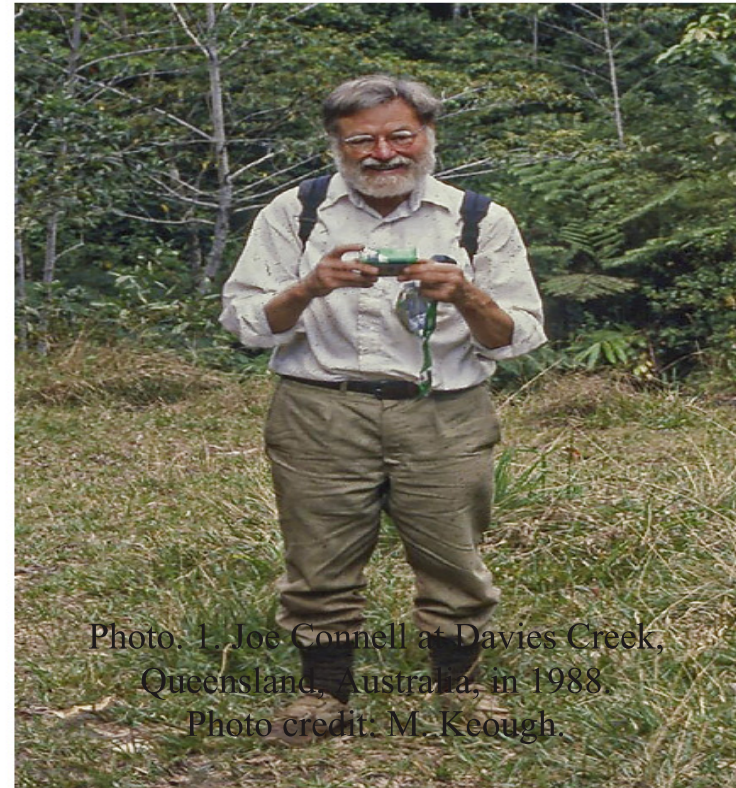


Resolution of Respect

Joseph Hurd Connell
(1923–2020)



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cused conceptual perspectives of the discipline, constructively challenged status quo paradigms, and identified important questions for future researchers.

An insatiably curious, highly creative, warmly gregarious, and wickedly funny human being, Joe enriched and forever changed the lives of hundreds of friends and scientific colleagues, not to mention literally thousands of professional ecologists and their students who studied his publications or learned about his research from the pages of every ecology textbook and many introductory biology texts. In this essay, we share and celebrate the rich history of his life and his contributions to science and its practice. Some of the personal details we include come from the invited autobiographical accounts he wrote for *Current Contents* in recognition of five papers that had been designated “Citation Classics” (Connell 1981, 1987, 1988, 1989, 1992) and a personal profile he wrote for Peter Stiling’s textbook, “Ecology: Theories and Applications” (Stiling 2002, pp. 118–119). These essays reveal a lot about his motivations and personal circumstances. Margaret Connell, Joe’s spouse, generously provided additional details and helped us complete the timelines.

His Early Life

Joe’s path to an extraordinary career in ecology was far from linear and included a rich assortment of life experiences. He was born the fifth of October 1923 in Gary, Indiana, USA, and attended a Catholic elementary school in Fort Wayne, Indiana, USA. Later, his family moved to Ellwood City, outside Pittsburg, Pennsylvania, USA, where his father was employed as an engineer in the steel manufacturing industry. Joe attended high school there. In fall 1941, he enrolled at Carnegie Institute of Technology, planning on becoming an engineer like his father. However, his life changed dramatically after the attack on Pearl Harbor and the United States’ entry into WWII in December 1941. In the following year, he joined the war effort and enlisted in the US Army Air Corps in December 1942. The Air Corps had a critical need for weather forecasters, so Joe was enrolled in a specialized training program in Meteorology at the University of Chicago (1943–1944). He was then stationed in the Azores as a commissioned officer (1944–1946) with the 1st Weather Reconnaissance Squadron, serving as meteorologist



Photo. 2. Joe and Margaret Connell at the celebration of Joe's 90th birthday in 2013. Photo credit: S. Holbrook.

