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This Week's Citation Classic®

Menge B A & Sutherland J P. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Amer. Naturalist* 110:351-69, 1976.
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Community structure, including species diversity, depends on both local- and large-scale factors. Within food webs, competition should control top predators, and predation should control sessile organisms. With increasing environmental variation, predation should become less and competition more important in controlling food web structure. [The *SCI*® and *SSCI*® indicate that this paper has been cited in over 265 publications.]

Predation, Competition, and Community Regulation

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In the early 1970s, whether or not community structure was determined by competition or predation was a hot topic in ecology. Bolstered by a body of elegant theory, many ecologists held that competition maintained diversity, determined distribution and abundance, and regulated differences in sizes of coexisting organisms.[1] A smaller group, citing experimental field studies, held that predation had the greater effect on community structure.[2]

In 1971 I took a position at the University of Massachusetts, Boston. One motivation for this move was the opportunity to investigate the factors controlling community structure along the rocky shores of New England. This interest was stimulated by several factors. First, my dissertation research involved a study of the population ecology of a predatory seastar living in rocky intertidal habitats in Washington State. One of my discoveries was that the small size of this beast was due in part to its losing out in competition with the much larger seastar *Pisaster ochraceus*. Thus, competition was important in structuring populations of these top predators. Second, the elegant experiments of J.H. Connell, R.T. Paine, and my fellow graduate student P.K. Dayton showed that predation had a prevasive effect on prey community structure in this same general habitat (see, for example, references 3 and 4).

Inspired by these results on the West Coast, I wondered what the relative influences of competition and predation might be on the structure of the much less diverse communities in the much more severe environments of the New England coast. My subsequent field experiments indicated that competition was much more important among prey species in New England than in the Pacific Northwest, especially on wave-exposed shores where predators were rendered ineffective by the severe conditions there. Predation was important, however, under the more benign conditions of more sheltered shores. I thus began formulating a general model of community structure, in which the relative influences of competition and predation depended on the trophic status of the species (whether consumer or prey) and on environmental variation.

I presented some of these ideas at the first East Coast Benthic Ecology meetings in 1975 at Durham, New Hampshire. There, my eventual coauthor, J.P. Sutherland of Duke University, approached me with some very similar, independently conceived ideas. We agreed to coauthor a paper and to submit it to the *American Naturalist*. We did so, and to my surprise, it was accepted rather quickly with moderate revision despite its somewhat controversial subject. Interestingly, and unbeknownst to us, Connell was also in the process of a similar synthesis, and his contribution actually preceded ours by several months.[2]

I believe that the paper has been frequently cited because it was one of the first arguments that community regulation depends on a continuum of several factors of varying relative strengths (competition, predation, *and* environmental variation) rather than a dichotomy of two factors (competition *or* predation). This view has gradually become widely accepted.[5] Sutherland and I have recently expanded the model to incorporate the roles of disturbance and recruitment and have proposed several methods by which to test it.[6]

1. **MacArthur R H.** *Geographical ecology*. New York: Harper and Row, 1972. 269 p. (Cited 1,330 times.)
2. **Connell J H.** Some mechanisms producing structure in natural communities: a model and evidence from field experiments. (Cody M L & Diamond J M, eds.) *Ecology and evolution of communities*. Cambridge, MA: Belknap Press, 1975. p. 460-90. (Cited 460 times.) [See also: **Connell J H.** Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* 19(30):16, 25 July 1988.]
3. **Paine R T.** Food web complexity and species diversity. *Amer. Naturalist* 100:65-75, 1966. (Cited 820 times.) [See also: **Paine R T.** Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 155.]
4. **Dayton P K.** Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41:351-89, 1971. (Cited 685 times.) [See also: **Dayton P K.** Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences*. Philadelphia: ISI Press, 1986. p. 156.]
5. **Diamond J & Case T J.** *Community ecology*. New York: Harper and Row, 1986. 665 p.
6. **Menge B A & Sutherland J P.** Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Amer. Naturalist* 130:730-57, 1987.

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