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Edward O. Wilson (1929-2021)

Naturalist, synthesizer and conservation champion.

Professor Edward O. Wilson, who died on 26 December 2021 at the age of 92, was one of the leading biologists of the twentieth and twenty-first centuries. His contributions to science were wide ranging, including theories to explain biological diversity, establishing the evolutionary underpinnings of social behaviour and advocating powerfully for conservation. His accessible writing extended his impact far beyond academia and inspired countless readers to follow a career in science. He did this while always retaining the kindness and generosity of a true 'southern gentleman'.

Growing up among the woods and bayous of Alabama, Wilson's passion for the natural world arose early. However, his broad interest in natural history was dramatically circumscribed when he was just seven: a fishing accident resulted in the loss of vision in one eye. Wilson noted that the other eye had enhanced acuity, which helped him to specialize on the "the little things that run the world". He began his first insect collection at the age of 9, and at 13, he reported to state authorities the first US colonies of the invasive red imported fire ant (*Solenopsis invicta*).

Wilson gained undergraduate and master's degrees from the University of Alabama. He was poised for a PhD at the University of Tennessee before diverting to Harvard, encouraged by correspondence with William L. Brown Jr, a fellow myrmecologist and curatorial assistant in the Museum of Comparative Zoology at Harvard University. He completed his PhD there in 1955, and married the love of his life, Irene 'Renee' Kelley, the same year. After graduation Wilson joined the Harvard faculty, which he served for 41 years until he retired in 1996; even then he was an unusually active emeritus member for another 25 years.

As a graduate student, Wilson was elected to the Harvard Society of Fellows, a small but intense group of scholars drawn from all disciplines across the university who gather each week to discuss their work. The society played a formative role in cultivating his cross-disciplinary thinking as well as funding his exploration of the natural world, including a year-long expedition to study ants on islands throughout Melanesia. This experience provided first-hand empirical evidence to fuel his understanding of how new species are formed, and helped to



Credit: Andrew Berry

generate a series of significant publications including a paper on character displacement with Bill Brown (*System. Zool.* 5, 49–64; 1956) describing how species with overlapping ranges typically differ most distinctively from each other in the region of overlap, and another on the taxon cycle (*Am. Nat.* 95, 169–193; 1961) describing how colonizing species frequently undergo cycles of range expansion and contraction, often associated with shifts in ecological distribution.

Wilson was fond of explaining to students that biologists fall along a spectrum. At one extreme is a student with a passion for a group of organisms, such as ants, whose goal is to learn everything possible about ants and build a career around ants. At the other extreme is a student with a passion for theory, whose goal is to find the perfect system with which to test hypotheses. Wilson pointed out that these complementary approaches to studying the natural world are necessary and sufficient, but work best together, and he celebrated both the empiricists and the theoreticians.

Wilson himself traversed both ends of this spectrum. He was a world authority on ants and social insects in general, and yet he never lost sight of the big picture, repeatedly marshalling enormous amounts of data to test hypotheses, many of them grand and unifying. A scan of his publications, which include more than 400 research papers and 30 books, illustrates this pattern: *The Theory of Island Biogeography* with Robert MacArthur (1967) remains one of the most influential books in population biology; The Insect Societies (1971) is the standard work on the subject; and Sociobiology: The New Synthesis (1975) is perhaps the most influential book on animal behaviour and behavioural ecology ever written. Wilson won two Pulitzer Prizes, for On Human Nature (1979) and The Ants (1990), with his long-time collaborator and friend, Bert Hölldobler. Wilson's double embrace of theory and empiricism is well illustrated by the contrast between Biophilia (1984) on the vital importance of the natural world to human health, and Pheidole in the New World: A Dominant, Hyperdiverse Ant Genus (2003), which includes formal descriptions of 341 new ant species.

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His work was not without controversy and Wilson relished a good fight. Sociobiology: The New Synthesis features 23 chapters devoted to an exploration of the adaptive basis of social behaviour in different animal groups. The final chapter on the implications for human behaviour provoked a firestorm of criticism complete with evocations of eugenics, culminating in a group of protestors from the organization Science for the People pouring a pitcher of cold water on his head at the 1978 meeting of the American Association for the Advancement of Science (AAAS). The stunt backfired badly as Wilson was in a cast because of a broken leg, and the audience applauded when he nevertheless carried on with his lecture.

In 2010, Wilson became embroiled in another controversy when he published a paper in Nature (466, 1057–1062; 2010) entitled 'The evolution of eusociality', with Martin Nowak and Corina Tarnita, which argued that even the most extreme form of social organization, such as that seen in ants, bees and wasps, could be explained without invoking kin selection. Despite having been an early advocate of William D. Hamilton's concept of inclusive fitness as a possible explanation for why many insects with haplodiploid sex determination and correspondingly elevated levels of within-colony relatedness show a high degree of social behaviour, Wilson concluded that there are too many exceptions for this to be an adequate explanation. He preferred instead a group selection model advocated by David Sloan

Wilson. This abrupt change of opinion provoked another high-profile altercation, although this time Wilson's opponents opted for the correspondence columns of *Nature* over the jug-of-water: a letter condemning the article was signed by 137 experts.

Potentially the most significant of Wilson's contributions have come from his tireless work for conservation. He thought every person on the planet should appreciate the biological diversity both in their own backyards as well on the other side of the globe, and firmly believed that we have a duty to protect it. He established the Encyclopedia of Life, which aims to host a webpage for every species. He reached out to unlikely allies in his mission to save the natural world, working with politicians, movie stars and religious leaders to advocate for conservation of the Creation. Most recently he threw down the gauntlet by initiating the Half-Earth Project, where he made the bold proposition that we should set aside 50% of the planet for conservation.

Despite all his accomplishments, including winning almost every award a scientist can receive. Wilson remained a genuinely humble and warm person. He always took the time to autograph books and to talk with students and fans about their own interests. He loved to engage in what he described as 'old geezer talk', reminiscing about growing up in the southern US, waxing eloquent about the biological wonders of the Alabama woods, spinning out plot lines of B movies on ants (the 1954 sci-fi horror film Them was a favourite) and occasionally indulging his students with moon pies, a sweet delicacy from the southern US.

Wilson was a deep thinker and synthesizer, a true mentor, a friend. His writings inspired generations of scientists, and his efforts on behalf of biodiversity will continue to galvanize our fight to save the planet. He also loved to surprise. The famed ant expert would announce to students that sharks were his other favourite organisms: both groups, he pointed out, included species ranging from top predators to lowly scavengers. His favourite field experience came when he was working to test island biogeography theory using small mangrove islands off the coast of Florida. There, he could stand in the shallow water with small sharks nosing around his feet while he picked ants off the mangroves above. "That's my idea of heaven!" he said.

Wilson's wife of 66 years, Irene, died on 7 August 2021; they are survived by their daughter, Catherine I. Gargill, who lives in Florida.

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Published online: 03 February 2022 https://doi.org/10.1038/s41559-022-01680-8