* spp.) abundance and overconsumption of kelp (Laminariales) and other macroalgae [12]. Further inspiration for trophic cascades research in marine systems was advanced several years later when, in 1980, Paine explored 'the design of natural webs,' and in so doing recounted cases of strong trophic interactions that started at upper trophic levels and cascaded downward across lower trophic levels, causing impacts near the base of the food web [5]. Paine first used the term 'trophic cascade' to describe the effects of predation in intertidal food webs as 'a series of nested strong interactions'. Although he did not explicitly define the term, this usage clearly associated trophic cascades with ecological processes being controlled from the top down through coupled trophic interactions. This view of food-web structure and the propagation of indirect effects through a series of nested direct interactions set the stage for what would become an entirely new branch of community ecology. It is noteworthy that, unlike the Green World Hypothesis, the chain of interactions in Paine's original definition did not require the effects to propagate to autotrophs. Later usage of the term did require effects reaching primary producers, beginning in 1985 with Carpenter *et al.*'s examination of interactions in a four-level web (piscivore–planktivore–zooplankton–phytoplankton) within lake systems of the northern Midwest USA [13]. These authors noted that population densities across each subsequent trophic level exhibited alternating patterns of fluctuation as densities of piscivorous fish increased. Power similarly showed that the presence or absence of steelhead (*Oncorhynchus mykiss*), a top predator in a four-level stream trophic chain, ultimately led to predictable variation in primary production [14].

Due in part to the preponderance of early empirical evidence from aquatic systems, in 1992 Strong concluded that 'true' trophic cascades were less prevalent in the terrestrial realm [15]. As a result, there was an almost exclusive research focus on freshwater systems during the early 1990s (Figure 1). Trophic cascades were thought to be less important in terrestrial communities because the purportedly species-rich terrestrial food webs were imagined as being more extensively interconnected, a pattern termed 'trophic tangles' to contrast with aquatic trophic cascades [15,16]. In 1999, Pace *et al.* reviewed trophic cascades and described the conditions that promote and inhibit the transmission of predator effects, including the presence of refuges, the productivity of ecosystems, and the potential for compensation [17]. Additionally, they illustrated how trophic cascades occur in a diversity of terrestrial and marine ecosystems.

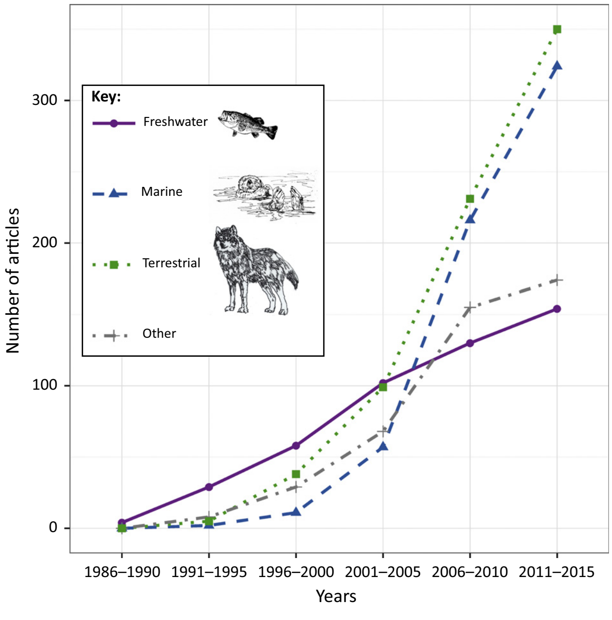

Figure 1. Trends in the Number of Articles Published on Trophic Cascades by Ecosystem Type. Around the turn of the 21st century, trophic cascades research shifted from being freshwater dominated to being dominated by studies in both terrestrial and marine systems. The articles counted in this figure are based on a Web of Science search for articles with topic (title, abstract, or keyword) 'trophic cascade(s)' published between 1965 and 2015. Each of the 2244 articles returned in this search was categorized according to ecosystem type using the article title, journal, and abstract. We used the 'other' category in cases when the ecosystem type was not clear, the article was purely theoretical, or the article covered multiple ecosystem types.

However, Polis *et al.* argued that top-down effects would quickly dissipate through the more complex networks of trophic interactions in terrestrial food webs compared with their downward propagation as trophic cascades in the comparatively simple and more linear aquatic food chains [16]. It was further argued that plant antiherbivore defenses and variability in plant palatability in terrestrial ecosystems were sufficient to prevent runaway plant consumption by herbivores in the absence of predators. By contrast, dozens of studies during this time had revealed the occurrence of trophic cascades in terrestrial systems [18], and researchers documented some of the first cases of strong cascades involving a large terrestrial carnivore: the gray wolf (*Canis lupus*) [19,20]. Moreover, aquatic food webs can be highly diverse (e.g., coral reefs or the Benguela food web), and plant antiherbivore defenses and variation in palatability are expressed in many aquatic plants [21,22]. This growing body of evidence cast doubt on proposed dichotomies between terrestrial and aquatic food webs.