The temperate zone years

Supported by funds from the GI Bill, Joe enrolled in a master's program in Zoology at UC Berkeley in 1947 and earned his MSc degree in 1953 under the supervision of wildlife biologist Dr. Aldo Starker Leopold. For his master's thesis, he set out to document the movements and home range of the brush rabbit, *Sylvilagus bachmani*, in a chaparral-grassland-dominated canyon just east of the Berkeley campus. Leopold recommended this study organism because he thought the rabbit was abundant and a potential game animal that had been little studied. As it turned out, this proved to be dubious advice. The rabbits were very difficult to capture; over the course of his 14-month study (March 1948 to May 1949), he sampled for 2251 trap nights, but caught only 40 rabbits, and several of these became "trap-happy," returning 6-14 times to the same trap (Connell 1954). Although his findings were an important contribution to our knowledge of brush rabbit natural history at that time, Joe found the project "frustrating" and the results "pretty dull" (Connell 1981, Stiling 2002, p. 118). This discouraging experience may explain why, after collecting his rabbit trapping data in 1948–1949, it was not until June 1953 that Joe filed his master's thesis. (By then, he had already started, in 1952, to collect data for his doctoral dissertation!) The serendipitous consequence of this tedious rabbit project was that Joe "vowed then to adopt a simple rule of thumb, namely, never again to study anything bigger than my thumb" (Connell 1981). This pledge and a fortuitous introduction to the little-known field experimental studies of the French marine ecologist, Harry Hatton (Hatton 1938) motivated Joe's famous study of competitive interactions between two species of barnacles on the shores of Scotland, described below. Ironically, he later immersed himself in long-term studies of corals and rain-forest trees, which spend only a small fraction of their lives at a size smaller than a human thumb. Unlike brush rabbits, however, they stay put and it is relatively easy to collect data from many of them!

Taking a needed break from research after his master's work, Joe tried his hand at secondary school teaching and taught biology for two years (1949–1951) at C. K. McClatchy Senior High School in Sacramento, California, USA. Teaching was hard work, but rewarding, and he might have continued in that profession had he not received notice that he had one year left of his GI Bill funds to use immediately or lose (Stiling 2002, p. 118). Two experiences he had while in graduate school at Berkeley were pivotal in determining his next career move (Connell 1992, Stiling 2002, p. 118–119). The first was a graduate seminar he had taken



Fig. 3. Joe Connell preparing to photograph a 1-m² plot on the coral reef flat at Heron Island, Great Barrier Reef, Australia, in 1967. The wooden frame around the quadrat reduces water surface rippling, improving the clarity of the image. Photo credit: D. Potts.

Deevey's review paper and Hatton's research greatly inspired Joe, who always gave credit where credit was due: "my career was shifted into a new direction by Hatton and Deevey, unbeknownst to them" (Connell 1992). Since Hatton had studied the effects of physical factors in controlling barnacle distributions across the tidal gradient, Joe decided to focus on the effects of biotic interactions on the same barnacle species, initially planning to investigate predation and intraspecific competition. Professor Yonge thought this an appropriate scope for Joe's PhD dissertation, and cautioned him not to take on too much (Connell 1981). Joe, however, had taken a field ecology course at Oxford University, taught by Charles Elton, which convinced him that competition between species was an important biotic interaction structuring natural communities. Disregarding his advisor's counsel, Joe surreptitiously added an experimental study of interspecific competition for space between *B. balanoides* and *C. stellatus*, species that were differentially distributed along the gradient of tidal height (Connell 1961a). Amazingly, this "side study" was not included in his dissertation, but turned into probably the most widely cited and influential study that Joe conducted. Joe surmised (Connell 1981) that this study received so much attention because there was a growing body of theory about interspecific competition, but little in the way of direct experimental tests demonstrating its influence on a natural animal population. Joe felt that the central study of his dissertation (Connell 1961b), while cited less frequently, was a more substantial and better paper. The two studies are highly complementary and employed controlled manipulations of barnacle densities, transplant experiments, and predator exclusion treatments to demonstrate the impacts of competition for space and predation on density and size structure.

