

When is a trophic cascade a trophic cascade?

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Trophic cascades are the time-honored focal point of food-web dynamics. They are the best loved example of indirect effects in undergraduate ecology textbooks and they represent a potentially useful application of theory. Researchers have found them from the Arctic to the tropics. But, can we agree on what they are? Here, we seek to clarify the terminology of trophic cascades and call for a consensus on how to quantify cascading effects in the future.

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Food webs occupy a central organizing position in community and ecosystem ecology. The discovery of trophic cascades and the delineation of their dynamics by empiricists and theorists represent some of the most exciting successes of food-web ecology. Over the past 40 years, debate on the prevalence and importance of trophic cascades has produced numerous thoughtful arguments and theoretical analyses; however, although experimental studies have addressed this subject in a variety of habitats, the topic remains controversial. A new meta-analysis by Schmitz *et al.*¹ might add clarity to the murky waters of this dialogue. By drawing together data from 41 studies, Schmitz *et al.* review our current knowledge of cascade dynamics in terrestrial habitats and indicate features that are common among diverse systems. Of particular note, Schmitz *et al.* illustrate the need for ecologists to be explicit in their definition of trophic cascades. Similar to other terms that once had specific significance in ecology (such as 'stability', 'regulation' and 'keystone species'), 'trophic cascade' has lost meaning as it has become more generally used.

Although Paine was the first to use the term 'trophic cascade'², the concept can be traced back to the tri-trophic Green World Hypothesis (GWH) proposed by Hairston *et al.*³ in 1960. This was later generalized to systems of one to five trophic levels – the Exploitative Ecosystem Hypothesis (EEH) of Fretwell⁴ and Oksanen *et al.*⁵

Owing to the great complexity of food webs, the GWH and EEH suggested that, to study general patterns in natural systems,

one could aggregate species that had similar feeding relationships into discrete trophic levels (herbivores, primary carnivores and top carnivores). Hairston *et al.* used this simplification to explain why the world is green – carnivores suppress herbivores, thus indirectly allowing plants to grow unimpeded by predation. Since this seminal paper was published, trophic ecologists have elaborated hypotheses concerning the diversity and extent of indirect effects on food-web dynamics, with linear trophic cascades being one of many possible interaction types⁶.

Recently, Pace *et al.*⁷ suggested that empirical studies from a variety of systems indicate that trophic cascades are widespread, although many factors regulate their occurrence. This suggestion was dependent on two significant departures from the GWH and EEH. First, they reasoned that it is unrealistic to simplify communities into food chains – communities are composed of complex food webs not simple chains. Second, they describe trophic cascades as 'strong interactions within food webs that influence the properties of the system', thereby including a much wider spectrum of interactions. Thus, 'trophic cascades' of new are no longer 'trophic cascades' of old.

To avoid ambiguity, Polis⁸ recently suggested that we distinguish between species-level and community-level cascades. '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 throughout an entire system, in a manner consistent with both the GWH and EEH. Note that although these definitions refer explicitly to predators, herbivores and plants (following the GWH convention), they also apply to any multilink linear food-web interaction.

The Pace *et al.* definition of trophic cascades carries important consequences. First, it qualifies every strong multitrophic interaction as a trophic cascade, regardless of the exact mechanism by which the indirect interaction occurs (e.g. trophic cascades would include strong effects arising from indirect interactions, such as keystone or intraguild predation). Second, this definition (which includes both species-level and community-level cascades) makes a trophic cascade independent of the strength of its impact on community dynamics. Thus, a strong interaction, even among minor species within a compartment or subset of a complex web, is elevated to the status of a trophic cascade. Given this new definition, trophic cascades would indeed be more widespread than previously argued (see Refs 8–10 for arguments against the commonness of 'old' trophic cascades). Third, and most importantly, species-level trophic cascades do not carry the same significance for ecosystem processes as the GWH and EEH predict for community-level trophic cascades. Species-level cascades do not usually explain habitat-wide changes in biomass distribution between plants and animals.

