Yes, Ecology is Hard

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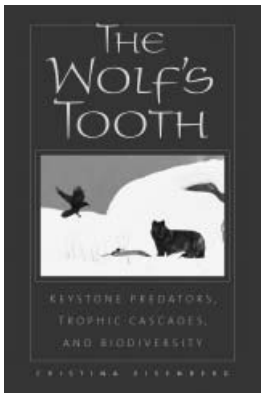
The Wolf's Tooth: Keystone Predators, Trophic Cascades, and Biodiversity. Cristina Eisenberg. Island Press, 2010. 248 pp., illus. $35.00 (ISBN 9781597263979 cloth).

Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature. John Terborgh and James A. Estes, eds. Island Press, 2010. 488 pp., illus. $45.00 (ISBN 9781597264877 paper).

Resolving Ecosystem Complexity. Oswald J. Schmitz. Princeton University Press, 2010. 176 pp., illus. $35.00 (ISBN 9780691128498 paper).

It would be difficult to argue that *Homo sapiens* has not known about trophic cascades at least since the Neolithic Revolution—ancient Chinese farmers, for example, are known to have understood that when birds eat coccinellid beetles, the latter's control over the aphids that affect crops is diminished. Such observations of trophic cascades are recorded in archeological sites the world over, reflecting the fact that the idea has been around for a long time. Consequently, understanding the concept within traditions of Western science is a historically complicated subject, yet it offers important lessons for contemporary ecologists. Three intersecting lines of development are clearly recognizable in recent history.

First, there is a rich base in historical natural history study that should not be bypassed. Citing Darwin's humble bees (as I frequently do) consecrates the idea as ordained by the master, yet humble farmers and humble hunters and gatherers before them undoubtedly took as a matter of course the notion that an enemy of my enemy is my friend. Indeed, one can hardly think about predators and their prey or herbivores and their plant food without casting one's thoughts in this evident framework.



Second, a rich base in experimental ecology has developed, demonstrating that action at one trophic level may have indirect consequences at some other level. Again citing the master, Darwin's famous experiments showing that his lawn mower (well, the equivalent) could have an effect on the competitive interactions among the plants attacked by that artificial herbivore were perhaps the first systematic demonstration of a trophic cascade, although one could imagine that ancient Chinese farmer killing a few birds and watching the aphids decline, thus being ecology's true master. Since the 1960s, experimental ecology has acquired its own imprimatur as the methodological imperative of modern research, and the experimental documentation of trophic cascades has been a major theme.

The third line of historical development is clearly much more recent. In the mid-1920s, Lotka and Volterra independently wrote down two very simple equations that demonstrated the profound truth that predators and their prey must oscillate with respect to one another. Although those ancient farmers may have realized this fact, it is not as obvious as the ecological shibboleth that my enemy's enemy is my friend. Furthermore, it is not so much the initial insight gained from these two equations, which many ecologists today would claim as independently obvious, but the enormous amount of theoretical ecology that has emerged from their detailed study. This fact is especially important since, as a result of the pioneering work of MacArthur and Levins, theoretical ecology is now a field unto itself, growing in mathematical sophistication even if it is a bit lacking in empirical grounding.

Today, we stand at the threshold (perhaps we are always there) of a quantum jump in our understanding about community ecology. A Venn diagram illustrating the intersection of these three trends would, I believe, guide us to the brink of making that jump. Unfortunately, these three trends seem to have generated the perception of a continuum rather than an intersection. Community ecologists are frequently thought of as existing on a continuum ranging from natural history, through experimental ecology, to theoretical ecology, with the normative value increasing along that continuum for the theoreticians but decreasing for the natural historians and being bell-shaped for the empiricists. But the problem, in my view, is not a prejudicial evaluation of which point on the continuum represents an ideal point of reference; rather, the problem is in the framework itself. These trends are not, and should not be thought of as, a continuum. They should be visualized as the overlapping set of a Venn diagram. The creative intersection of natural history, experimental ecology, and theoretical ecology is where the truth will be found.

A wonderful example of the inspiration that comes from the natural history set can be found in Cristina Eisenberg's *The Wolf's Tooth: Keystone Predators, Trophic Cascades, and*

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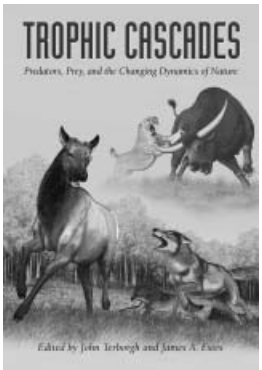
Biodiversity. Eisenberg knows wolves, and as is supremely evident from her narrative, she loves them as well. Using wolves both directly and as metaphor (e.g., "orcas are the wolves of the sea"), she describes some of the more fascinating indirect effects of trophic interactions in a variety of ecosystems and makes a noble attempt to tie our understanding of trophic cascades and similar indirect effects to our ability to manage ecosystems sustainably. In her first and most obvious objective—to make us appreciate wolves and their role in trophic cascades—she is extremely successful. Obviously written with a popular audience in mind, the book is peppered with enough personal anecdotes and poetic portraiture to keep the layperson interested but enough straight factual reporting to convey science to the assembled readership. Her attempt to tie such knowledge to our ability to plan sustainable management is less convincing, although I acknowledge that it is a valiant effort, and hope I can be shown to be in error by wise future planning informed thusly.

Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature, a collection of chapters edited by John Terborgh and James A. Estes, is, like all such collections, a mixed bag. In the introductory chapter, cowritten by the editors and Bob Holt, we see a surprising—and, I might add, slightly irritating—point of view. Symptomatic of this view is one particular sentence illustrating an intolerant rejection of ideas because they seem too specialized or erudite. There is a reference to *homoclinic orbit* as an apparently evident case of a term not relevant enough even for Google search. Curiously, in chapter 7, again cowritten by Bob Holt, we find a most casual reference to a heteroclinic orbit. One must wonder if the Professor Holt of chapter 3 is irritated with the Professor Holt of chapter 7. This explicit rejection of advanced theory is not wise; it seems to unwittingly pigeonhole trophic cascades into a "theory-free" box, effectively accepting the continuum characterization of trophic cascades, rather than seeking the intersection in the Venn diagram.



The chapters themselves of *Trophic Cascades* are generally excellent summaries of some corner of—mainly—experimental work on trophic cascades and—frequently—more general indirect interactions of one form or another. The example of Carpenter's studies of lake cascades is particularly striking. It is one of the most celebrated sets of ecological experiments, and it is all too briefly summarized in one chapter and alluded to in several others. Especially noteworthy is chapter 17, by Marten Scheffer, which is actually a quick summary of his 2009 book *Critical Transitions in Nature and Society.* Scheffer's chapter—and especially his book—focuses on a question that has emerged as both theoretically fascinating and of enormous practical importance. Given that ecosystems frequently occur in alternative states or "regimes" (which is undoubtedly true), can we predict when a system will switch from one regime to another, and, more importantly, can we devise practical ways of judging from real world data when a regime shift is on the horizon? Melting Arctic ice could change global ocean currents such that all of Northern Europe would become almost uninhabitable, and, furthermore, such a shift could occur quite suddenly. Will we be able to detect when that change is about to happen? Will a canary suddenly die in the coal mine? Relying on a broad range of theoretical ecology, the tentative conclusion is that careful monitoring of the correct variables could indeed provide us with advance notice of an imminent crisis. Even though the arguments are all correct and the insights dramatic, *Critical Transitions* leaves open the disturbing fact that many of the same theoretical formulations Sheffer uses to devise "signals" of imminent transitions also suggest broad parameter ranges in which there will be no signal at all, in principle. That is, for many systems, the fundamental principle may be the "inevitability of surprise."

In the end, the empirical examples in *Trophic Cascades*, from both aquatic and terrestrial ecosystems, as well as a variety of specialized topics, leave little doubt about the ubiquity and importance of the phenomenon. As in the case of *The Wolf's Tooth*, the arguments regarding how our knowledge of cascades will lead to better management are less convincing, even though Soulé makes a valiant attempt in chapter 20, although even here, the analysis is perhaps hampered by naively emphasizing our "Pleistocene impulses."

Resolving Ecosystem Complexity by Oswald J. Schmitz attempts a more cohesive presentation not only of trophic cascades, but also of a smattering of other well-known ecological catchwords, many of which stem from his own extensive experiments in old-field communities. Although they are strongly focused on the experimental side of ecology, the range of topics covered in this book is large and coupled with at least initial experimental evidence, sometimes with fascinating hypothesis-generating extrapolations. If there is a central theme, it has to do with scaling up from individual behavior through the perpetual game of solving the inherent trade-off between foraging and predation risk. In a larger context, the book is laudable for its emphasis on "diligence in natural history study...as an important prelude to experimentation," but it fails, in my view, to strive for new theoretical foundations.

If *The Wolf's Tooth* emphasizes natural history, *Trophic Cascades* the experimental, and *Resolving Ecosystem*

Complexity a bit of both, none of these three titles sufficiently summarizes past theory or breaks new theoretical ground. This is certainly not a critique, since none of them claims to have done so, and they are all arguably excellent books for what they seek to do.

Are there trophic cascades? Of course. How important are they for understanding ecosystem complexity? The jury is still out. As part of a more general idea of ecological complexity, they are certainly essential, but more fundamental structures enter into modern food-web theory—issues such as chaotic competition, phase locking, critical transitions, and, yes, even homoclinic cycles—suggesting that we are only beginning to understand what we need to understand. Why is it that astrophysicists can predict so many things about their subject matter while ecologists remain mainly baffled by things like unexpected pest outbreaks or the sudden disappearance of entire populations and are unable to say with any degree of certainty what will happen when the next invasive species arrives in the Great Lakes? When an astrophysicist friend was asked that question, he replied, "Because ecology is hard."

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Reference cited

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