

Schoener T W. The controversy over interspecific competition. *Amer. Sci.* 70:586-95, 1982.  
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A detailed examination shows that most real communities have lower niche overlap during times of resource scarcity than abundance; this supports the argument that selection for divergent phenotypes is relatively strong and effective during the former times. [The *SCI*<sup>®</sup> indicates that this paper has been cited in more than 215 publications.]

## How Important Is Competition?

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In 1977, J.A. Wiens<sup>1</sup> published a very important paper in *American Scientist*, arguing that, much of the time, populations are well below carrying capacities; therefore the evolutionary impact of interspecific competition (e.g., selection producing character displacement) should be small. My immediate reaction was that if selection were intense enough during what Wiens called "crunch" periods, i.e., times when species were pressing their carrying capacities and competing, this could give, over the long term, patterns that were evolutionarily affected by competition; moreover, crunches may not be all that infrequent. Wiens's article inspired me to try a kind of response in the same journal, but large amounts of field work postponed this for about four years. By then, nearly all of the evidence and ideas concerning interspecific competition were being questioned, sometimes vigorously. So, I decided to do a more general treatment, covering what I considered the most important aspects of the competition controversy rather than simply the variable-environment portion. The resulting paper attempted to present all points of view, though it was inevitably colored by my "competitionist" background.

Thus, the paper was mainly a review, likely accounting in part for its frequent citation. Also contributing may have been a compilation and evaluation of studies on niche overlap during time of resource scarcity vs. plenty (extending earlier work by Smith, the Grants, and the Abbotts).<sup>2</sup> Rather impressively, organisms as diverse as insects, frogs, fishes, lizards, birds,

and mammals mostly showed less niche overlap during "lean" than "fat" times. This suggested that, specifically during lean times, strong selection resulting from interspecific competition produces in each species adaptations most suited for resources used relatively exclusively; hence, during those times, each species would manifest the relatively nonoverlapping niche to which its phenotype was best adapted. In fat times, diverse phenotypes would all find it optimal to feed on the same superabundant food types, thereby producing high niche overlap.

How were those aspects of the competition controversy I reviewed in 1982 treated subsequently in the literature? First, I concluded that mathematical theory was more diverse in its predictions than was apparently realized; this trend has continued. General mathematical theory about interspecific competition, as opposed to mechanistical theory, has not proliferated much recently; mathematical theories of all kinds continue to be largely untested. Second, the use of "null models" to aid in statistical evaluation of community patterns that, by hypothesis, result from competition was rather frequent in the mid-1980s but has now also diminished, perhaps because such studies are so data-intensive. Results were mixed, but a remarkably well-executed recent study supportive of competition is by J.L. Eldridge and D.H. Johnson<sup>3</sup> on shorebirds. Third, the question of how niche overlap relates to competition can now be seen as necessitating a "decision-tree" approach,<sup>4</sup> rather than as having a single answer. Fourth, the strength of competition was then, and continues to be, described as variable over time; P.R. Grant<sup>5</sup> showed that although selection is not continuous and is rarely intense in Galápagos finches, competition theory can still apply. A major new theory by N.J. Gotelli and W.H. Bossert<sup>6</sup> supported my conjecture that, even in rather strongly fluctuating environments, selection for character displacement can be substantial. Fifth, views on ecological interactions have become more pluralistic, logical connections between predation and competition are now more appreciated, and field experiments have often demonstrated both.<sup>7,8</sup> Investigators today seem more focused upon the details rather than the existence of competition.

1. Wiens J A. On competition and variable environments. *Amer. Sci.* 65:590-7, 1977. (Cited 455 times.) [See also: Wiens J A. Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 22(14):10, 8 April 1991.]

2. Smith J N M, Grant P R, Grant B R, Abbott I J & Abbott L K. Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* 59:1137-50, 1978.

3. Eldridge J L & Johnson D H. Size differences in migrant sandpiper flocks: ghosts in ephemeral guilds. *Oecologia* 77:433-4, 1988.

4. Schoener T W. The ecological niche. (Cherrett J M, ed.) *Ecological concepts*. London: Blackwell, 1989. p. 79-113.

5. Grant P R. Interspecific competition in fluctuating environments. (Diamond J & Case T, eds.) *Community ecology*. New York: Harper and Row, 1986. p. 175-91.

6. Gotelli N J & Bossert W H. Ecological character displacement in a variable environment. *Theor. Pop. Biol.* 39:49-62, 1991.

7. Sih A, Crowley P, McPeck M, Petranka J & Strohmeier K. Predation, competition and prey communities: a review of field experiments. *Annu. Rev. Ecol. Syst.* 16:269-311, 1985.

8. Schoener T W. Field experiments on interspecific competition. *Amer. Naturalist* 122:240-85, 1983. (Cited 365 times.) Received January 21, 1992