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Historical events are shown to influence structure in a variety of natural communities. Examples include the order of larval recruitment and the events determining the presence or absence of important consumers. Structure is then maintained by dynamic processes such as competition or predation. [The *SCI*® indicates that this paper has been cited in over 195 publications.]

Historical Events Can Influence Community Structure

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In the early 1970s, I was a new PhD, scientifically born and bred on the rocky shores of the West Coast but with a new job in North Carolina where there was little naturally occurring hard substrate. However, a diverse and interesting epibenthic community (the fouling community) grew subtidally on man-made structures such as pilings and jetties. Following in the footsteps of K.D. McDougall,[1] I decided to submerge tiles beneath the Duke University Marine Laboratory dock in order to study the process of community development. I was impressed with the degree to which tiles submerged in successive months developed entirely different assemblages, as did tiles submerged in the same months in different years. In addition, I noticed that species would settle in abundance on newly submerged tiles but not on older nearby tiles already occupied by the adults of other species. Thus, while I started out to study succession, I found little evidence for an orderly process of community development. Instead, the process seemed driven largely by the vagaries of larval recruitment and specific interactions between larvae and resident adults.

In the fall of 1972, I visited Steve Hubbell at the University of Michigan. Steve was my office-mate in graduate school at Berkeley and had invited me up to give a seminar. While discussing my results he remarked, "You're not looking at classical succession, John. You've got evidence there for alternate steady states. Here, read this paper by Lewontin[2] and see if you don't agree." Indeed, the R.C. Lewontin paper did outline the appropriate theoretical construct within which to view not only my results, but the results of many others.

I returned to Beaufort and over the next several months wrote the paper that I sent to the *American Naturalist*. Why not go for the gold? I was delighted when it was provisionally accepted (I was up for tenure), but publication was delayed because the editor, Robert Sokal, rightly insisted that I plot my results rather than place them in tables. I resisted only because I couldn't think of a way to plot percentage data that had been transformed to arcsines. I finally got the idea of transforming the y axis itself, much as is done with logarithmic plots, and the last hurdle was passed.

The basic idea was that different communities could be produced during succession by chance differences in the order of arrival of community members. Different communities could also be produced by perturbations causing "permanent" change, usually those affecting the presence or absence of important consumers. These different communities (multiple stable points, alternate stable-states, or alternative community states) persist in the face of other perturbations because of dynamic processes such as competition or predation. However, these processes do not confer resistance to all possible perturbations so communities are only conditionally stable; multiple stable points are not stable in the generic sense. To understand why the system is at a particular stable point we must know (1) the history of the order of species invasions and/or (2) the history of perturbations that cause "permanent" change. Longer term studies that include this historical component have increasingly supported this point of view.[3-6]

1. **McDougall K D.** Sessile marine invertebrates at Beaufort, North Carolina. *Ecol. Monogr.* 13:321-74, 1943. (Cited 65 times since 1945.)
2. **Lewontin R C.** The meaning of stability. (Woodwell G M & Smith H H, eds.) *Diversity and stability in ecological systems: report of symposium held May 26-28, 1969*. Upton, NY: Biology Department, Brookhaven National Laboratory, 1969. p. 13-24. (Cited 40 times.)
3. **Simenstad C A, Estes J A & Kenyon K W.** Aleuts, sea otters, and alternative stable-state communities. *Science* 200:403-11, 1978. (Cited 65 times.)
4. **Sutherland J P.** The fouling community at Beaufort, North Carolina: a study in stability. *Amer. Naturalist* 118:499-519, 1981. (Cited 35 times.)
5. **Paine R T, Castilla J C & Cancino J.** Perturbation and recovery patterns of starfish-dominated intertidal assemblages in Chile, New Zealand, and Washington State. *Amer. Naturalist* 125:679-91, 1985. (Cited 15 times.)
6. **Johnson C R & Mann K H.** Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecol. Monogr.* 58:129-54, 1988.

IA-12