# Perspectives

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# A keystone ecologist: Robert Treat Paine, 1933–2016

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Robert T. Paine with an ochre star, *Pisaster ochraceus*. Photo taken on 17 January 2016, Santa Cruz, California, USA. Courtesy of Amy Miller.

*Abstract*. Robert T. Paine, who passed away on 13 June 2016, is among the most influential people in the history of ecology. Paine was an experimentalist, a theoretician, a practitioner, and proponent of the "ecology of place," and a deep believer in the importance of natural history to ecological understanding. His scientific legacy grew from the discovery of a link

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between top-down forcing and species diversity, a breakthrough that led to the ideas of both keystone species and trophic cascades, and to our early understanding of the mosaic nature of biological communities, causes of zonation across physical gradients, and the intermediate-disturbance hypothesis of species diversity. Paine's influence as a mentor was equally important to the growth of ecological thinking, natural resource conservation, and policy. He served ecology as an Ecological Society of America president, an editor of the Society's journals, a member of and contributor to the National Academy of Sciences and the National Research Council, and an in-demand advisor to various state and federal agencies. Paine's broad interests, enthusiasm, charisma, and humor deeply affected our lives and the lives of so many others.

*Key words: intermediate disturbance; keystone species; mentor; patch dynamics; tribute to life; trophic cascade; zonation.*



This year marks the 50th anniversary of Robert T. Paine's most cited paper (Paine 1966), a startling breakthrough that put the science of ecology on a new course. It was also the last year of his remarkable life. Paine was among the most influential ecologists of all time, in part for his scientific contributions, in part for his mentoring skills, and in part for his personality and character. From his frenetic work ethic in the field to his love of ecological concepts, working with Paine was a combination of spartan field conditions, bold experiments about new ideas, and deep respect for the privilege of having NSF (United States National Science Foundation) funding for his research. There were no extravagances, except when it came to ideas.

As a graduate student in Frederick E. Smith's lab at the University of Michigan during the mid to late 1950s, Paine was strongly influenced by Hairston et al.'s (1960) Green-World Hypothesis (which, at the time, was just taking form) and by the ongoing quest to understand ecological drivers of species diversity (Hutchinson 1959; Smith was a student of G. E. Hutchinson). Paine's spark of inspiration was to link the two ideas, that "top-down" effects (*á la* HSS) might influence species diversity. A second realization, likely influenced by Joe Connell's (1961*a*, *b*) experimental studies, was that the most powerful approach to test these ideas was to manipulate the system. Paine joined the Zoology Department at the University of Washington as a new assistant professor in 1962 and soon thereafter began searching out field sites for teaching and research. From his initial observations of the rocky intertidal community on Washington's spectacularly diverse outer coast, Paine recognized that *Pisaster ochraceus* (a large, predatory, sea star) fed extensively on mussels (*Mytilus californianus*) as part of a diverse diet including barnacles, limpets, chitons, and snails in a system that supported numerous invertebrate and algal species.

Paine's synthesis of nascent ideas and field observations led to his now-famous *Pisaster* removal experiment, begun in 1963. The experimental design was elegantly simple, but the results revolutionary. To determine the degree to which *Pisaster* influenced the distribution and abundance of species, Paine chose two similar stretches of rocky shoreline, removed *Pisaster* from one of these (via a long-term "press" perturbation), and left the other as an unmanipulated control. In the absence of *Pisaster*, mussels (*Pisaster*'s preferred prey and the system's dominant space competitor) expanded their range downward on the shore, overgrowing or crowding out algae, barnacles, and other low intertidal species as the system changed to a near-monoculture of mussels. The original experiment at Makah Bay was later repeated on Tatoosh Island with similar results.

