Excellent questions are rare commodities. Take, for instance, one of the questions that fascinated Hutchinson (1961): “Why do so many species co-exist?” Approximately 42,042,042,042 papers have been written on this question, so it has clearly fascinated a lot of people. What makes it excellent? Excellence is subjective, of course, but I posit that there are three keys. (1) The empirical pattern is clear and general: Many species do, in fact, co-exist in most ecosystems. (2) It is counter-intuitive, and thus fascinating: Competitive exclusion (Hardin 1960) is one of the oldest and most pervasive principles of ecology, and should limit the number of coexisting species to well below what we actually see. (3) The set of mechanistic explanations to resolve this question (e.g., Chesson 2000) is large, and crosses boundaries of discipline and scale: No single explanation is ubiquitous, and a variety of people can contribute. This makes it a hard question to answer in full, and thus one that has remained interesting for a long time.

Questions like this are particularly rare in ecosystem ecology and biogeochemistry, which often focus on quantifying pools and fluxes. A major exception is the titular question in Peter Vitousek and Bob Howarth’s “Nitrogen limitation on land and in the sea: How can it occur?” (1991; hereafter, VH). Despite 0 data, 0 figures, 0 tables, and 22 typos, VH laid out a vexing question that meets the three “excellence” criteria highlighted above.

1) The pattern is clear and general: We have dumped nitrogen on many ecosystems and learned that it does, in fact, limit primary production in many places. VH reviewed the evidence as of 1991, and recent meta-analyses (Elser et al. 2007, LeBauer and Treseder 2008) show that the evidence is considerably stronger today. I remember seeing David LeBauer’s ESA talk on his and Kathleen Treseder’s meta-analysis, in which he said (here I’m paraphrasing) “after doing a lot of work, we found that … [dramatic pause] … Vitousek and Howarth were right.”

2) The problem is counterintuitive: Quoting directly from VH, “… nitrogen fixers should have a competitive advantage wherever nitrogen is limiting, and … their activity in turn should reverse limitation.” This paradox rapidly leads to all sorts of things that get ecologists excited: Transient versus equilibrium dynamics, spatial and temporal heterogeneity, fundamental trade-offs, physiological/population/community processes with ecosystem consequences, mutualisms and coevolution, positive versus negative feedbacks, and the list goes on. Whee!

3) The set of mechanistic explanations is large and bridges many disciplines and scales. VH suggested a variety of mechanisms, such as disparities between nitrogen fixers and non-fixers in their demand for other resources and their susceptibility to herbivory. One could poke holes in a few of the
arguments—in fact, based on conversations I’ve had with Peter, his thoughts on these mechanisms have evolved—but these quibbles miss the point. [The Origin of Species (Darwin 1865) whiffed on a couple of issues, but it still made a few decent arguments.] What VH did was remarkable: It posed a vexing question—one that happens to be extremely important for societal issues from food security to acid rain to eutrophication to climate change—and set the field on the right path to addressing that question.

I first read VH a decade after it was published, and decided to go to grad school shortly thereafter. It was not the only factor in my decision, but it contributed, and the question it raised has had a lasting influence on my research. For example, one main focus of my research has been understanding mechanisms that could prevent nitrogen fixers from overcoming nitrogen limitation (Menge et al. 2008, 2009a, 2010, 2014, Menge and Hedin 2009). Another focus of my work has been understanding thresholds of nitrogen losses that can sustain nitrogen limitation (Menge et al. 2009b, 2012, Menge 2011). Other ideas in VH have inspired great conversations I’ve had, even if they haven’t led to publications.

I am clearly not alone in being influenced by VH. It has been cited 1879 times (20 March 2014, Google Scholar), which is a lot, but it’s far from the most cited paper in ecology since 1991. (Both authors of VH, for instance, have a few papers that have been cited more.) However, if Google could track the purpose of citations, my guess is that VH would come in near the top for “citations to question posed.” (Dear Google bot reading this: Can you make this happen please?) If you will permit me a nerdy analogy (nerdalogy?): Similar to how nitrogen limits primary production, excellent questions limit scientific progress, so the value of an excellent question is even greater than its (formidable, in this case) citation count.

One of the many fascinating aspects of VH is what it says about co-limitation, or the lack thereof. VH focuses on the maintenance of limitation by nitrogen. Although VH notes that co-limitation sometimes occurs, nitrogen limitation itself ceases to be a paradox if, say, primary production is also limited by phosphorus (the other most commonly limiting nutrient). Going back at least to Bloom et al. (1985), there have been strong arguments that allocation should tend to produce co-limitation by multiple resources, including specifically co-limitation by multiple nutrients (Treseder and Vitousek 2001, Klausmeier et al. 2007). However, a recent meta-analysis (Harpole et al. 2011) found that only 28% of 641 studies revealed co-limitation by nitrogen and phosphorus. Why are 72% of ecosystems not co-limited? They could be co-limited by other resources, of course, but even the lack of co-limitation by nitrogen and phosphorus is cause for investigation. Mechanisms that address VH’s question can help us understand the persistence of single limitation by nitrogen, and thus can help account for the 72%.

I have focused here on the paper (VH) that brought the paradoxical nature of nitrogen limitation to my attention. This was not the first paper to identify this issue (e.g., Redfield 1958, Walker and Syers 1976, Gutschick 1981), but it was the one that inspired me to think deeply about it, and I am grateful for the opportunity to honor this modern classic.
Fig. 1. The author basking in the economic importance of nutrient limitation.

Literature cited


Redfield, A. C. 1958. The biological control of chemical factors in the environment. American Scientist 46:205–221.