This brings us to a central question: why are community cascades, such as those predicted by the GWH and EEH, apparently absent or rare in terrestrial habitats^{8–10}? All the cascades that Schmitz *et al.* unearthed in terrestrial systems measured interactions within subsets of a community. Recent empirical and theoretical studies suggest that a variety of factors can influence the strength and occurrence of trophic cascades (Table 1); for example, 'apparent' trophic cascades might occur when predators are subsidized with prey from the detritivore channel^{10,11}. Many of the impediments to community-level cascades arise from the complexity of natural systems. Aquatic systems are more apt to fit within the GWH and EEH because they are more likely to possess characteristics that match the simplifying assumptions implicit within these theoretical models. The idealized models best fit the small set of relatively simple aquatic systems where community-level cascades occur. Such systems should possess the following characteristics: (1) habitats are relatively discrete and homogeneous; (2) prey population dynamics are fast relative to predator dynamics (i.e. rapid algal turnover);

Table 1. Factors and processes that influence the occurrence of trophic cascades

| Factors | Net effect on cascade ^a | Refs |
|---|------------------------------------|------------|
| Self-regulation of guilds and/or trophic levels | | |
| Cannibalism | – | 10,18,21 |
| Interference competition | – | 28,29 |
| Territoriality | – | 30 |
| Intraguild predation | – | 31 |
| Regulation across trophic levels | | |
| Omnivory | + or – | 8,10,18,32 |
| Intraguild predation | + or – | 10,31 |
| Predator-mediated coexistence | – | 23 |
| Apparent competition | + or – | 33,34 |
| Induced responses | – | 21,35 |
| Behavioral responses | + or – | 36 |
| Positive interactions | + or – | 26,37 |
| Consumer age structure | + or – | 38 |
| Food-web complexity | – | 5,8–10,23 |
| Resource availability and quality | | |
| Temporal heterogeneity | + or – | 38 |
| Resource quality is low | – | 9,21,39,40 |
| Resource edibility is high | + | 8,9,21 |
| Resources are dominated by few species | + | 8,9,21 |
| Nutrients recycle rapidly | + | 41 |
| Size refugia | – | 42 |
| Landscape factors | | |
| Spatial subsidies | + or – | 43,11 |
| Refugia | – | 44 |
| Disturbance patterns | + or – | 45 |

^a–, negative effect; +, positive effect.

(3) common prey are more or less uniformly edible; and (4) the systems are simple and trophically stratified, with strong interactions between species. Many aquatic systems lack these community characteristics and do not exhibit trophic cascades. In comparison, most terrestrial systems are much more complex: (1) habitats are heterogeneous with fuzzy boundaries; (2) they exhibit variable prey population dynamics, some much faster than predator dynamics and some much slower; (3) prey are almost never uniformly edible to a single consumer; and (4) systems are reticulate and complex, and interactions between species tend to be weak and diffuse. To the extent that all natural systems deviate from the simplifying assumptions of the GWH and EEH, they tend to depart from clear community-level trophic cascades.

Terrestrial agricultural systems might be the exception that proves the rule. The biological control industry is founded on the idea that the natural enemies of herbivores (e.g. parasitoid wasps, ladybird beetles and *Bacillus thuringiensis*) reduce plant damage¹². In the past century, millions of dollars were spent in an effort to develop and promote this type of trophic cascade, which has had a significant impact on many crops, as well as some disastrous results¹³. As a rule, agrosystems tend to be homogeneous monocultures

of a single plant species, with low diversity among consumer types and abrupt boundaries. Crop plants are bred for high production and (before genetic engineering) are rarely bred for pest resistance, thus increasing their edibility relative to nondomesticated plants. The extreme simplification imposed on these systems often allows strong species interactions. It is in these unnaturally simplified habitats that we find a semblance of community-level cascades. Herbivores have an inordinate effect on plants and predators can have a powerful effect on herbivores. The short linear food chains of biological control differ from similar food webs, in which the modal pattern is a reticulation of trophic relationships rather than a simple trophic cascade^{9,10,14}. This is consistent with other arguments, to the end that more diverse communities are tied together by multiple trophic influences among species. In general, community-level cascades appear to occur only when the affected plant species is a particularly dominant component of a system, as is the case for agricultural systems, subtidal kelp¹⁵, stream algae¹⁶ or lake phytoplankton^{17,18}.

