Robert Treat Paine III (1933–2016)

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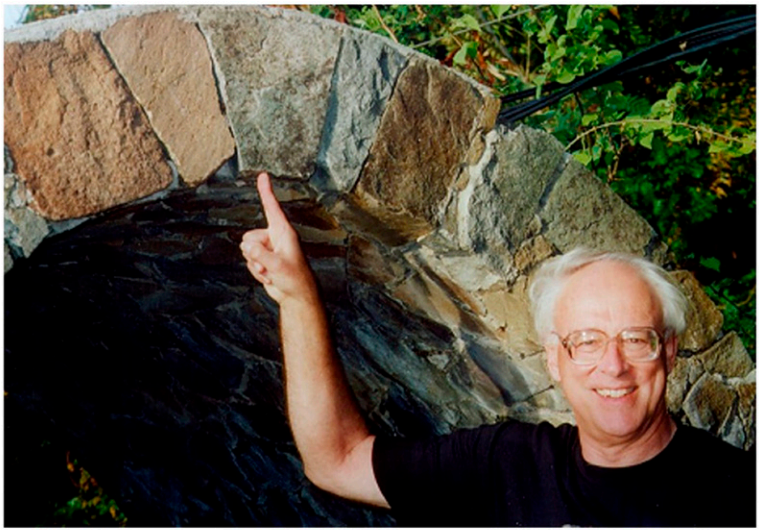
Robert Treat Paine III passed away June 13 in Seattle surrounded by family and friends. RTP, as he was known, was an emeritus Professor at the University of Washington, where he developed a career that helped define the field of community ecology. Ever an avid naturalist who paid close attention to the specifics of a bird song or a starfish's diet, RTP's best-known contributions were the concepts of keystone species and trophic cascades. Keystone species have effects on communities or ecosystems that are much larger than their abundances would suggest. Trophic cascades are the many changes in species diversity or abundance that ensue when a consumer is removed from an ecosystem (see ref. 1 for a more detailed synopsis). RTP was also well-known as a champion of the use of experimental methods in field ecology, helping to show that simple experiments in complex natural communities could reveal a wealth of information about how species interacted with one another. Another enduring dimension of his legacy was his mentoring and inspiration of several generations of graduate students and postdocorates in the adventure of working out the complex wiring of species interactions, all within the wild dynamics of natural ecosystems.

RTP was a descendent of a celebrated clan in Boston that included Thomas Paine and Robert Treat Paine Sr., a signer of the US Declaration of Independence, as well as the great mathematician George Birkhoff. RTP grew up in Boston as an avid naturalist and bird watcher, and attended Harvard. His initial graduate work was in paleontology at the University of Michigan, but he became fascinated by ecology in courses led by ecologist Fred Smith, so ended up doing an ecological study of a modern-day brachiopod. After a postdoctorate at The Scripps Research Institute in San Diego, California, he took a faculty position at the University of Washington, where he began working on the complex invertebrate communities of the highly productive and species-rich northeastern Pacific intertidal zone.

In the welter of the interactions of hundreds of species, RTP focused on predator–prey interactions, charting out the species that were consumed by others.



Robert Treat Paine III. Image courtesy of Robert Steneck (University of Maine, Orono, ME).

In this, RTP found a simple metric for predation by a large abundant species: By turning over purple sea stars, he could record the diets of hundreds of individuals. This led to a simple question about the impact of predation on intertidal communities, which RTP studied by experimentally manipulating densities of purple sea stars along rocky shores. The fundamental changes in communities without stars focused RTP on the role of predators controlling community composition. Some species could be removed without huge effect. Others were key to community composition, and without them the communities collapsed. From this realization, RTP used the analogy of a keystone—the central shaped stone holding up an arch—to describe the importance of keystone predators. In a short note published early in 1969, RTP coined a term that has since become intrinsic to the lexicon of ecology (2).

