

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's<sup>18</sup> '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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#### References

- Polis, G.A. *et al.* (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86, 3–15
- Murdoch, W.W. (1966) Community structure, population control, and competition – a critique. *Am. Nat.* 100, 219–226
- Hairton, N.G. *et al.* (1960) Community structure, population control, and competition. *Am. Nat.* 94, 421–425
- Slobodkin, L.C. (1967) Regulation in terrestrial ecosystems and the implied balance of nature. *Am. Nat.* 101, 109–124
- Ehrlich, P.R. and Birch, L.C. (1967) The balance of nature and population control. *Am. Nat.* 101, 97–107
- Marks, J.C. *et al.* (2000) Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos* 90, 20–27
- Schmitz, O.J. *et al.* (2000) Trophic cascades in terrestrial systems. A review of the effects of carnivore removals on plants. *Am. Nat.* 155, 141–153
- Warner, R.R. and Chesson, P.L. (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *Am. Nat.* 125, 769–787
- Terborgh, J. *et al.* (1997) Transitory states in relaxing ecosystems of landbridge islands. In *Tropical Forest Fragments* (Laurance, W.F. and Bierregaard, R.O., eds), pp. 256–274, University of Chicago Press
- Zimov, S.A. *et al.* (1995) Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.* 146, 765–794
- Silver, M.W. *et al.* (1995) Marine snow, what it is and how it affects ecosystem functioning. In *Linking Species and Ecosystems* (Jones, C.G. and Lawton, J.H., eds), pp. 45–51, Chapman & Hall
- Allredge, A.L. and Cohen, Y. (1987) Can microscale chemical patches persist in the sea? Microelectrode study of marine snow, fecal pellets. *Science* 235, 689–691
- Powell, T.M. (1989) Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. In *Perspectives in Ecological Theory* (Roughgarden, J. *et al.*, eds), pp. 157–176, Princeton University Press
- Power, M.E. *et al.* (1996) Disturbance and food chain length in rivers. In *Food Webs, Integration of Patterns and Dynamics* (Polis, G.A. and Winemiller, K.O., eds), pp. 286–297, Chapman & Hall
- Barkai, A. and McQuaid, C. (1988) Predator-prey role reversal in a marine benthic ecosystem. *Science* 242, 62–64
- Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73, 747–754
- Carpenter, S.R. *et al.* (1999) Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* 9, 751–771
- Paine, R.T. (1980) Food webs, linkage, interaction strength and community infrastructure. *J. Anim. Ecol.* 49, 667–685

## 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'<sup>1</sup> and the 'propagation of indirect mutualisms between nonadjacent levels in a food chain'<sup>2</sup>. 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<sup>1,3</sup>. 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 Polis<sup>4</sup> 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'<sup>5</sup>. 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.*<sup>3</sup>, 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.*<sup>6</sup> in Canadian boreal forest. Mammalian and avian predators were excluded to examine indirect impacts upon vegetation.

This study is much larger in scale than most ecological experiments, both in space (1-km<sup>2</sup> blocks) and time (10 years). Predators had clear direct effects on herbivore abundance (mainly snowshoe hare and arctic ground squirrel), but little indirect effect upon plant biomass (largely shrubby willow and birch). Sinclair *et al.*<sup>6</sup> suggest that this reflects compensatory plant growth. However, the consumed plants are relatively long-lived and co-occur with black spruce. Ten years is a long time for experimental community ecology, but is rather short measured against the generation length of spruce trees. A longer-running experiment might find a shift in plant community composition owing to altered competitive abilities of birch and willow against spruce. Another important effect at longer timescales is that species not even present in the local community might be able to invade, following a reduction in predation or an increase in herbivory. Dispersal on land is sluggish compared with aquatic systems, thus effects that emerge from reshuffling of the species pool will play out only over long timescales in terrestrial ecosystems.