Many of the findings of Schmitz *et al.* confirm this observation. They found that the magnitude of effect of predator removal on plant damage was significantly greater in systems with low herbivore

diversity. The effect of predator removal on plant reproduction also tended to be greater in low diversity systems. However, in many cases, researchers did not provide a mechanism for these effects. Recent theoretical work suggests that complex systems are more stable than less diverse systems^{19,20}. One reason might be that high diversity systems have significantly more redundancy and it is these factors that limit the strength of trophic cascades. Leibold *et al.*²¹ argued that, in trophic cascade experiments, there is a strong response over short timescales; however, over time, species that have greater defenses against predation and/or herbivory become more dominant, weakening the link between predators and prey. This phenomenon is well known by freshwater ecologists; in systems with strong consumption, inedible green algae and cyanobacteria (blue-green algae) become more dominant over time. Moreover, the addition of planktivorous fish causes a shift towards zooplankton that are less susceptible to visual predators. Less complex systems (e.g. agricultural systems) do not contain the redundancy and diversity to allow these shifts towards less susceptible prey.

So, when is a trophic cascade a trophic cascade? In most cases cited by Schmitz *et al.*, although the response by terrestrial plants to predator manipulations is 'statistically significant', changes in plant biomass and/or productivity carry little or no biological significance from a community or ecosystem point of view (in the sense of producing a substantial change in plant biomass or productivity). This is also the case from a population point of view. Few experimental studies showed that predator removal decreased terrestrial plant abundance. Instead, experimentally induced cascades usually produce some decrement in plant performance^{22–24}. Whether such increased plant damage actually translates into meaningful reductions in plant abundance is an open question. For plant–insect herbivore interactions in general, we know in only a few cases how nonlethal effects of herbivory influence plant populations^{25–27}.

Given that most experimental demonstrations of terrestrial trophic cascades fail to show any meaningful population-level impacts on plants, we argue that support even for species-level cascades is limited in terrestrial systems. Schmitz *et al.* make a similar point: predators had a much greater effect on plant damage than on plant biomass or reproductive output. They caution that conclusions about the strength of top-down effects can often be an artifact of the plant-response variable being measured. To this caution must be added the reminder that negative evidence is seldom reported. This is an unmeasured

factor that would tend to increase the statistical frequency and strength of trophic interactions in the published literature, above that actually occurring in nature.

As a community, trophic ecologists ought to agree upon some specific criteria that provide evidence for a cascading effect. Strong⁹ previously argued that one characteristic of what we will now call community-level cascades is 'runaway consumption'. If we accept this as a criterion, we must come to a consensus about what it means. A traditional index to demonstrate a community cascade is the change in plant biomass; another index, not modeled by the GWH or EEH, could be the change in plant-community composition. But, how much change (e.g. 20, 40 or 80%) is it necessary to show? Is it possible (or desirable) to establish a subjective percentage? Like good artwork, most ecologists would recognize (and agree on) a trophic cascade when they see one. However, to become a more predictive science, we should set a more testable basis for quantitative analysis. This might be difficult to achieve because statistically significant effects might not be biologically meaningful. Likewise, effects that are biologically important can be difficult to demonstrate statistically because it is difficult to conduct and replicate large experiments.

In conclusion, analyses such as those of Schmitz *et al.* provide insight towards how we can improve our science. Their study has highlighted the importance of discriminating between species and community cascades, the importance of establishing mechanisms for indirect effects and the importance of choosing appropriate response variables. This is a valuable step towards synthesizing our current knowledge of terrestrial trophic cascades, especially by examining the effects of diversity and testing for causes of attenuation or propagation of the indirect effects at the center of trophic cascades. Perhaps most importantly, this review, as well as recent papers by Polis⁸ and Pace *et al.*⁷, demonstrates our current need for consensus in trophic ecology, beginning with a standard vocabulary and moving towards a standard criterion of importance.

Acknowledgements

We would like to thank P. Stapp, F. Sanchez-Pinero, M. Rose, A. Boulton and J. Vander Zanden for thought-provoking discussions and constructive criticism. We would also like to thank O. Schmitz for his thoughtful advice and encouragement, as well as M. Pace and two anonymous reviewers whose comments improved this paper. We acknowledge the support from NSF grants DEB9527888 and DEB9806657 to GAP and from an NSF Graduate Research Fellowship to ALWS.

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