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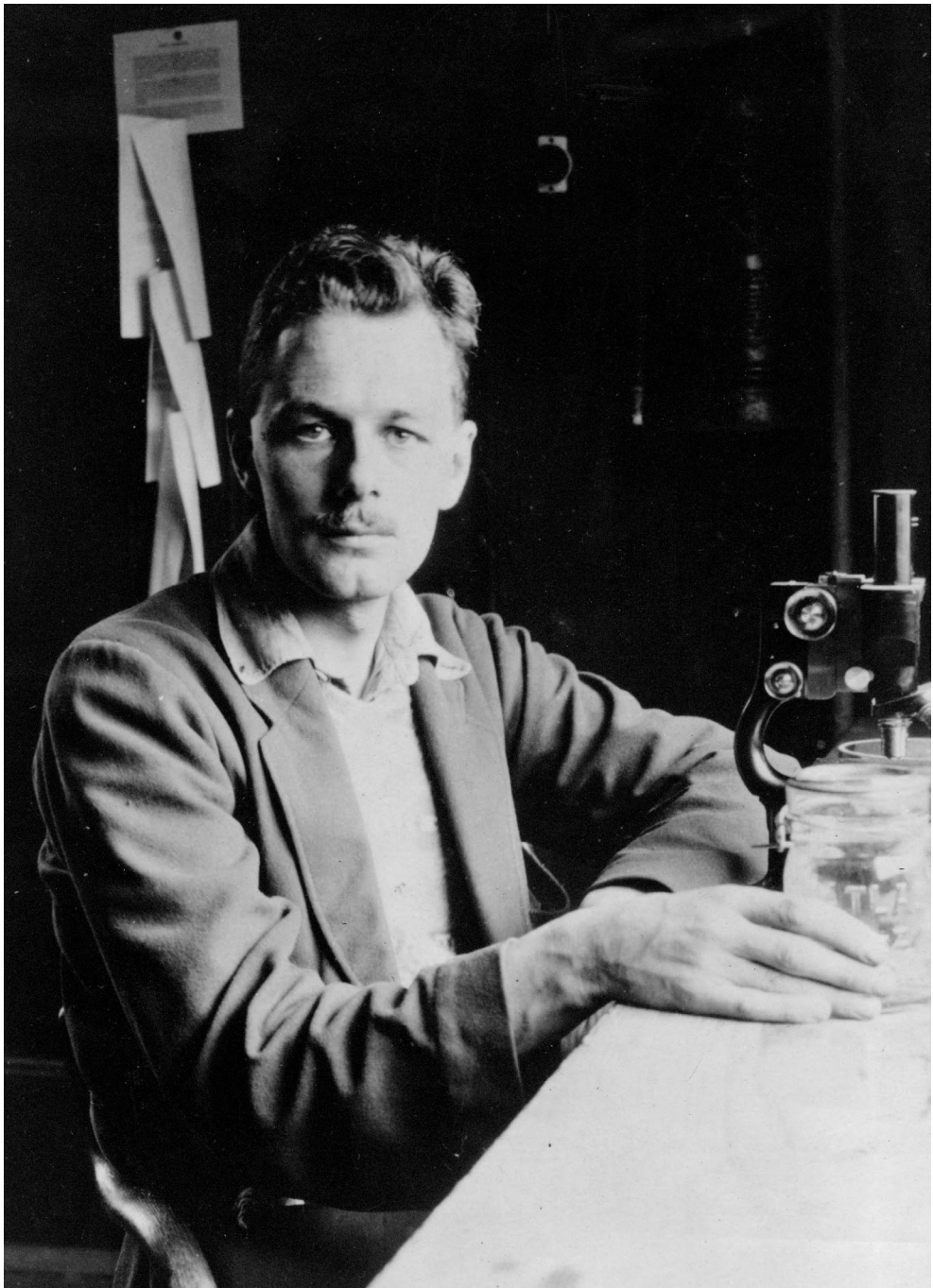
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Elected ForMemRS 1983

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George Evelyn Hutchinson, born on 13 January 1903 in Cambridge, is considered by many to be the father of modern ecology because he infused the science with theory that was anchored in natural history. When called the father of ecology in 1973 on receiving the very first Tyler Prize, he instantly demurred, saying that credit should go to Darwin and Charles Elton, and further that what he was really proud of was the string of wonderfully bright students who had studied with him. Nonetheless in many senses and to a major extent Hutchinson can be credited with transforming natural history into a science. He spent most of his professional years at Yale and returned to England in 1991 for the last months of his life.