Paine's 1966 paper had a strong and lasting influence on ecology. The paper was one of the early demonstrations that experimentation was not limited to the laboratory, but could provide powerful insights in field settings, thereby helping establish ecology as an experimental science. Ecologists had done experiments before, primarily in the laboratory, but most of those experiments failed to address such topical and forward-thinking conceptual issues. The paper also advocated a role for predation and top-down forcing in the regulation of local species diversity, a concept later termed the "predation hypothesis." Here again, Paine was not the first to recognize a defining role for predation. Such insights traced back at least a century to Darwin's (1859) account of the interplay among cats, mice, bees, and clover in the English countryside. The ecological importance of predators was reinforced through famous books by Charles Elton (*Animal Ecology*; Elton 1927) and Paul Errington (*Of Predation and Life*; Errington 1967), and by Aldo Leopold's conclusion that the removal of wolves and other large predators led to irruptions of deer and the decline of plants across much of the United States during the 1930s and 1940s (Leopold et al. 1947). Despite the prominence of these authors, the notion of top-down control evidently did not resonate deeply with the ecological community. Although it took several years, Paine's 1966 paper propelled this idea into the intellectual fabric of ecology. Finally, Paine (1966) was the first to establish (albeit implicitly) the importance of indirect effects (indirect interactions between two species are those that involve one or more intervening species) in food web dynamics. Publication of this paper was a watershed moment for ecology.

A number of other important elements of ecology's lexicon and conceptual infrastructure grew from Paine's work and his views of nature. One was the idea of *keystone species* (Paine 1969), a "repurposed" term reflecting the idea that the influence of certain individual species can be so great as to hold their ecosystems together, much as a keystone prevents an arch from collapsing. Both the idea and the term took hold, but eventually the term was applied so broadly that its usefulness was questioned. In response to this broad but loosely applied usage in the scientific and popular literature, Power et al. (1996) formally defined keystones as "species that are relatively rare but have disproportionately large effects on their associated ecosystems." Many ecologists now see deep truth in this view of nature. The keystone species concept provided an alternative hypothesis to the predominant view in the mid 1960s: that diversity was determined by competition-driven coexistence. Robert MacArthur, a strong proponent of the view that competition determined community structure, immediately realized the importance of Paine (1966): three months after its publication, he reportedly wrote Paine a letter saying "This changes everything" (Roberts 2016).

A second important term to emerge from Paine's work and thinking is that of the *trophic cascade*, introduced in his 1979 Tansley Lecture to the British Ecological Society (Paine 1980). By his own admission, this term was born "out of desperation" (Paine 2010:23). Although he did not explain the nature of that desperation in detail, those of us who knew him well understand that it was motivated by at least four factors. First, he felt a need to provide a contrast to the strong bottom-up view that had come to prevail in many circles of ecology. Second, the term elegantly described the findings of his experimental studies, namely the indirect influences of *Pisaster* predation in rocky intertidal communities. Third, it called attention to the growing number of case studies of other species and ecosystems in which similar patterns and processes were being demonstrated. And fourth, it helped emphasize his realization that indirect effects were pervasive in nature. In addition to trophic cascades, Paine's Tansley Lecture emphasized the importance of understanding the topology of trophic webs, and the notion that those webs contain modules of tightly interacting species that interact more weakly with other modules. These latter concepts also became focal research areas for sub-disciplines of ecology.

Keystone species and trophic cascades are only a part of Paine's conceptual legacy. Many of his writings also emphasized his view of biological communities as mosaics of patches in different stages of succession. The concept of patch dynamics, anticipated in A. S. Watt's 1947 Tansley Lecture, married MacArthur and Wilson's equilibrium theory of island biogeography with Levins' metapopulation framework. The result was a non-equilibrium theory that captured the dynamics of the mosaic of intertidal landscapes (Levin and Paine 1974) and complemented an emerging view in other systems (Bormann and Likens 1979).

