Radiation ecology, systems ecology and the management of the environment
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Radiation ecology, systems ecology and the management of the environment

CHUNGLIN KWA

This paper is about two subdisciplines of ecology, radiation ecology and systems ecology, and about two institutions, the ecology groups at Oak Ridge National Laboratory and at the University of Georgia. In these two institutions, systems ecology emerged out of radiation ecology. Yet, it seems these two subdisciplines could not be more different. Radiation ecology is problem and technique oriented. In contrast, systems ecology can best be described as a social movement. A general emphasis on newness combined with varying degrees of missionary zeal, rather than precisely stated goals, served to excite newly won disciples in an effort to reform an outdated discipline. Systems ecologists meant to ‘revolutionize’ ecology, its concepts as well as its practices. How can we understand the nature of the transition of radiation ecology to systems ecology?

Eugene Odum, Professor of Zoology at the University of Georgia, coined the term ‘radiation ecology’ in 1956, a number of years after it came into existence. It arose in response to problems of radioactive waste and fallout, which slowly, too slowly, emerged as problems at the end of World War II. The term ‘systems ecology’ was also first used by Eugene Odum, who hailed it in 1964 as the ‘new ecology’. A paper published in 1962 at Oak Ridge...
National Laboratory has retrospectively been called the first systems ecological paper.4

To define systems ecology seems harder than to give its chronology. Indeed, many different definitions have been offered. The most elusive points out that it is a ‘new ecology’, characterized by ‘the accumulation of the techniques, instruments and wherewithal for analysis of ecosystems as a whole’.5 One aspect of this definition highlights systems ecology as a modernization movement. Another aspect links it to ecosystem ecology, and this is indeed what ‘systems ecology’ in the United States has come to denote; as a ‘systems science’ it is more than anything else connected with the analysis of large and complex ‘ wholes’ such as ecosystems. But systems ecology has many other connotations as well, as appear for example in the definition of two other system ecologists: ‘Systems ecology is a robust hybrid of engineering, mathematics, operations research, cybernetics, and ecology.’6

Systems ecology in the United States, however, has been a much more coherent endeavor than the above definitions at first suggest. A few years after systems ecology came into existence, systems ecological projects constituted the bulk of the American contribution to the International Biological Programme (1968–1974), and a separate programme for systems ecology was set up at the National Science Foundation that equalled or surpassed the one existing NSF programme for the rest of ecology.7 The ecological programmes at the University of Georgia and Oak Ridge National Laboratory were among its most important beneficiaries. One might say that the history of these two institutions coincide to a large extent with the early history of systems ecology, i.e. until the beginning of the IBP, the final point to which the account in this paper will be carried.

**US ecology around mid-century**

In 1956 the ecological programmes at the UGa and ORNL occupied peripheral positions within the discipline of ecology, and not only because they were newly built. The UGa was a small land-grant university of modest

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reputation and without a long-standing programme in ecology. ORNL was primarily a physics laboratory and its endeavors into other realms were of marginal interest by necessity.

A second shared feature is that they were strongly limited to applied ecological problems, and this seemed enough to prevent them from taking a place in mainstream ecology. Both the UGa and ORNL were entirely or almost entirely dependent on funding by the Atomic Energy Commission, and this draws attention to the extraordinary fact that, prior to 1970, the AEC was the most important patron of American ecology.

Thirdly, there was a sense in which the ecological research at the UGa and ORNL was nevertheless 'mainstream'. The early work was as solidly descriptive as the work being done at the intellectual centers of ecology such as the University of Chicago and Yale University. The effects of radiation on the environment opened, as it were, a new territory for pre-existing ecological approaches and practices. Its practitioners regarded radiation ecology as a subdiscipline of ecology in its own right.