Of course, these thoughts about the Sinclair *et al.*<sup>6</sup> experiment are speculative. However, there is suggestive correlative evidence in many terrestrial ecosystems (e.g. high tundra<sup>7</sup> and USA woodlands<sup>8</sup>) that removal of top predators (including human hunting) does lead to upsurges in the abundance of mammalian herbivores at decadal scales, with worrying long-term consequences for forest dynamics<sup>9–11</sup>. For instance, Terborgh<sup>9,10</sup> has observed that on islands in the manmade Lago Guri in Venezuela, where top predators are now absent, mammalian herbivores are abundant; there is little recruitment via seedlings and saplings of canopy trees compared with controls on the nearby mainland. To date, there has been little effect of predator elimination on total plant biomass or species composition of the adult trees; but, if these conditions continue, one can predict that within a century there will be a radical alteration in the composition and character of the vegetation on these islands.

Another serious limitation of the current evidence base is that manipulative experiments (for sensible reasons) focus on a small subset of predatory taxa. Imagine the following gruesome thought experiment: an evil scientist takes vegetarianism to its logical extreme and creates a ray gun that he uses to kill all the carnivores (vertebrate predators, invertebrate predators, parasitoids and entomophagous nematodes – all of them) of a large ecosystem (pick your favorite ecosystem or, if you prefer, your least favorite

ecosystem), but leaves behind all the folivorous and root-munching herbivores. What happens to this morally purified ecosystem when we wait long enough (as defined by plant generation length) to gauge shifts in plant communities, including invasions from larger regional species pools of both plants and herbivores? If trophic cascades are ubiquitous, there should be large impacts of increased herbivory in these ecosystems dominated by vegetarian consumers. If not, then everything will look much the same as before, with minor and idiosyncratic waxings and wanings of a small number of plant species. My own suspicion is that one would see a range of effects but rarely will there be no, or just very minor, effects; often there will be huge changes in the plant communities, albeit on average probably less dramatic than observed in many aquatic systems. Moreover, at times, heterogeneities and reticulateness in webs will indeed weaken cascades, but at other times will prove to enhance them. As an example of the latter effect, note that webs with generalists are, by definition, more reticulate than webs with specialists. If top predator removal permits upsurges in generalist herbivores, some plant species might be vulnerable to exclusion via apparent competition. This is not expected in webs dominated by specialist herbivores.

But, this is just a hunch and I could well be completely wrong about the importance of trophic cascades in terrestrial ecosystems. It is humbling that here, at the beginning of the 21st century, we ecologists cannot do much better than that. Ideas presented by Polis<sup>4</sup>, Pace *et al.*<sup>1</sup>, Oksanen<sup>7</sup>, Strong<sup>5</sup> and others provide key pointers towards a predictive theory of food-web impacts on plant communities, but this theory is still rather embryonic. However, I can predict more confidently that as ecologists grapple with elucidating the consequences of food-web dynamics for plant community structure and ecosystem functioning, the ideas that

Gary Polis so successfully championed – his emphasis upon the reticulate nature of food webs, his concern with the spatio-temporal dimension and ecosystem contexts of food web dynamics, and his deep appreciation of the need to weave the idiosyncratic details of natural history into the conceptual fabric of our science – will continue to inform and inspire our discipline for many years to come.

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#### References

- 1 Pace, M.L. *et al.* (1999) Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.* 14, 483–488
- 2 Persson, L. (1999) Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85, 385–397
- 3 Schmitz, O.J. *et al.* (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.* 155, 141–153
- 4 Polis, G.A. (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86, 3–15
- 5 Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73, 747–754
- 6 Sinclair, A.R.E. *et al.* (2000) Testing hypotheses of trophic level interactions: a boreal forest ecosystems. *Oikos* 89, 313–328
- 7 Oksanen, L. and Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *Am. Nat.* 155, 703–723
- 8 Alverson, W.S. and Waller, D.M. (1988) Forests too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2, 75–92
- 9 Terborgh, J. (1999) *Requiem for Nature*, Island Press
- 10 Terborgh, J. *et al.* (1997) Transitory states in relaxing ecosystems of landbridge islands. In *Tropical Forest Fragments* (Laurance, W.F. and Bierregaard, R.O., eds), pp. 256–274, University of Chicago Press
- 11 Miller, S.G. *et al.* (1992) Impacts of white-tailed deer on endangered and threatened vascular plants. *Nat. Areas J.* 12, 67–74

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