

## Ecosystem Succession and Nutrient Retention: Vitousek and Reiners' Hypothesis

Donald R. Zak

University of Michigan, Ann Arbor, Michigan

What mechanisms mediate the flow of energy and cycling of nutrients during ecological succession? Are they linked in time and across space? In 1969, Eugene P. Odum proposed a series of hypotheses that caused the ecological community to think critically about patterns and processes (*sensu* Watt 1947) during ecological succession and how they might be linked in a causal manner. Odum's perspective on the process of succession, or "the strategy of ecosystem development" as he termed it, was undoubtedly shaped by the intellectual influence of his mentor, Victor Shelford, as well as Shelford's contemporaries such as Fredrick Clements. They shared the idea that ecological communities possessed emergent properties, wherein the whole is greater than the sum of its parts (*sensu* Phillips 1934). Inasmuch, the 24 hypotheses Odum (1969) articulated were an amalgam of holism and reductionism that created his rationale for the way energy flows and nutrients cycle within ecosystems. It is within this context that Peter Vitousek and Bill Reiners derived ideas that are fundamental to our understanding of energy flow and nutrient cycling in terrestrial ecosystems, ideas that have profoundly shaped my thinking as an ecologist.

In his classic paper, Odum (1969) eloquently drew parallels between successional patterns of biomass accumulation in laboratory microcosms and forests, and, moreover, explained how biomass accumulation ceased late in succession because respiration consumed the products of photosynthesis; patterns and processes that he proposed were shared among all ecosystems. He argued further that the "conservation" of growth-limiting plant nutrients should be low in simple, species-poor, early-successional ecosystems, whereas nutrient conservation should be greatest in late-successional ecosystems due to the complexity of biotic interactions among a diverse set of organisms. In retrospect, Odum's rationale regarding the *emergence* of nutrient conservation from the complexity of late successional ecosystems was probably shaped by a holistic perspective likely derived from his intellectual upbringing, whereas his ideas regarding biomass accumulation were based on physiological observations (e.g., microcosms) and insightful extrapolation (e.g., forests). Odum's attempt to derive pattern from process, or vice versa, fueled the critical thinking of many ecologists, and over the following decades, set in motion events that have generated great insight into ecosystem-level processes. I believe one of the most important was the Nutrient Retention Hypothesis proposed by Peter Vitousek and Bill Reiners.

Vitousek and Reiners (1975) revealed a critical disconnect in Odum's rationale for patterns of biomass accumulation and nutrient conservation during secondary succession; Odum failed to realize they were linked, wherein one drove the other. Vitousek and Reiners (1975) argued that, if biomass accumulation in an ecosystem ceased late in secondary succession, then, in contrast to Odum's prediction, nutrient conservation should be low, because the net incorporation of growth-limiting nutrients into living plant biomass also must cease (Fig. 1). This led to the prediction that nutrient retention, or "conservation" as Odum had termed it, should be greatest early in succession when ecosystems are accumulating biomass (i.e., net ecosystem productivity is greater than zero; Fig. 1).

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Whereas nutrient retention should be low in late-successional ecosystems, because the pace of biomass accumulation has ceased, (i.e., net ecosystem productivity = 0), thereby creating a low demand for growth-limiting plant nutrients; the input of nutrients should therefore be equivalent to their loss (Fig. 1). This simple, elegant, and mechanistic logic simultaneously united the flow of energy and cycling of nutrients within ecosystems, albeit Lindemann (1942) had made remarkable headway on this matter several decades earlier.

What set Vitousek and Reiners' work apart from others was devising a true ecosystem-level experiment that provided a statistical test of their hypothesis. If their *Nutrient Retention Hypothesis* was correct, then the export of growth-limiting plant nutrients should be greatest in late-successional ecosystems and dramatically lower in early-successional ecosystems in which biomass was accumulating. But, how does one test this at the scale of an entire ecosystem? Vitousek and Reiners cleverly used a paired-watershed approach in which the size, topography, and geologic characteristics of two adjacent watersheds were as identical as possible and only differed from one another in the successional stage of the dominant vegetation; in this case, high elevation spruce forest in the northeastern United States. Using these "natural" experiments, they identified paired watersheds that were sealed by underlying bedrock and drained by a single stream, making stream flow the only means for nutrients to exit these watersheds. Monitoring the concentration of growth-limiting ( $\text{NO}_3^-$ ), essential (Ca), and nonessential (Na) plant nutrients in stream flow over time enabled them to test their hypothesis, and the competing hypothesis proposed by Odum (1969). Their work revealed that the concentration of  $\text{NO}_3^-$ , a growth-limiting nutrient, in stream flow exiting late-successional spruce-dominated watersheds was significantly greater than that exiting watersheds blanketed by early-successional forest. Moreover, they observed no difference in the concentration of a nonessential plant nutrient (i.e., Na) in the stream water draining from early- and late-successional watersheds, providing evidence that the rate of biomass accumulation caused patterns of nutrient retention and loss. With a mechanistic rationale and an ecosystem-scale "natural" experiment, Vitousek and Reiners (1975) demonstrated that the flow of energy and cycling of nutrients were indeed linked in time.