New Perspectives on Trophic Cascades

We conducted a survey of the literature using Web of Science for articles with the term 'trophic cascade(s)' in the title, abstract, or keywords. Results showed an exponential rise since the 1990s in use of the term 'trophic cascade' in studies of marine and terrestrial systems, while the rise in usage was slower in studies of freshwater systems (Figure 1). The dramatic increase in the number of trophic cascades studies in terrestrial systems reflects a shift from earlier thinking that trophic cascades only occur in aquatic systems. At the same time, each new discovery has added layers of complexity and has increased the potential for confusion or misuse of the term 'trophic cascade'.

The earliest empirical analyses of trophic cascades focused on the potential for predators to limit herbivore abundance through consumptive effects. However, numerous trophic cascades triggered by nonconsumptive effects have since been documented [23]. Many of these cascades involve predator-induced changes in herbivore vigilance and foraging behavior that result in their altered impacts on plant communities [24,25]. Studies have also uncovered trophic cascades via mesopredator release, where the loss of top predators allows mid-sized (meso) predator abundances to increase, with concomitant effects on the prey of the mesopredators [26]. Mesopredator release is now a common phenomenon in many places worldwide because of the extensive extirpation of top predators [27].

Early work had a singular focus: to test whether communities were controlled by top predators. This was an alternative to the prevailing view that food chains are largely under bottom-up (e.g., nutrient input) control. Top-down and bottom-up factors are now widely recognized to operate simultaneously [28], which requires more deliberate effort to carefully test the relative importance of top-down and bottom-up factors, how they interact to drive community structure, and the circumstances under which top-down regulation has the greater role [29].

The proliferation of descriptions of these and other kinds of trophic cascade means that there is no commonly accepted definition of the term. This has, in turn, resulted in imprecise usage and thinking (Box 1). As a consequence, empirical evidence risks becoming equivocal, with ensuing debates pivoting on which definition is used or on perceived meanings of the concept. Much is at stake because the concept of 'trophic cascade' is now being considered in management planning for ecosystems. It is especially relevant to conservation-based assessments of marine protected areas and the reintroduction of predators to terrestrial systems [2,30,31]. The concept provides a useful lens for moving beyond mere species protection to conserving the functional integrity of species interactions and entire ecological systems [2,31]. The increasingly central importance of the trophic cascades concept in ecological science, conservation, and management demands that trophic cascades be carefully and explicitly defined.

Defining Trophic Cascades

Therefore, we propose the following definition (see Box 2 for related terms): 'Trophic cascades are indirect species interactions that originate with predators and spread downward through food webs'.

This definition is consistent with Paine's original conception of nested sets of species interactions [5]. It further holds that trophic cascades must involve 'indirect effects', defined as the influence of one species upon another through one or more intermediary species [32]. Our definition is less restrictive than several others [23,29] in that it requires neither that trophic cascades begin with apex predators nor that they end with autotrophs.

Crucial to our definition of trophic cascades is strict adherence to top-down forcing. Food-web control through bottom-up forcing should not be viewed as a trophic cascade. Our intention in proposing this distinction is not to promote a regressive, dichotomous view of trophic control of communities and ecosystems, but rather to distinguish between trophic processes in which the distribution and abundance of species are controlled by the negative influences of consumers on their prey on the one hand, and the positive influences of prey on their consumers on the other. This proposal does not diminish the importance of bottom-up forcing and neither does it imply a

Box 2. Definitions of Terms Related to Trophic Cascades

Autotrophs: organisms, also known as primary producers, that create organic molecules from inorganic carbon through photo- or chemosynthesis.

Biotic resources: living organisms or once-living organisms that are consumed or utilized by other organisms.

Bottom-up forces: the dimension of consumer–prey interactions in which the prey has an enhancing influence on its consumer.

Consumptive effect: lethal effect of a predator on prey due to predation mortality.

Direct effect: the result of a direct interaction.

Direct interaction: an interaction between two species with no interceding species (one link in an interaction chain).

Indirect effect: the result of an indirect interaction.

Indirect interaction: an interaction between two species with one or more interceding species (involving two or more adjacent links in an interaction chain).

Knock-on effects: cascading effects that are not trophically downward because they spin-off from the main interaction chain.

Mesopredator release: the loss of a top predator causes an increase in a mid-sized (meso) predator.

Nonconsumptive effect: nonlethal effect of a predator on prey due to changes in prey behavior or other traits in response to perceived predation risk by prey.

Primary consumers: animals that eat primary producers.

Secondary consumers (predators): animals that eat other animals.

Top-down forces: the dimension of consumer–prey interactions in which the consumer has a limiting influence on its prey.

