

In the following two invited News & Comment articles, Mary Power and Robert Holt comment on the Perspective article by Gary Polis *et al.* in this issue (pp. 473–476). Gary Polis, Michael Rose (a postgraduate researcher at UC Davis with Gary Polis) and three visiting colleagues – Shigeru Nakano, Takuya Abe and Masahiko Higinshi – were tragically killed in a boating accident on 27 March this year.

What enables trophic cascades? Commentary on Polis *et al.*

Polis and colleagues, in both a 1999 paper¹ and in this issue of *TREE* (pp. 473–476), have made the case for a needed distinction between community-level and species-level trophic cascades. Confusion over the level of aggregation in studies of predator impacts on prey and plants has muddied this issue for more than 30 years. Murdoch², in his critique of Hairston *et al.*³, pointed out the need to specify the unit of study: 'It might be, for example, a single population or a group of populations of a recognizable type, etc.' He argued that if fossil fuels didn't accumulate, this needn't imply food limitation for all detritivores, because some of these populations could be limited by predators or other factors below the level that would have been set by their food, leaving other populations to 'eat up the "left-over" food'. Slobodkin *et al.*⁴ rebutted that they weren't concerned in their 1960 paper with a majority vote (how many individual consumer or producer species were regulated by food, predators or some other factor), but rather with how their collective trophic level biomass responded. Ehrlich and Birch⁵ argued that, contrary to the generalization that herbivores were generally not food limited, specialists such as the cabbage white butterfly might be. If the world were planted with more cabbages, its population would increase. Slobodkin *et al.*⁴ again replied by saying that if the world were planted with more cabbages, other plants, and their associated herbivores, would decrease as a result of cabbage competition, causing collective trophic level abundance to respond as they predicted.

Different questions require different levels of aggregation. The similar spectral irradiances of manzanita and marijuana might not matter to scientists interested in remote sensing of chaparral plant cover, but are inconvenient for drug enforcement officers. Community ecologists often seek some intermediate level of resolution (e.g. 'edible' and 'inedible' members of a trophic level⁶). Our

conceptual pigeonholes accommodate natural continua and variation very imperfectly. Improving our approximations requires specific research on which differences are trivial, and which are crucial, for a particular prediction. If ecologists accept the community- versus species-level cascade terminology proposed by Polis and colleagues, we could at least better communicate which phenomena we are attempting to predict.

We still have a lot to learn about the distribution and abundance of both types of cascades, and the community characteristics that enable them. Schmitz *et al.*⁷ found trophic cascades frequent in published terrestrial studies (45/60 cases), with carnivore impacts on plants and herbivores equal to or stronger than those documented in aquatic systems. Polis *et al.* (in this issue) point out that the studies they reviewed documented species-level cascades. Documenting community-level cascades on land requires large spatial and temporal scales, in part because of the storage effect⁸ imposed by long-lived terrestrial producers⁹. By an ingenious synthesis of paleoecology and contemporary Siberian pony manipulations, Zimov and colleagues¹⁰ argued persuasively for top-down mediation of vegetation transition from steppe graminoids to mossy tundra over Beringia, following the extermination by human hunters of Pleistocene grazing megafauna. Here, however, plant biomass did not increase, and a key mechanism (trampling) was nontrophic.

Polis and other terrestrial ecologists here and elsewhere have argued that aquatic ecosystems that are homogeneous, simple and closed are more likely to cascade. Aquatic ecologists, however, have been impressed with the subtle heterogeneity that structures even pelagic communities, where thermal convection cells, gelatinous surfaces of salps, or algal aggregates provide key boundaries that delimit and intensify processes and interactions^{11–13}. The jury is still out on how diversity differs between aquatic and terrestrial systems, pending more

thorough inventories, including of microbial species identities, in both. It is common for a benthic or planktonic algal sample of a few cm³ to contain >30 species; however, a producer species density is difficult to match in a terrestrial sample of a similar volume. Size disparity between consumers and resources, and relatively fast prey dynamics, can sometimes enable cascades (Refs 1,14 and on pp. 473–476). Fast resource dynamics allow aquatic systems to respond to consumer or nutrient manipulations over short timescales convenient for experimentalists, but could work against top-down control by permitting demographic escape. The small size of freshwater algae might make them more uniformly ingestible but, with high resource loading, algae can accrue enough biomass to outcompete animals for oxygen, putting an abrupt end to top-down control. Similar density related escapes were reported for whelks, which when abundant turn the tables on spiny lobsters, their former predators, and collectively rasp them to death¹⁵. This 'run away production' is the converse of Strong's¹⁶ 'run away consumption', and is yet another manifestation of strong nonlinearity in ecological relationships.