The Cambridge of his childhood and youth was one of the great intellectual epicentres of the world. Hutchinson characterized it as ‘inhabited by genius, possibly more significant intellect per thousand inhabitants than any place has had before or since.’ His father, Arthur Hutchinson, was a mineralogist and later Master of Pembroke, and would have been the discoverer of radioactivity and terrestrial helium had he not insisted on first finishing some work at hand. His mother, Evaline, a ‘strong but not militant feminist’, provided lifelong encouragement. His uncle, Sir Arthur Shipley, was a noted zoologist and Master of Christ’s College. The discovery of mummified black rats in the walls of the Master’s Lodge led to an early awareness of species interactions because it had been displaced by the brown Norway rat. Typically, Hutchinson used this example with an actual illustration many decades later in a scientific essay.

At eight years of age he was sent to St Faith’s, a boys’ school in Cambridge. The curriculum included mathematics, Greek and Latin as well as poetry. At the time Hutchinson and his friends organized the Cambridge Junior Natural History Society. It focused on the collection

of all sorts including fossils, insects and vertebrates. When provided with a killing bottle for butterflies and moths by his father, he very soon started to specialize in aquatic insects and in particular aquatic bugs (Hemiptera). These became one of the foci for the rest of his life and in a sense led to his becoming the foremost authority on limnology of his time.

When eight or nine years old, he and his younger brother Leslie managed to lock Sir George and Lady Darwin, his parents and other dinner guests in the dining room and turn off the power. He enjoyed recounting this ‘disgraceful’ behaviour as well as having first noted the buoyancy of water when he pushed a little girl into a shallow pool. Other than those anecdotes his youth seemed to have focused on the vibrant intellectual environment in which he was immersed.

Hutchinson was sent for secondary school to Gresham’s in Holt, Norfolk, which, among other things, was strong in physical science. As a consequence he entered Cambridge with a strong background in chemistry and physics—a background that made it natural to include chemistry and geology in limnological studies not long afterwards in South Africa and later in Connecticut. Gresham’s also had a strong natural history society in which he excelled: in one year he was the only student elected to all sections of the society. It was there at age 15 he published his first paper on a swimming grasshopper.

Hutchinson took his Cambridge entrance exams in mathematics and physical science and graduated in 1925 with double firsts in zoology. This gave him the basic underpinnings for his intellectual trajectory: the physical and biological sciences for ecology, and mathematics for theoretical frameworks. Although the courses he took included one from J. B. S. Haldane (FRS 1932), who played a major role in the modern synthesis in evolutionary biology, he also benefited a great deal from unstructured activity outside the classroom, including field trips. He, Grace Pickford and Gregory Bateson were founding members of the Cambridge University Biological Tea Club. Discussion over tea remained a punctuation point in his day for the remainder of his life.

He clearly could have gone on for a PhD degree at Cambridge but chose not to do so. There is no clear indication of why he did this, but it is likely that he was ahead of his time in wanting to combine the physical sciences and geology with biology and that there were probably obstacles to doing that. His sheer brilliance rendered the lack of a PhD no impediment. Indeed, neither he nor Charles Elton (FRS 1953) had PhD degrees. Hutchinson then went on a Rockefeller Fellowship to the Stazione Zoologica in Naples. Although he was not successful in his research on the octopus endocrine system, he did develop a special affinity for Italy and Italian culture.

He subsequently went as a senior lecturer to the University of Witwatersrand in Johannesburg despite warnings from his parents about the already infamously difficult zoology professor, H. B. Fantham, who indeed fired him from his teaching post. (The university decades later named a hall in Hutchinson’s honour). The university was still bound by the contract to pay him, so this released him to do field work. Grace Pickford was in South Africa on her own fellowship, and they married. Together they studied the shallow and dry lakes or *vleis* and their chemical properties in particular: Hutchinson wrote, ‘at last, I had found what I wanted to do’—namely, limnology.