Paine's insight from his intertidal work joined with Connell's (1961*a*, *b*) findings to upend the classical notions of causes of zonation, or bands of species occurring at different places along an environmental gradient. The principal paradigm was that physiological tolerances determined the spatial locations of species. Species low on the shore (or at lower altitudes on a mountain side) were thought to be best suited to those specific environmental conditions, whereas species higher on the shore (or mountain side) were considered better suited to the different physical conditions in those places. Paine's demonstration that mussels readily invaded downwards following removal of their predator, *Pisaster*, combined with Connell's experiments demonstrating that predation and competition set lower limits of barnacles, challenged this existing paradigm. The faster growth of mussels and barnacles that colonized the lower intertidal suggested that this sub-habitat was actually better from a physiological point of view than the midshore, and led to the revelation that biological factors controlled the lower limits of these species. Subsequent work in many systems has shown that both biotic and abiotic factors, acting alone or together, can determine local distribution and range limits of species.

Finally, Paine and his collaborators recognized that predation could have effects comparable to those of other kinds of disturbance—wave damage on rocky shores or treefall in forests, for instance—which reset a successional process. Paine and Vadas (1969) expanded this hypothesis to sea urchin herbivory of algae. The general idea, which postulated that local diversity was maximized at intermediate levels of predation (Paine 1977), complemented the views of Connell (1978) and Janzen (1970), who independently proposed the intermediate disturbance hypothesis. The intermediate disturbance hypothesis eventually became another ecological paradigm that has weathered the test of time.

The collective influence of Paine's early field studies and the ideas they spawned in his then-developing view of ecology have been monumentally important over the past half century. Despite the runaway usage of *keystone species* in the 1970s and 1980s, Paine's (1969) use of the term conveys a fundamental truth about natural systems that continues to structure our thinking. All species surely are not keystones, but keystone species are just as surely widespread in nature. Despite some bantering of meaning and usage, the same can be said of *trophic cascades*. Seventeen years ago, Pace et al. (1999) surveyed the evidence and declared that trophic cascades occur in diverse ecosystems. That view, and its powerful implications for natural resource conservation and management, has continued to gain force (Schmitz et al. 2000, Shurin et al. 2002, Borer et al. 2005). Similarly, patch dynamics has become a central concept in the study of communities and ecosystems, and ecologists' notions of causes of zonation have evolved to include biological and physical factors. It would be difficult to imagine any introductory ecology class in which students weren't exposed to keystone species, trophic cascades, patch dynamics, zonation, and the intermediate disturbance hypothesis. From the perspective of his contributions to ecology, Paine was both a keystone and a foundation thinker.

Paine's forceful influence on ecology came not only from his own research and thinking, but also through his mentoring and the many important contributions by his students and others that he unselfishly helped along the way. Spending so much time with students and colleagues at his beloved field site, Tatoosh Island, triggered interactions that included not only prolonged debate of ecological ideas, but also practical knowledge of field research methods. The Paine tribe is famous for their ingenious, sometimes amusing, devices for enclosing or excluding species and manipulating environmental conditions, many of which were inexpensive items scrounged from grocery, hardware, and variety stores: "What can I do with this dog dish?" In addition, Paine's commitment to long-term study of this one remarkable site led to deep understanding of annual to multi-decadal scale changes in biota and their environment, and instilled in his students a deep knowledge and respect for natural history as bedrock for ecology practiced in the real world. Paine tested the generality of his discoveries in the intertidal zones of Chile, New Zealand, and other sites around the world, but he returned always to Tatoosh, where his irrevocable sense of place produced insights that apply in terrestrial, freshwater, and marine communities worldwide. Paine never stopped doing science, and was working until the end on several papers, including a project on the dispersal of spores of the seaweed *Postelsia* that was three decades in the making.