Adult *C. stellatus* are most abundant on the upper shore and rare below, even though their larvae recruit over a range of lower tidal levels. Conversely, *B. balanoides* adults are densest at mid-shore to low shore levels and rare at upper levels, despite their larvae settling over much of the tidal range. Joe's experiments demonstrated that, while predation by the snail, *Thais* (= *Nucella*) *lapillus*, reduced the density of large *B. balanoides*, their preferred prey, the mortality they caused was not sufficient to prevent the faster-growing *B. balanoides* from competitively excluding *C. stellatus* from the mid-shore to low shore. When *B. balanoides* were manually removed from the mid-shore plots, *C. stellatus* survived

Joe received his PhD in Zoology from the University of Glasgow in 1956. Following a postdoctoral study at Woods Hole Oceanographic Institute (1955–1956), where he studied the spatial distribution of two species of clams, he accepted a two-year instructorship in Zoology (1956–1958) at the University of California, Santa Barbara (UCSB), and was subsequently hired as an Assistant Professor of Zoology in 1958. He spent the rest of his career at UCSB, earning tenure to Associate Professor of Zoology in 1961, and a promotion to Full Professor of Zoology in 1966. He retired in 1991 as Professor Emeritus of Zoology and held the appointment of Research Professor of Biology from 1996 to the time of his death.

When he returned to the west coast of the United States, Joe sought to test the generality of the patterns he had documented in Scotland. Soon after being appointed to the faculty at UCSB, Joe headed north to the Friday Harbor Marine Laboratories on San Juan Island off the northwest coast of Washington State, where a comparable assemblage of barnacles and their snail predators occupy the intertidal zone. Working at two sites on the shore of San Juan Island, Joe conducted a series of experiments, similar to those he had used in Scotland, to study the impact of competition for space among three species of barnacles. The interactions proved quite different in this site, where three species of predatory snails (*Thais* spp.) preyed on the barnacles, as opposed to the single species of predatory *Thais* in Scotland. Their combined impact strongly reduced the density of the most common barnacle species, *Balanus glandula*, so that competition for space among barnacle species on the low to mid-shore was insignificant (Connell 1970), a very different outcome than Joe observed in his dissertation research. This study was among the first to demonstrate that predation can mediate the intensity of interspecific competition and thereby promote the coexistence of potentially competing prey species. The site-dependent nature of the interactions that Joe documented in Scotland versus Washington State became a major conceptual theme (i.e., context-dependence) in community ecology 40 years later.

The tropical years

After being awarded tenure in 1961, Joe decided he “would strike out in a new research direction—try something new or outrageous—without worrying about whether it might cause a hiatus in my publication record” (Connell 1987). After studying relatively low-diversity temperate marine intertidal eco-