The limnological work had been sponsored by Lancelot Hogben (FRS 1936) of the University of Cape Town and it was he who informed Hutchinson of the possibility of a Seesel Anonymous Fellowship at Yale. Hutchinson applied by cable but missed the deadline and was offered a lectureship (again by cable) instead—in part because of support from Alexander Petrunkevich (an arachnologist, and the last student of August Weissman). And so in 1928 he began his time at Yale, where he remained until 1990 (figure 1). He was appointed Sterling Professor of Zoology in 1965 and in 1971 Sterling Professor Emeritus.



Figure 1. G. Evelyn Hutchinson in his laboratory at Yale in the 1960s with a giant tortoise from Aldabra (a gift from A. J. Kohn and Willard Hartman). Hutchinson had been very active in saving that island from conversion to a military base. (Photograph by Phyllis Crowley.)

He went to New Haven via Cambridge, where he acquired two important books: August Thienemann's *Die Binnengewässer Mitteleuropas* on European limnology, and Charles Elton's *Animal ecology* with its important work on food chains (Elton 1927). (A conflicting report indicates that he read the Elton book while in South Africa.) Grace Pickford went with him and eventually did her PhD, while department chairman Ross Granville Harrison encouraged the young instructor in limnology and ecology.

In 1932 he went to Kashmir and Ladakh as the biologist on the Yale North India Expedition, a strenuous trip that included crossing over passes above 18 000 feet. Although he fulfilled the purpose of making collections from *Daphnia* to mammals, he did not content himself with merely recording species new to science. In particular he was asking questions about the various lakes and their chemistry and biology, later publishing a paper in *Nature* (1)* comparing high-altitude lakes in north India and Europe. By the age of 30 he had studied lakes on four continents.

* Numbers in this form refer to the bibliography at the end of the text.

On his return to New Haven, limnology was clearly a central research theme. Indeed, Hutchinson could have had an exceedingly distinguished career in limnology alone. He was the first to use radioactive molecules (phosphorus in the first instance) to illuminate the dynamics of lake chemistry, and he thus founded radioecology. With his early student Edward Deevey he initiated the field of palaeoecology. He, Deevey and collaborators were very interested in how lake sediments reflected both natural change and human history in the watershed. There was a series of papers on cores from Lake Huleh in Israel and Laguna Petenxil in Guatemala and Lago di Monterosi (the latter in Roman times). He was long interested in the phenomenon of cyclomorphosis in certain plankton species and sought causal explanation in temperature; ultimately one of his former undergraduate students, Stanley Dodson, demonstrated predation to be the driving cause.

His four-volume *A treatise on limnology* (7, 14, 15, 18) is a work of astounding breadth and depth (volume 1 (1957) on geography, physics and chemistry; volume 2 (1967) on lake biology and limnoplankton; volume 3 (1975) on limnological botany; and volume 4 (1993) on the zoobenthos). It remains a useful reference to this day.

From the limnological work clearly spring the more theoretical aspects of Hutchinson's work that provided the foundation of modern ecology, starting with the important influence of the Lotka–Volterra equations and Gause's experiments in competition. The latter include situations in which competitive exclusion is at work and situations in which it might not, all of which led to his definition of the ecological niche in his 'Concluding remarks' paper of 1957 (8). This paper brought the niche from its original definition by Grinnell (1917), which was basically the habitat of a species, and from the role of the species in the community as subsequently defined by Elton (1927) (who phrased it famously as 'There goes the vicar') to something that was explicitly quantitative, namely the n -dimensional hypervolume (8).

In its turn this new quantitative basis for the niche set the stage for mathematical considerations of competitive exclusion (when it works and when in non-equilibrium situations it does not (10)), fugitive species (a forerunner of the metapopulation concept) and character displacement, and the famous seminal paper on biodiversity 'Homage to Santa Rosalia or Why are there so many kinds of animals?' (9), in which Hutchinson explored factors contributing to and limiting diversity in nature. The suggestion in that paper that there might be a minimum ratio of difference for two species (of 1.3:1) led to a burst of research that in the end demonstrated that it was not so broadly applicable as originally thought, but nevertheless helped build better insights into species richness and community ecology. By focusing on what might set distinctions between competing species, Hutchinson also drew attention to the topic of species diversity. His student Robert MacArthur pursued this first in his dissertation work with North American Wood Warblers and then in subsequent papers.

