Robert Treat Paine

(1933–2016)

Ecologist who established concept of keystone species.

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In the 1960s, ecology was dominated by descriptions of patterns in nature and assertions that these patterns were determined by physiological tolerances, energy flows through ecosystems or competition among similar species.

Robert Treat Paine changed the field's course with a simple experiment. He removed ochre starfish (*Pisaster ochraceus*) from a seashore in Washington state, revealing that a single predator could control the abundance, diversity and distribution of other organisms sharing its ecosystem. Thus was born Paine's concept of a 'keystone species' — one that influences most of the other species in its community, just as the wedge-shaped stone at the top of an arch holds the structure in place.

Paine, who died on 13 June, was born in Cambridge, Massachusetts, in 1933; his mother was a photographer and writer, his father an art historian. As a boy, he spent hours exploring the woods, acquiring a feel for the rhythms of nature and honing his powers of observation.

Paine developed a passion for palaeontology as an undergraduate at Harvard University in Cambridge. But his plan to study fossils as a graduate — at the University of Michigan in Ann Arbor — was derailed after he started attending classes taught by ecologist Frederick E. Smith. Smith was unafraid to ask provocative questions about patterns in nature. Switching to ecology, Paine studied a living fossil: a species of lamp shell, or brachiopod, for his 1961 PhD.

Following a postdoctoral fellowship at the Scripps Institution of Oceanography in La Jolla, California, in 1962, Paine joined the zoology faculty at the University of Washington in Seattle. There he conducted his now-classic starfish experiments, developed other transformative ideas and established a dynasty of experimental ecologists up to and beyond his official retirement 36 years later.

Paine's studies at Michigan coincided with the development of an avant garde idea in ecology. Challenging conventional wisdom that the availability of prey regulated predators, the zoology faculty troika of Smith and his colleagues Nelson Hairston and Lawrence Slobodkin proposed in 1960 the 'green world hypothesis'. In their view, the world was green because herbivores, who could otherwise consume all plant (green) matter, were regulated by their predators (N. G. Hairston *et al. Am. Nat.* **94,** 421–425; 1960). The paper attracted considerable attention, but like all conceptual and most field ecology at the time, lacked solid field evidence.

Enter Paine's starfish. Paine demonstrated conclusively that, at least on one rocky shore, the top predator both controlled its prey and affected most of the other species in the community (R. T. Paine *Am. Nat.* **100,** 65–75; 1966). The ochre starfish is a generalist predator, consuming barnacles, snails, limpets and more. Its favourite food is the California mussel — the dominant competitor for space on the rocks. By controlling mussel numbers, starfish enable a wide diversity of species to co-exist, including other prey species, and an array of seaweeds, sponges and anemones that the starfish do not consume. When Paine removed the stars from the system, mussels quickly crowded out other species. Comparable dynamics were later demonstrated for keystone species in other marine, terrestrial and freshwater ecosystems.

Paine expanded these ideas to include the concept of 'trophic cascades' — the rippling through a community of strong, top-down effects that affect multiple ecosystem levels and species. These ideas upended established theories about the dominance of 'bottom-up' effects, such as those mediated by changes in rainfall or nutrients. Experimental evidence is hard to argue against, and it was clear from Paine's experiments that single species could matter.

His findings had a major effect on conservation. Sharks, for example, are now understood to have key roles in controlling the distribution, abundance and diversity of many species in ocean ecosystems.

Paine delighted in romping around the rocky intertidal zone, especially at his long-term study site on Tatoosh Island off the Olympic peninsula of Washington. He was in his element in the field — steering his outboard motor boat through swells, navigating his two-metre frame over slippery algae, hauling supplies up steep cliff faces, peppering everyone with observations, and generally outpacing students decades younger than him. He also took intense pleasure in devising ways to adapt hardware supplies to manipulate the abundance of species with different characteristics. A home-made fence or cage had to achieve its intended ecological purpose as well as withstand pounding waves and storm surges of a not-so-pacific ocean.

Bob's legacy is defined by his charisma and his brilliant mentoring of generations of ecologists, as much as by his research. He kindled curiosity, independent thinking and a willingness to observe closely and then manipulate nature to discern her secrets. Even after retiring, Bob actively supported his ever-expanding family of academic (as well as biological) children, grandchildren and great-grandchildren.

Now recognized as one of the greatest ecologists in history, Bob was not afraid to be provocative, but understood that what mattered were results — especially experimental ones. His towering stature easily intimidated students until they spent time with him and discovered an encouraging and inspiring mentor and often a friend.

Even early on, another giant in ecology, Robert MacArthur, who in the 1960s had championed the importance of competition in structuring ecological communities, understood how profound Bob's keystone-species findings were. Writing to him three months after the initial starfish results were published, MacArthur stated simply: "This changes everything." And so it did. ■

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