It is the juxtaposition of these competing hypotheses that has impressed on me how one's intellectual upbringing can shape their ecological "world view" and the importance of questioning the underlying assumptions of one's own thinking. Further, it exemplified how ecological knowledge is iteratively built from a foundation set in place by others, as well as the importance of devising a complete connection between an ecologically important hypothesis and a clever experiment that provides the appropriate statistical test. Vitousek and Reiners' work exemplifies these essential scientific characteristics, strengthening ecology as a science and increasing our understanding of how ecosystems function. For me, it served as a scientific model to emulate and helped me understand *how* and *why* biogeochemical cycles are linked in time and space. Most importantly, the ecological dynamics depicted in Vitousek and Reiners' Nutrient Retention Hypothesis lie at the heart of understanding a myriad of human influences on biogeochemical cycles, including coastal eutrophication, nitrogen saturation of terrestrial ecosystems (Aber et al. 1989, 1998), as well as the accumulation of anthropogenic carbon dioxide in the Earth's atmosphere. As we further embark through a time period in which humans have dramatically altered the flow of energy and cycling of nutrients at a global scale, it is our foundational knowledge of ecosystem processes, like that generated by Vitousek and Reiners (1975), which enables us to understand, anticipate, and hopefully limit our collective impact on the planet.

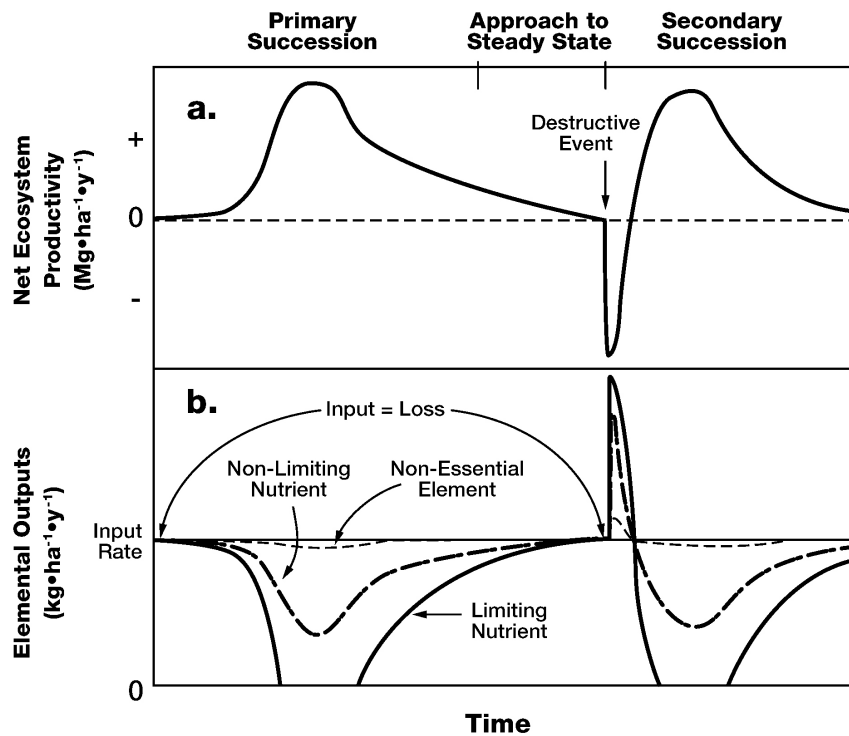


Fig. 1. A conceptual diagram depicting Vitousek and Reiners' (1975) *nutrient retention hypothesis*, which links the flow of energy and the cycling of nutrients in terrestrial ecosystems. Panel a illustrates the rate at which biomass accumulates (i.e., net ecosystem productivity) during primary and secondary succession, which is the balance between rates of net primary productivity and microbial decay. Early in succession, biomass accumulates because net primary productivity exceeds the rate of decay (i.e., net ecosystem productivity  $> 0$ ). In contrast, rates of net primary productivity and decomposition are equivalent late in succession; here, biomass ceases to accumulate and net ecosystem productivity approaches 0. Panel b illustrates how the loss of growth-limiting, non-limiting, and nonessential nutrients correspond to patterns of ecosystem biomass accumulation in Panel a. An assumption is that rates of nutrient input remain constant over successional time, as illustrated in Panel b (see nutrient input rate). When net ecosystem productivity is positive during succession (i.e., net primary productivity  $>$  microbial decay), the loss of growth-limiting plant nutrients approaches zero, because growth-limiting nutrients are needed to build accumulating biomass. In contrast, the loss of non-limiting nutrients is less affected by patterns of net ecosystem productivity, because there is a lower biological need for them; nonessential nutrients are not affected by ecosystem productivity. An important prediction encapsulated in the nutrient retention hypothesis is that the loss of nutrients from terrestrial ecosystem is greatest following disturbance. In this situation, rates of decay dramatically exceed net primary productivity; therefore net ecosystem productivity is  $< 0$ . This causes the mineralization of nutrients from decaying organic matter to exceed biological demand, and nutrient loss attains a maximum. Human activity has intentionally and unintentionally manipulated net ecosystem productivity on a global basis, and has therefore also altered the rates at which nutrients are retained and lost from terrestrial ecosystems.

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