RTP's gift was to take a simple field experiment on marine invertebrates and turn it into a broad lesson in ecological organization that struck a chord across

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almost all ecosystems. Adoption of the idea came very quickly. Early adopters of RTP's 1966 paper on the control of diversity by predators (3) included famous papers from 1966 and 1967 on species diversity gradients (4) and the limits of similarity between species (5). As a result, the concept of keystone species is one of the simplest, yet most fundamental, in community ecology.

The idea of trophic cascades was presented in the Tansley Lecture to the British Ecological Society (6). Here, RTP focused on the stability of ecosystems with hundreds of species or more, after perturbation of one or a few top predators or grazers. The parade of studies discussed in this paper painted a heuristic model of the eddies of ecological interaction in the sea of species. Again, some species were dramatically more important than others in maintaining ecosystem stability. And once the keystone species were perturbed, dramatic changes cascaded down the food web. This concept has found strong support across many ecosystems, and over the ensuing decades has focused attention of the role of humans in controlling diversity, abundance, and productivity (7).

One of RTP's gifts was to marry patterns of species abundance with the results of field manipulations, and discern ecological processes that transcended his focal taxa or community. In addition to food web theory, these experiments focused on the role of disturbance and patch size on diversity, interaction strengths and their importance to community stability, the role of predation in controlling primary production, causes of zonation along physical gradients, and many more insights. RTP worked intently with mathematicians to turn his intuition about ecological process into well-tested theory, but also returned the favor by helping them to savor the messy details of fieldwork.

The dual themes of experimental ecology and process-oriented ecology were to be the hallmark of RTP's subsequent academic contributions. RTP taught that great ecological insight could grow out of observing pattern (in the field) and discerning process (experimentally). But along the way he used his gift for conducting experiments in remote field settings to train, inspire, and befriend a Who's Who of community ecologists: graduate students, undergraduates, postdoctorates, collaborators, and artists. RTP established a long-term research site at Tatoosh Island in Washington, in collaboration with the local Makah Native Americans. The wilderness location without power or running water was nevertheless RTP's home nearly every low tide all summer for decades. And there was a bevy of students, researchers, and visitors clamoring for the honor of being included in a Tatoosh Trip. There, the work of starting, monitoring, and maintaining various intertidal experiments intersected with long conversations about natural history, community ecology, and the more prosaic business of camp housekeeping in the perpetual fog of the outer coast of Washington. This university on the rocks produced a steady stream of papers, doctorates, inspiration, and an academic genealogy that spans ecology, evolution, invertebrate biology, mathematical biology, and environmental biology. Sometimes students learned the experimental method too well, as when a group of us (who hardly knew one bird from another) decided to conduct an experiment on whether RTP could indeed identify birds only by their songs, as he boisterously claimed. Late one evening, we snuck away from our camp and played the sound of a bird known strictly to be from the United States east coast. RTP bounded off his chair and raced into the bush toward the tape player, yelling "Chuck-will's widow!"—proving both his complete command of bird watching detail and the value of a good, well-placed experiment.

Throughout his career, RTP emphasized the importance of his work to basic ecology; but he was equally concerned with the impact of humans on biodiversity, and contributed substantially to preserving the planet's resources through service to the Ecological Society of America, the National Academy of Sciences, and government agencies. Indeed, RTP was chosen as the Chair—and performed exceptionally effectively—of the National Oceanic and Atmospheric Administration Fisheries' Salmon Recovery Science Review Panel, as well as other committees assessing environmental impacts.

Robert Treat Paine III was one of the great ecologists of history, whose legacy through research and mentoring reshaped the discipline, and helped it evolve from descriptive natural history to an experimental and quantitative science. RTP maintained his devotion to his daughters and his gardens and his friends and always assumed that everyone and everything would be a delicate tangle of interactions and effects. He has left many strong interactions behind, and a cascade of admiration for his contributions to our science and our lives.

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