ments that Joe had so successfully used on rocky seashores to identify the mechanisms structuring those communities. Nevertheless, he and colleagues were able to conduct manipulations of avian and mammalian seed predators and litter disturbers at his forest site in North Queensland to assess their effects on seedling assemblages (Theimer et al. 2011). The major results of his tropical work, however, come from the analysis of long-term census records collected from permanent plots established on the Great Barrier Reef and in two rainforest sites in the state of Queensland. In 1962, during his first visit to Australia, Joe established replicate permanent 1-m² plots, line-intercept transects, and belt transects in several different sub-habitats across the reef on Heron Island near the southern end of the Great Barrier Reef. Changes in the 1-m² plots, including the recruitment of new colonies, were quantified from 35-mm color slides taken with an SLR camera positioned vertically over each plot during 36 visits in 26 of the 38 years between 1962 and 2000 (Fig. 3; Connell et al. 1997a, 2004, Tanner et al. 2009). A year later in 1963, Joe, working with Tracey and Webb, laid out two large permanent rainforest plots, one (1.7 ha) at Davies Creek in tropical North Queensland southwest of Cairns, and the other (1.9 ha) in subtropical South Queensland near O'Reilly's Rainforest Resort within Lamington National Park just south of Brisbane (Connell et al. 1984, Connell and Green 2000, Green et al. 2014). Seedlings and small saplings were identified, measured, and mapped within several belt transects at each location, and larger trees were individually marked and censused throughout both plots. These plots have been re-censused by teams of field assistants every few years; surviving trees are remeasured, new recruits tagged, and deaths recorded (Figs. 4–6). Through the years, literally hundreds of graduate students and postdocs "groveled" on the rainforest floor with Joe, measuring seedlings and getting leech bites as part of a ritual for aspiring field biologists. In celebration of the 50th anniversary of the establishment of these plots, Harms and Green (2014) published a description of the history and contributions of what is now known as the Connell Plots Rainforest Network. These records of community structure and dynamics may be the longest ever collected from these habitat types.

Joe immediately recognized that, to make meaningful headway in studying the mechanisms maintaining diversity in these hyper-diverse communities, he needed the expertise of skilled taxonomists to accurately distinguish the many morphologically similar species co-occurring in each habitat. In addition to being accomplished ecologists, Tracey and Webb were experts at identifying rainforest plants,



Photo. 4. Joe Connell carefully mapping a treefall gap in the Davies Creek rainforest plot in 1999. Photo credit: K. Harms.



Photo 5. Joe Connell (right) and Geoff Vico (left) censusing seedlings along a transect at the Davies Creek rainforest site in 1977. Photo credit: W. Sousa.

including their juvenile stages. Drawing on his extensive field observations and his help compiling large sets of forest survey data, Webb had published the first physiognomic structural classification of Australian rainforest vegetation in the *Journal of Ecology* in 1959. On the coral side, Dr. Carden Wallace, of James Cook University and the Museum of Tropical Queensland, provided essential help identifying corals in his plots and belt transects.

Several events raised questions in Joe's mind about the generalization that tropical communities should be considered equilibrational or "balanced" systems, tightly regulated by density or frequency-dependent biotic interactions such as interspecific competition for limited resources, predation, and disease. The first was a teatime conversation Joe had with the renowned Australian population biologist, Charles Birch, during which Joe presented his working hypothesis of stable, tightly regulated tropical communities. Birch replied: "Fine, but also keep your eyes open for tropical weather up in Queensland—some of those cyclones might shake things up a bit" (Connell 1987). The second event that challenged his assumption was in fact the impact of a severe cyclone that passed over both Heron Island and one of his rainforest plots in 1967, causing considerable damage (Connell et al. 1997a, 2004). At that time, many researchers considered these episodes rare, annoying events that "wrecked my study," rather than drivers of community dynamics whose effects might not be recognized without long-term monitoring



Photo 6. Davies Creek rainforest plot census crew in 1977. Photo credit: Wrasche

studies. Joe subsequently broadened his view of the possible mechanisms that could maintain diversity in these systems to include disturbance.

Joe's detailed coral and rainforest studies yielded novel insights into the processes that maintain the extraordinary levels of species diversity in these two tropical ecosystems. The studies challenged the long-standing view that these were equilibrial assemblages of tightly co-evolved species. From his 38-year record of changes in the coral system (Connell et al. 1997a, 2004, Tanner et al. 2009), Joe documented the damage caused by multiple cyclones and subsequent patterns of recovery. Large storm waves associated with these storms battered the reef, breaking and displacing colonies, while shifting sediments harmfully abraded them. Partial or complete death and displacement of colonies opened space for new recruits; competitively dominant species were knocked back and recolonization by competitively inferior species enriched the coral assemblage. This episodic reset of coral assemblages to a younger, more diverse state by disturbances of intermediate frequency and intensity as a general mechanism by which diversity is maintained is what Joe called the "Intermediate Disturbance Hypothesis" (Connell 1978).