Hutchinson assisted his postdoctoral student Raymond Lindeman with the publication of the famous paper 'The trophic–dynamic aspect of ecology' (Lindeman 1942), which laid the foundation for systems ecology. It described the energy relationships between different trophic levels of a lacustrine ecosystem and was soundly rejected by the editors of *Ecology*, in part because one reviewer opined that it would not be worth publishing until data had been collected for 50–100 lakes. Hutchinson encouraged Lindeman to revise it and sent a strong letter making the case that if ecology aspired to advance as physics does it needed to embrace theory (Cook 1977). *Ecology* did accept the revised manuscript but Lindeman was struggling with a fatal hepatitis and did not live to see it in print. McIntosh (1985) considered this a watershed paper in the history of ecology. In addition, its significance is recognized by the

Lindeman Award of the American Society of Limnology and Oceanography, which honours young scientists.

Hutchinson became interested in information theory and cybernetics and participated with a friend and colleague from university days, Gregory Bateson, in a conference on cybernetics, contributing a paper 'Circular causal systems in ecology' (4). This represented his continuing interest in unifying principles, which in many senses fostered the infant science of mathematical ecology in which his students Robert MacArthur and Egbert Leigh were noted pioneers.

In a sense as a global-scale extrapolation of his interest in the interaction of the physical and biological elements of ecosystems, Hutchinson championed the biospheric concept of Vernadsky by giving attention to global biogeochemical cycles. For several years he edited a series of volumes on biogeochemistry published by the American Museum of Natural History, among them one he authored principally on guano islands and entitled 'The biogeochemistry of vertebrate excretion' (5).

One of the cornerstones of Hutchinson's work was the link between natural science fact and theoretical constructs. The reality of nature was the real test of any intellectual construct, and even his most mathematical student Robert MacArthur adhered to this: Hutchinson liked to say that MacArthur really knew his warblers. As his early student Gordon Riley put it, 'every fact should be useful but no fact will be useful until it is used.' Indeed, Hutchinson's interest in the odd and unusual ('The giraffe: most improbable') was because such oddities had, in the end, to fit into an intellectual framework—rather like the exception proving the rule. This tight link with the reality of nature is in part why most of his work has stood the test of time so well.

This principle is clearly evident in *An introduction to population ecology* (16), a splendid summary of population ecology at that time. A *tour de force* based on his famous course on ecological principles and the knowledge and insights gained over a lifetime, it is equally valuable for its extensive footnotes that cover everything from William of Ockham to the history of the concept of territory in animals (essentially a two-page footnote). An appendix, 'Ratiocinator infantium', provides the necessary calculus for readers to understand the theoretical insights (and he loved to observe that differential calculus is more interesting because it 'describes how things change').

Hutchinson is noted for the extraordinary set of students he inspired and enabled over time (figure 2). He led by example, inspiration and good questions, and at any given time there would be students working on a great variety of problems and a great variety of organisms. The accent was on the positive, for example 'there is no such thing as a completely bad paper' or 'that was right but for the wrong reason'. It was in fact a bit like being in the atelier of a great Renaissance artist except in this case the artist's aspiration was for each of us to shine in our own right. Hutchinson created an atmosphere in which we all aspired to do our very best and nothing was more important than the occasional approbation, usually phrased as 'marvellous'. All he would need to do is say he was a little worried about something for us to immediately redo a bit of work.

Hutchinson delighted in the diversity of his students and their research. In the late 1960s the National Science Foundation expressed concern that graduate students were constrained in their intellectual inquiry by virtue of serving as research assistants on NSF grants. He sent a one-sentence reply that he was not interested in making 'smudged carbon copies' of himself.

The first set of students was already at Yale or in New Haven: Gordon Riley, Edward Deevey, Thomas Edmondson and Max Dunbar. Later ones came specifically to study with the

being the essay ‘The cream in the gooseberry fool’ (12). That related to the gooseberry moth *Abraxas grossulariata* and a collection of the moths originally put together just to document the variety of wing patterns, for which crazed collectors were willing to pay high prices, but which ultimately were the basis of studies that ‘underpinned the modern chromosomal theory of inheritance, the work of E. B. Ford on natural selection in the wild and “all that has happened subsequently in genetics”’ (Donoghue & Pickering 2010).