Polis and colleagues (and many others) have pointed out that trophic cascades might be more likely in a homogeneous, closed ecosystem. These reasonable arguments are not supported by a model of Carpenter *et al.*¹⁷, in which they summarize conditions influencing whether eutrophication of lakes could be reversed (e.g. by biomanipulations of higher trophic levels). Eutrophication becomes irreversible when nutrient fluxes from the watershed, or from internal recycling, overwhelm nutrient sinks (higher trophic levels, sedimentation out of the euphotic zone or flushing through outflowing rivers). In their model, heterogeneity (having a sediment compartment in which nutrients become unavailable to algae) or an open system (river washout of excess nutrients) enable rather than preclude trophic cascades that allow higher trophic levels to affect plant biomass. As always, we need specific understanding of causal processes to predict trophic cascades, or any other community or species-level phenomena.

What we are really struggling to understand in our investigations of trophic cascades is how and why the strength of ecological interactions varies over space and time and across taxa. Our understanding clearly is contingent on the scales (scope and resolution) of our investigation, both taxonomic (lumping versus splitting and how much of the web to include) and spatio-temporal (how to delimit systems in space and time and how intensively to sample them). Gary Polis stimulated the quest for clarity and larger understanding of these issues tremendously, and led by example to provoke community ecologists to 'stop looking at our feet', and ecosystem ecologists to deepen their consideration of natural history. As we continue Paine's¹⁸ 'profitably frustrating' quest for predictive understanding of trophic dynamics, Gary Polis' insights and impetus will continue to energize and illuminate food web research.

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Trophic cascades in terrestrial ecosystems. Reflections on Polis *et al.*

In its simplest form, the concept of a 'trophic cascade' is an ecological variant of a basic truism, 'the enemy of my enemy is my friend'. Recent definitions of the term 'trophic cascade' include: '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'¹ and the 'propagation of indirect mutualisms between nonadjacent levels in a food chain'². In principle, these definitions apply throughout a food web, but, in practice, there has been a focus on indirect carnivore impacts on plants via shifts in herbivore abundance and activity^{1,3}. This emphasis reflects a fundamental ecological question: to understand the forces that govern plant community composition and dynamics, must one pay attention to the food webs supported by those plant communities? If trophic cascades are ubiquitous and large in magnitude, the answer is 'yes'.

Gary Polis⁴ and his colleagues (see pp. 473–476, this issue) sensibly observe that it is important to distinguish between 'species-level' and 'community-level' cascades. In species-level cascades, altering predator numbers indirectly influences just one or a few plant species; whereas, in community-level cascades, there is a substantial impact on plant biomass distribution for entire communities. They urge ecologists to agree on objective measures of strengths of cascades. In addition to these useful methodological and terminological suggestions, Polis *et al.* suggest that 'community cascades...[are] apparently absent or rare in terrestrial habitats' as compared with aquatic habitats and that 'support for even species-level cascades is limited in terrestrial systems'⁵. They argue that this putative difference between biomes reflects the great complexity of terrestrial ecosystems and the reticulate patterning of food webs. I would like to

respectfully suggest that the jury is still out on these substantive claims.

Unfortunately, the proper timescale for assessing trophic cascades at the plant community level extends well beyond that of typical field studies. In the recent review of terrestrial studies by Schmitz *et al.*³, 81% of the studies involved measurements within a single annual growing season of the focal plants, many of which were long-lived shrubs or trees. A fair test of trophic cascades would have to extend over multiple plant generations. Extending the timescale could either enhance or weaken cascades. A small increase in herbivory that seems 'insignificant' in any given year could be greatly magnified in its ultimate impact (for instance, if it lowers the competitive ability of a plant species). Or, a large impact within a single growing season might induce compensatory or defensive mechanisms, or act at life stages unimportant in determining density, and thus become weakened over longer timescales.

The timescale issue in terrestrial studies is a tough nut to crack. For instance, consider the ambitious, large-scale study reported recently by Sinclair *et al.*⁶ in Canadian boreal forest. Mammalian and avian predators were excluded to examine indirect impacts upon vegetation.