In the Queensland rainforests, a different story emerged. When storms and other natural disturbances damaged or killed trees (Connell et al. 1997b), they opened light gaps that enhanced local recruitment

Joe's empirical findings and conceptual writings forever changed the science of ecology. With a well-deserved nod to his little-known predecessor Harry Hatton, Joe deserves credit for introducing and popularizing the use of controlled, replicated experiments to investigate ecological hypotheses in nature. One measure of the impact of his work on the discipline is how heavily his papers have been referenced by other scientists: 11 papers or book chapters have been cited over 1,000 times each. To date, these 11 papers combined have been cited 32,136 times!

Joe also made major contributions to the growth of ecological theory and concepts by writing highly synthetic and critical reviews that evaluated published research results pertinent to key ecological phenomena. Especially impactful reviews addressed the role of natural enemies in preventing competitive exclusion (Connell 1971), community interactions on rocky intertidal shores (Connell 1972), shifts in species interactions along environmental gradients (Connell 1975), mechanisms of ecological succession (Connell and Slatyer 1977), hypotheses explaining the maintenance of high diversity in tropical communities (Connell 1978), the prevalence and relative importance of interspecific competition (Connell 1983), and the evidence needed to judge ecological stability and persistence (Connell and Sousa 1983). Each of these reviews has been cited more than 1,000 times to date, with the succession paper receiving more than 5,200 citations and the tropical diversity paper receiving more than 11,600!

Ironically, while Joe provided perhaps the most famous demonstration that interspecific competition can shape community structure and species distributions, he also actively challenged the notion that it was the overriding and ubiquitous factor structuring communities. Several of his reviews questioned this prevailing perspective (Connell 1980, 1983) and provoked those invested in the "competition" paradigm.

In the arena of applied ecology, Joe served as inaugural Chair of the Marine Review Committee (1974–1990), which was charged by the California Coastal Commission with assessment of the environmental impacts of the San Onofre Nuclear Power Plant on the coast of southern California.

also highly egalitarian in his interactions with students and colleagues, especially when it came to seeking critical comments on his manuscripts. He would relentlessly pepper colleagues and students with multiple drafts of every paper he wrote. He carefully considered every comment, no matter whether it came from an undergrad or a full professor. If something was unclear, it was his fault, not the reader's. He worked hard to clearly communicate his results and conceptual ideas in his writing,

Joe as Mentor, Colleague, and Friend

Joe gave his graduate students a lot of freedom in their choice of study organisms and field sites. He mostly cared that the questions and hypotheses were clearly stated and testable and that the findings would make a novel and valuable contribution to our understanding of the natural world. Of his 18 PhD and 2 MA thesis students, 12 worked in marine rocky intertidal habitats, two in marine soft-sediment environments, two in subtidal kelp forests, one in chaparral shrubland, one studied salmon in aquatic habitats, one studied terrestrial snails, and one studied stream flatworms.

Fifteen postdoctoral researchers worked with Joe. Most collaborated on data collection, data analysis, or manuscript writing associated with either his coral reef or rainforest study. Several were involved with assessment of the potential impacts of the San Onofre Nuclear Power Plant. Others pursued their own research projects. Joe considered them peers and their collaboration greatly enhanced and expedited the analysis and publication of some of his most important research results.

Joe gave detailed feedback on his students' work. When he finished working over their papers, the bath of red ink could be visually and psychologically jarring, but the feedback always resulted in a clearer exposition of ideas. Some of his most frequent corrections were marked "No NUAs" (nouns used as adjectives) or "EUW" (eliminate unnecessary words), mixed with a few good-natured curse words. Learning to accept constructive criticism was a key part of his regimen of scientific training.

He was so committed to the value of scientific data that he actually wrote up and published the dissertation chapters of two of his PhD students who were unable to do so, assigning himself second authorship.



Photo. 7. Lunchtime break for the 1977 census crew at Davies Creek. Note the classic Australian billycan in left foreground. Photo credit: W. Sousa.

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