Hutchinson was a true polymath with wide-ranging interests and extraordinary knowledge beyond science itself. His topics included the biology in medieval manuscripts, art history, anthropology, religion, folklore and even the scientific view of water divining (rhabdomancy) and considerations of computers and artificial intelligence. His writing was of literary quality, as became evident in his first book, *The clear mirror* (2), based on his time in North India and Goa in 1932. He was a regular contributor to *American Scientist* with a column entitled ‘Marginalia’ (named for the marginal illustrations in medieval manuscripts). Many of these were republished in books by Yale University Press (*The itinerant ivory tower* (6), *The enchanted voyage and other studies* (11) and *The ecological theater and the evolutionary play* (13)). He also became a close friend of Rebecca West and served as her literary executor. At Yale he was a long-time member (and twice President) of the Elizabethan Club and a regular at Fellows’ events at Saybrook College.

There was also a continuing concern about the environment. His close friend and colleague Ruth Patrick was famous for both her work in theoretical ecology and her work on the effects of pollution on the ecology of rivers; beginning in the 1940s she demonstrated that the biodiversity of a river reflected not only the natural condition but also the human impacts on the watershed. Hutchinson personally intervened through the Royal Society to protect the Aldabra tortoise from the threat of Aldabra being made an airbase.

As early as the 1940s he was teaching about greenhouse gases and climate change. On receiving the Franklin Medal he said he hoped ‘the various things we are doing to the atmosphere will cancel each other out’. His very first ‘Marginalia’ column (3) stated, ‘... the most practical lasting benefit science can now offer is to teach man how to avoid destruction of his own environment ...’

In 1970, when in hospital for an operation for a hernia (he referred to it as a small parting of the body wall) he started to write an essay on what it was like to grow up in Cambridge at the start of the twentieth century. He soon realized that he had started an autobiography, and *The kindly fruits of the earth—recollections of an embryo ecologist* (17) was published in 1979. The account ended in 1930; it contained no opinions of living persons and did not mention Grace Pickford.

He received many honours. In addition to the Franklin Medal (1979), he was the first to receive the John and Alice Tyler Ecology Award (1974) and was awarded the Kyoto Prize in Basic Science in 1986. I had tea with him just before the Tyler Award evening. He had just returned from a tree-planting ceremony that the then administering institution Pepperdine University liked visiting notables to perform. With amusement he told me that Ronald Reagan (who was infamous for a dismissive statement that if you had seen one redwood you had seen them all) had also been asked to plant a tree ‘and it was a redwood. And it died.’

He received the National Academy of Science’s Cottrell Award for Environment, and in 1984 the National Academy’s Daniel Giraud Elliot Medal with the citation ‘Hutchinson was admired as limnologist, biochemist, ecologist, evolutionist art historian, and ranks among our zoological giants.’ He declined to receive the National Medal of Science from Richard Nixon.



Figure 3. G. Evelyn Hutchinson and sister-in-law Hannah Hutchinson in 1981 upon receiving an honorary DSc from Cambridge. (G. Evelyn Hutchinson Papers (MS 649), Manuscripts and Archives, Yale University Library.)

He received honorary degrees from Harvard, Princeton and Duke, among others, and in 1981 from Cambridge (figure 3). There is a Hutchinson Lake in northwestern Ontario.

His first marriage to Grace Pickford ended in divorce in 1932. In 1933 he married another Englishwoman, Margaret Seal, with whom he shared deep interests in music and art; she died of complications from Alzheimer's in 1983. During World War II they looked after a young girl, Yemail Ovid, from Britain, to whom Hutchinson was devoted for the rest of his life. In 1985 he married Anne Washington Twitty Goldsby. She died in December 1990, at which point he returned to his family in England before dying in London on 17 May 1991, survived by his younger sister, Dorothea. In 2010 Yale University Press published a definitive biography (Slack 2010) and an anthology of famous papers with associated topical essays (Skelly *et al.* 2010).

Hutchinson left behind the science of modern ecology fashioned from physical science, mathematics and the reality of natural history. He did so within his view that 'everywhere in education we should aim at seeing life as a sacred dance in which the champions are those who give most beauty, truth and love to the other players.'

ACKNOWLEDGEMENT

The frontispiece photograph was taken at Woods Hole in the 1930s and is reproduced courtesy of Yale University Archives.

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