

Wiens J A. On competition and variable environments. *Amer. Sci.* 65:590-7, 1977.
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In variable environments, resource levels fluctuate between superabundance and scarcity. Interspecific competition may be important only during the lean times ("ecological crunches"). Consequently, populations and communities often may not be in equilibrium, selection on resource-utilization traits may be intermittent, and patterns predicted from competition-based theory frequently may be absent. [The *SC*® indicates that this paper has been cited in more than 445 publications, making it the most-cited paper from this journal.]

Ecological Crunches and Competition

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During the 1960s and early 1970s, ecologists generally believed that natural communities were in equilibrium and their structure was determined by competitive interactions. I grew up, academically, fervently embracing this view and conducted a PhD study of grassland birds in Wisconsin¹ that showed (I thought) how subtle the niche partitioning produced by these interactions could be. After I moved west to a faculty position in Oregon, I began a long-term study of breeding bird communities in the Great Basin shrubsteppe, partly to extend the grassland studies into more complex habitats and partly to escape the rain of the Willamette Valley. Despite my best efforts and most probing analyses, the expected patterns failed to emerge. After several years of trying to fit the square peg of data into the round hole of theory, my student John Rotenberry and I realized (during a June snowstorm) that the conditions of resource limitation required by community theory probably occurred only intermittently in the shrubsteppe—much of the time the birds lived in a land of plenty.

The realization that environmental variations might weaken the effects of competition in communities was not new—the Australian ecologists

H.G. Andrewartha and L.C. Birch had espoused a similar view in 1954,² although their views had little impact on community ecology of the 1960s. Once we shed the preconceptions of competition-based theory, it was not difficult to find abundant evidence of environmental variability, of inconsistencies in community patterns in such environments, and to recognize some of the logical flaws in the traditional theory.³ A paper developing some of this thinking, along with some empirical documentation, was rejected by four mainstream ecological journals before being published in *Condor*,⁴ so when I prepared this paper, I submitted it to a more neutral journal, where it was promptly accepted.

After an initial phase of begrudging citations (i.e., "but see Wiens 1977"), the response was largely positive. Many authors cited the paper in support of their conclusions that competition occurs infrequently or that communities are not in equilibrium.⁵ I think that the paper was cited so frequently because it set forth an alternative to the prevailing competition paradigm whose tidiness and ubiquity were beginning to bother many ecologists who looked at nature and saw variation. This variation became more apparent as more investigators began to study particular communities for more than a year or two.

Now, the pervasiveness of competition is no longer accepted without question and several forms of equilibrium and nonequilibrium theory have been recognized.⁶ Results of our shrubsteppe studies remain consistent with the "ecological crunch" model,⁷ although another test of these ideas, Peter Grant's analysis of finch communities in the Galápagos Islands,⁸ demonstrated frequent competition in a highly variable environment. The major challenges posed by the paper still remain unresolved: how frequent and severe are ecological crunches; at what levels do resources become limiting; and how rapidly do population and community attributes change during the more benign periods between crunches?

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2. Andrewartha H G & Birch L C. *The distribution and abundance of animals*. Chicago, IL: University of Chicago Press, 1954. 782 p. (Cited 1,190 times.)
3. Wiens J A. Avian community ecology: an iconoclastic view. (Brush A H & Clark G A, eds.) *Perspectives in ornithology*. Cambridge, England: Cambridge University Press, 1983. p. 355-403. (Cited 40 times.)
4. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. *Condor* 76:385-400, 1974. (Cited 65 times.)
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7. Wiens J A. *The ecology of bird communities. Volume 2. Processes and variations*. Cambridge, England: Cambridge University Press, 1989. 316 p.

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