RETROSPECTIVE

Joseph H. Connell (1923–2020)

Innovative experimental ecologist

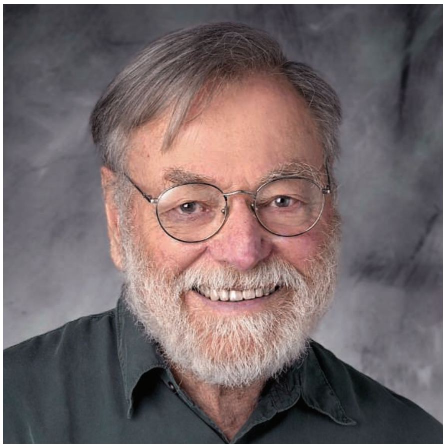
By **William W. Murdoch**[1] *and* **Wayne P. Sousa**[2]

Joseph ("Joe") H. Connell, a hugely creative ecologist, died on 1 September at the age of 96. Joe had a knack for devising simple yet rigorous ways to uncover the mechanisms behind the patterns and dynamics in natural communities. Perhaps the most influential experimental ecologist of his generation, he articulated theories explaining natural phenomena such as the maintenance of biological diversity.

Joe was born on 5 October 1923 in Gary, Indiana. After Pearl Harbor, in 1941, he enlisted in the U.S. Army Air Corps. He was sent to the University of Chicago for training in meteorology and then stationed in the Azores from 1943 to 1945 flying weather survey missions. In 1946, he completed his B.S. in meteorology at the University of Chicago, followed by an M.A. in zoology at the University of California, Berkeley, in 1953 and a Ph.D. at the University of Glasgow, United Kingdom, in 1956 under zoologist Charles Maurice Yonge. Postdoctoral research at Woods Hole Oceanographic Institution, Massachusetts, preceded his hiring in 1958 as an assistant professor by the University of California, Santa Barbara (UCSB), where he remained for the rest of his career.

Joe's groundbreaking early research led the transition of ecology from a largely descriptive to an experimental science. He addressed a ubiquitous pattern in nature: One species often abruptly replaces another along continuously changing physical gradients, such as up mountainsides. His Ph.D. research on the island of Cumbrae in Scotland investigated factors controlling such a pattern in the distribution of adults of two barnacle species in the intertidal zone on the rocky seashore. Joe conjectured that this zonation was maintained by physical competition between the barnacles for space rather than by different tolerances to physical stresses along the intertidal gradient. First, he showed that the distributions of newly settled larvae of both species overlapped broadly across the intertidal zone. He then confirmed his interspecific competition hypothesis by removing the larger, faster-growing species from small replicated plots on the mid- to low shore where it predominated; in contrast to controls, the smaller, slower-growing species in these plots survived to adulthood well outside the upper zone where its adults typically occur.

In his early Pacific coast research on San Juan Island, Washington, Joe examined two different intertidal barnacle species. Here, three species of predatory snails reduced the density of barnacles and precluded interspecific competition between them for space. Whereas larvae of the smaller species settled over much of the shore, adults were restricted to a refuge zone high on the shore, where predators were scarce. Adults of the larger barnacle species could grow large enough to be invulnerable to the snail predators, so they coexisted with snails on the mid- to low shore.



These simple yet revolutionary experiments were among the first to demonstrate the roles of interspecific competition, predation, and refuges in structuring natural communities. They are featured in every ecology textbook and have galvanized ecologists to investigate ecological patterns and processes through field experiments. They also foreshadowed extensive future investigations of the interaction between competition and predation.

At UCSB, Joe's interests turned to the immensely diverse tropical coral reefs and rainforests of Australia. He wondered how so many potentially competing species could coexist in habitats that had long been presumed to be environmentally stable. To answer this question, Joe established multiple permanent plots in forest and reef sites, where he monitored, over decades, the demography and interactions of marked or photographed individuals. Two major hypotheses emerged from these pioneering studies. The first was that recurrent disturbances can maintain species diversity by preventing local competition from progressing to completion. Joe demonstrated this by recording cyclone-induced damage and recovery on the Great Barrier Reef. The second hypothesis, elaborated for rainforests but potentially relevant to all assemblages of sessile organisms, posited that when seeds and seedlings of a particular species are locally abundant, host-specific enemies (such as herbivores and pathogens) preferentially thin those dense patches. By following the fates of individual seedlings for decades, Joe and colleagues verified this pattern of compensatory seedling mortality: Rarer species are favored over common ones, thereby helping maintain diversity.

In addition to his innovative empirical studies, Joe made enormous conceptual contributions to ecology. He wrote synthetic reviews evaluating published research on key ecological themes, and in doing so he influenced thinking on mechanisms maintaining species diversity, the role of recruitment in "open" systems, and the mechanisms causing successional changes in communities through time. The myriad honors and awards bestowed upon Joe included the Guggenheim Fellowship (twice), the Ecological Society of America's George Mercer and Eminent Ecologist awards, fellowship in the American Academy of Arts and Sciences, and membership in the Australian Academy of Science.

We both came to UCSB because Joe was there: W.W.M. in 1965 as a colleague and W.P.S. in 1973 as a graduate student. Joe was a wonderful senior colleague and adviser—supportive and never domineering. He was modest, without guile, irreverent, and hilarious. Antiauthority and antiestablishment, he was skeptical of general theories, especially if they were his own or had become dogma, until he found strong evidence or produced it himself. Joe was widely adored by his many graduate students and postdocs. As one of them observed, he enjoyed being questioned rather than worshipped and having his theories tested rather than hyped.

Joe brought to science a mind uncluttered by orthodoxy, a deep curiosity about how nature works, and a rich imagination for finding ways to satisfy that curiosity. He tackled each problem in the way that seemed to him most obvious and straightforward, yet his approaches were often surprisingly original. His research expanded our understanding of virtually all the major biological processes thought to control natural communities and inspired legions of ecologists to follow in his footsteps. ■

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