Limiting Factors, Competitive Exclusion, and a More Expansive View of Species Coexistence

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When I began graduate school in the 1980s, species interactions were viewed predominantly through the prism of resource competition. Species found together were largely understood to coexist because of how they segregated their use of the available spectrum of local resources. I entered this world of ideas wholeheartedly, but I was fascinated by why prey species are able to coexist with some predators and not others. Consequently, the central concept of my scientific discipline, Hutchinson's niche, seemed to have no bearing on my ecological fascinations. Predation was understood largely as a species interaction that ameliorated the effects of resource competition among the prey, and so its main consequence was to prevent competitive exclusion (Paine 1966).

In struggling to make sense of all this, I came across an article by Simon A. Levin in *The American Naturalist* (Levin 1970) that was a revelation to me. In it, Levin articulated many of my own misgivings about having resource competition as the sole basis for understanding species coexistence, and he offered a new vantage from which community organization could be understood.

The article begins with a presentation of the ideas underlying Gause's principle of competitive exclusion—the conceptual basis of Hutchinson's definition of the niche (1957, "Concluding remarks," *Cold Spring Harbor Symposium of Quantitative Biology* 22:415–427). The article is the epitome of scholarship, using many quotes from the relevant articles to build his argument. The motivation for the argument is Slobodkin's 1961 analysis of Gause's competitive exclusion principle and his evaluation of its test-

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ability (found in *Growth and Regulation of Animal Populations*, Holt, Rinehart & Winston, New York). Levin draws on Slobodkin's logical arguments to show that Gause's competitive exclusion principle results in a tautology. If the ecological niche is defined "as that space which no two species can continue to occupy for an indefinitely long period of time" (Slobodkin 1961), "no one can any longer dispute the Gause principle" (Levin 1970, p. 414).

He motivates the main analysis presented in the article by arguing that Hutchinson's "hypervolumes in multidimensional space" are not incorrect representations of species niches, but rather, we are incorrect in how we characterize the importance of various dimensions constituting a species' hypervolume and the relationships between the hypervolumes for multiple species:

> Which dimensions those are is determined by which factors are limiting those species, be those factors resources, predators, or others. Two species cannot coexist unless their limiting factors differ and are independent; this is the only criterion one need examine at a given time and place. (Levin 1970, p. 415)

This is a much more inclusive concept, embracing not only competition for food but also predation and any other type of interaction that may be important to a species. Also, the emphasis shifts the focus to factors that limit the abundance of each species. The implication here is that two species may have identical Hutchinsonian hypervolumes but still coexist if their abundances are limited by the factors associated with different dimensions of that hypervolume.

A general mathematical treatment of a community of interacting species is developed to make a simple but profound point. The population dynamics of each species is governed by a general equation that is a function of the abundances of the species in the system and variables defined by factors extrinsic to the community (e.g., abiotic variables; eq. [1] in Levin 1970). All of the contributing

terms in this function define the "limiting factors" for that species, and these limiting factors can be thought of singly or in combinations.

The article offers a simple mathematical proof to answer the primary question of how large must the minimum set of limiting factors be for a community of r species to coexist at either a stable point equilibrium or a stable limit cycle. The direct implications of this proof is the main result of the article: "In particular, no stable equilibrium is possible if some r species are limited by less than r factors" (Levin 1970, p. 419).

Along the way to this result, the nature of limiting factors, point equilibria versus limit cycles, perturbation analyses, deterministic versus random environments, and various forms of stability are discussed. In particular, the proof applies to all types of limiting ecological factors and not just resource limitation, and the conclusions apply equally well to systems with stable point equilibria and stable limit cycles.

The article concludes by first offering a reinterpretation of Paine's (1966) classic experiments. Typically, *Pisaster* predation is described as preventing competitive exclusion by *Mytilus* mussels of a number of inferior competitors (Paine 1966), but Levin shifts the focus to changes in sets of limiting factors. "Presumably, the presence of *Pisaster* had made possible the independent operation of a great many more limiting factors than was possible without *Pisaster*. In its absence, species which no longer had to contend with predation were now able to dominate several resources that could previously be divided among more species" (Levin 1970, p. 419).

The application of the main result to a number of ecological situations is then proffered. Neutral community dynamics is presaged in a discussion of dynamics when a system is short of limiting factors. Finally, the article deals with how predation and resource competition may interact to promote coexistence or limit community membership in a basic outline that foreshadows results on diamond-shaped and apparent-competition community modules.

Throughout my career, this article has been a touchstone to which I have returned continually. On first reading, it provided me with an alternative way to think about species coexistence unconstrained by resource competition. A decade later it provided me insights about what is required for coexistence of consumers that simultaneously compete for resources and are fed on by a common predator. Most recently, it offered me inspiration for why "intraspecific competition must be greater than interspecific competition" was an insufficient mindset for understanding coexistence.

Our conception of species coexistence in biological communities has moved far beyond the simplistic formulations based largely (or solely) on resource competition. However, the competitive exclusion principle and Hutchinson's niche concept still have a powerful hold on how we view nature and interpret species interactions. For me, the perspective that Levin (1970) first articulated is a conceptually richer and mathematically stronger foundation on which our queries about biological communities should be based. The question is not whether two species that are limited by the same set of factors can coexist. Rather, the correct question is whether these species differ in how they are limited by the same set of factors.

Finally, I also greatly admired this article for its sense of whimsy and humor. Too often science is dry, stiff, and humorless. To prove that it does not have to be so, I end by quoting from Levin's "Acknowledgments," and I draw your attention to the mathematician's joke at the end of the first sentence: "Finally, this paper cannot close without an exposition of certainly the most elegant form of the niche theorem (section 1) to appear anywhere (unfortunately without proof). The following is taken from Dr. Seuss's epic *On Beyond Zebra* (Geisel 1955 [Random House, New York])."

And NUH is the letter I use to spell Nutches
Who live in small caves, known as Nitches, for hutches.
These Nutches have troubles, the biggest of which is
The fact there are many more Nutches than Nitches.
Each Nutch in a Nitch knows that some other Nutch
Would like to move into his Nitch very much.
So each Nutch in a Nitch has to watch that small Nitch
Or Nutches who haven't got Nitches will snitch.

"W. L. Brown Jr. and R. Root were aware of this statement long before the author, but it should indeed have wider currency."

In *The American Naturalist*

Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. American Naturalist 104:413–423.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–76.