Paine's mentoring and teaching at the undergraduate level, at the University of Washington and around the world, were equally influential and legendary. His undergraduate "Principles of Ecology" class at the University of Wisconsin moved deftly between natural history observations from the 1920s to the latest mathematical papers, often enriched with a personal anecdote or cartoon (these were the days of overhead projectors and transparencies). Many students became ecologists and went on to graduate school because of Paine. Teaching with Paine in this course was like trying to keep up with a master of jazz improvisation. When it worked the students were dazzled, and even when it didn't, the class was never boring. Because he knew the literature so deeply and broadly, Paine had no rival in synthesizing dozens of different research threads into one theme. In talking about his own experiments, his enthusiasm was electric; and in talking about the field research of others, he would often remark, "it must have been a great adventure." Teaching was an adventure for Paine, as was everything.

Among the far-flung places Paine visited to do research, teach, or give seminars, he returned time and again to Chile. And his influence on Chilean ecology has been significant. The power of his ideas and his personality got students' attention, but his enthusiasm for exploring new shores and learning the natural history, ecology, culture, and history of a new place was infectious. The similarities and differences between the coasts of Chile and the U.S. Pacific Northwest triggered wide-ranging discussions that had a lasting impact on students' trajectories and science.

As of 2013, Paine's academic family included no fewer than 325 direct and extended offspring (Yong 2013), many of whom have risen to positions of influence in their own right and have trained their own students the same way they were mentored. Some of these people have continued to study the workings of rocky intertidal communities. Others have found their ways through scientific studies of other species and ecosystems. Still others have carried Paine's legacy into the policy arena where they have endeavored to impart a sense of truth and excellence in natural resource conservation and management. The list is too long to recount and any attempt to do so would necessarily shortchange the accomplishments of many.

Paine's influence on ecology is felt not only through his scientific contributions and the contributions of those he has mentored, but to an important degree because of his manner and character. Many of us who knew him as students and young scientists came to appreciate his sometimes brash proclamations and well known proclivity for not suffering fools lightly. But beneath this tough exterior was warmth, concern, and humor, all generously shared with those of worthy minds, motivations, and abilities to withstand a little honest criticism. His charisma was on stage at the 2015 (centennial) meeting of the Ecological Society of America, where Paine was frequently seen in the halls, surrounded by throngs of students, joyfully bantering and discussing whatever topics came up.

Paine had a profound love for nature, for ecology, and for the discipline that led him not only to follow his own path, but to encourage and inspire complementary approaches by others. He was in no sense a mathematician, though mathematics was in his Birkhoff genes on his mother's side. Yet he was a great theoretician, and recognized the importance of developing mathematical formalisms that allowed exploration of his theoretical ideas. His students and collaborators found working with Paine to be a wonderful and critical exchange of perspectives, almost always converging on something fresh and new. Paine served nature, ecology, and society through leadership roles in the Ecological Society of America and committees of the National Academy of Sciences and governmental agencies.

No tribute to Paine's life would be complete without brief mention of his passions outside the realm of ecology. He was a devoted father to his three daughters, and they in turn loved and revered him. A Bostonian by birth, he was a life-long Red Sox fan who reveled joyfully after the 2004 season that broke the 86-year-old "Curse of the Bambino." He maintained a vegetable garden in the backyard of his Seattle home and never seemed to tire of discussing his love of the produce and his secrets to successful gardening. Paine was deeply competitive by nature. Nowhere was this spirit more evident than in his unending mission to find the largest glass fishing float while prowling some remote shoreline, or in his quest to catch the biggest salmon. On one memorable occasion, Paine responded to a photograph one of us sent him of a 40-plus-pound chinook with just two words, "game hog."

To all who knew Paine, perhaps the most endearing memory is his great sense of humanity, compassion, and, above all, his immediate and wonderful sense of humor. He had a unique ability to find something funny in any situation. The defining characteristic of the clusters of people who always surrounded him was that they were always laughing. This was a very rare and important gift.

Robert T. Paine was a great ecologist and a great human being. We will miss him. But no life is forever and his was a life well lived. We are enriched by his gift to ecology, and from the gift of having known him.


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