Trophic level: the position of an organism in a food web.

view of the relative importance of bottom-up and top-down forcing. However, we do feel strongly that mixing top-down and bottom-up control in the definition of trophic cascades renders the term meaningless.

By our definition, the indirect effects of 'mesopredator release' are trophic cascades [33], so long as these indirect effects proceed downward across successively lower trophic levels. The process of 'mesopredator release' [27] is commonly ascribed to a decline or disappearance of an apex predator population resulting in population increases of mid-sized predators. Examples include exclusion of coyotes by wolves that releases pronghorn calves from extensive predation by the smaller canid [34] and, similarly, the release of small mammals from predation by foxes in the presence of dingoes [35]. 'Mesopredator release' research is set apart from the earlier classic trophic cascade descriptions by the absence of demonstrated effects on primary producers in most cases. This might be more from a lack of studies not measuring potential plant effects than the absence of a plant effect.

Our definition recognizes that trophic cascades are typically driven by consumptive (trophic) effects, otherwise predators would starve and prey would incur no risk of predation. However, cascades from many ecologically significant interactions do not involve killing and eating (trophic) events. The strength of consumptive effects can be modified by nonconsumptive effects, manifesting as changes in prey behavior or other traits in response to the perception of predation risk [23]. An example in which nonconsumptive effects predominate is the increase in seagrass productivity corresponding to a decline in foraging activity by dugongs (*Dugong dugon*) and sea turtles (*Chelonia mydasin*) in the presence of tiger sharks (*Galeocerdo cuvier*) [36].

Although trophic cascades necessarily begin with higher trophic level species and proceed downward through food webs via top-down forcing, the indirect effects of predators are not exclusively top down in nature. Inasmuch as trophic cascades commonly influence the distribution and abundance of autotrophs, further indirect effects from the altered plant communities are seemingly inevitable. We do not consider bottom-up effects to be part of a trophic cascade, even if they originate with species of high trophic status and are the consequence of a trophic cascade. While top-down predator effects can change the abundance and productivity of plants that in turn trigger a change in bottom-up effects of the plants on the food chain, we consider such responding bottom-up influences as 'knock-on effects' of trophic cascades rather than a part of the trophic cascade proper. Examples include the top-down influence of grey wolves to elk (*Cervus elaphus*) to berry-producing shrubs (a trophic cascade) to the consumption of berries by grizzly bears (*Ursus arctos*) (a knock-on effect) [37]; and the top-down influence of sea otters to sea urchins to kelp (a trophic cascade), to the effects of kelp on fish [38], herbivorous crabs (*Pugettia* spp.) [39], and atmospheric carbon dioxide [40] (all knock-on effects).

Detecting Trophic Cascades

Trophic cascades, while important in determining the distribution and abundance of species, are invisible in static or stationary systems where there is no change in predator status. Similar to any other species interactions, the consequences of trophic cascades can only be seen and measured when the controlling predator is perturbed. Normally, this is done by removing predators from systems in which they are abundant or adding them to systems in which they are rare or absent. Such predator perturbations can be accomplished in two ways: through time-series records from systems to which the predators are removed or added, or through snapshot comparisons of paired systems with and without predators, as a space for time substitution. In our view, the term 'trophic cascade' applies both to the dynamic response of the distribution and abundance of species to a change in the driving predator and to the dynamic processes that maintain the distribution and abundance of species in static or stationary systems.

Variations in Trophic Cascades

Trophic cascades will inevitably vary in both their operational timescales and strength of influence on component species. Effect sizes will vary by ecosystem type, initial perturbation magnitude and type (if applicable), and choice of response variables. Our definition does not specify a minimum effect size of the trophic cascade [17,41], beyond the obvious fact that it must be measurable. Moreover, timescales over which the influences of trophic cascades affect changes in the distribution and abundance of species following perturbations to the controlling consumer should be expected to vary considerably among ecosystems, depending on the generation times of the component species, especially those of the autotrophs. For example, predator effects on autotrophs through trophic cascades, which have been observed over time periods of weeks to months in lakes [41], streams [14], and coastal marine systems [42], can require decades or centuries in terrestrial systems where long-lived trees are the affected species [43]. This variation in timescales has been a source of much confusion and misunderstanding in studies of trophic cascades.

Concluding Remarks

Language precision in science can facilitate effective communication and accurate idea-sharing across disciplines. Terms must be defined as precisely as possible. However, in the interest of promoting rigorous tests of concepts, these terms must not be so specific as to seldom apply nor so broad as to always apply. The term ‘trophic cascade’ risks falling into the realm of uselessness for these very reasons. Over the 35 years since Paine's foundational work, the term has taken on many forms and has been subsumed by broad, inconsistent usage. While noteworthy efforts to provide clarity for this term have been made, the scientific community at large either chooses the definition that suits their system or no definition at all. We hope that our definition and related discussion captures the essential qualities of this important concept, and is both appropriately accurate and precise to describe an idea that represents one of the foundations of modern ecology.

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