In most American universities, if not all, ecology was (and still is) usually represented by one or more faculty members at Departments of Biology, Zoology, Botany, Forestry, etc. They had widely diverging backgrounds, reflecting the many sources that feed into ecology: zoology and botany, mathematical and field methods, taxonomic and physiological approaches. Furthermore, different foci can be discerned such as the familiar division between terrestrial and aquatic ecology, and, most importantly, the definition of the object of ecology as the population (groups of individuals of any one kind of organism), the community (all the populations occupying a given area) or the 'ecosystem', i.e., the community functioning together with its nonliving environment such as the various climatic factors.  

Viewed from the perspective of the protagonists in the account of this paper, this ecological scene was dominated by a few outstanding figures, mostly at elite universities. The University of Chicago was among the most important. Its tradition in ecology dates from the beginning of the century, and includes ecologists such as Henry Cowles, his student Victor Shelford and W. C. Allee. The latter formed the so-called Ecology Group, mostly consisting of his own former graduate students, which functioned until his retirement in 1950. Its theoretical position concerning population ecological problems earned it the designation of 'school'. Apart from Allee, the group

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consisted of Alfred Emerson, Thomas Park, and Karl Schmidt, and also included Orlando Park from nearby Northwestern University. The group at Chicago (the ecologists at the Botany Department not included) was relatively large compared to most universities. Eugene Odum and the Oak Ridge ecologist Stanley Auerbach received at least part of their education from Chicago or Chicago-related ecologists.

At the end of the 1940s, Yale occupied a similar position. G. Evelyn Hutchinson, who was at Yale from 1928 until his retirement in 1971, is perhaps the single most influential American ecologist of this century, through his own work and that of his graduate students. A high proportion of these students rank among the most important ecologists in the US. At the time, three of his former graduate students were on the staff at Yale, too, and they were sometimes designated as the 'Hutchinson School'. According to one of them, Gordon Riley, it was 'a loosely knit, informal group' that later on disbanded.10 Both at Yale and Chicago, the ecologists were highly committed to research, but though they were designated as 'schools', they did not form research groups that were tied together by a shared research programme. Much of the research was done in the context of education, and both Hutchinson and the Chicago ecologists wrote widely used textbooks. Thus their importance for American ecology far exceeded their numerical size, an importance which can also be inferred from the fact that for instance, the Chicago ecologists Emerson and Park held key positions such as the editorship of Ecology.11

As indicated by the enumeration of its various sources, ecology is an extremely heterogeneous field, with many subfields developing quite independently of one another. It has been commented recently that this situation probably precludes for ever any theoretical unification.12 To the extent that the most highly esteemed work in ecology was (and to some extent still is) descriptive, this hardly mattered. The journal Ecology refused theoretical papers with few exceptions until 1973, when the Board of Editors changed its policy.13 Traditional virtues such as a good background in taxonomy thus remained strong prerequisites for academic recognition.

So much for appearances during the 1950s. By the late 1960s the ORNL and the UGA had gained national prominence as centers of ecological research, and the factors that helped them to win that position were the very same factors that initially seemed to constrain them to the marginal position of the peculiar form of applied ecology known as radiation ecology. Seen

11 Mitman, op. cit. (9), p. 177 n.
retrospectively, the Atomic Energy Commission provided a context in which elements of what was later to emerge as systems ecology could be combined. The problems and perspectives of radiation ecology were broadened in a specific way so as to give rise to systems ecology. In this way, Eugene Odum and Stanley Auerbach, typical naturalists and outdoors ecologists lacking a mathematical background, were the founders of a subdiscipline of ecology that was strongly mathematical.

The role of the AEC and the institutional context it provided to the nascent science of radiation ecology can hardly be overestimated. In various ways, the particular setting of radiation ecology helped to select and shape its research directions. The AEC Division of Biology and Medicine (DBM) was first and foremost interested in the problems radiation posed for human health. The importance of the problems of health directed the attention of the AEC-hired ecologists at an early stage to the food chain. Radiation ecology, which was initially developed as research on the direct effects of radiation on organisms and their environment, thus provided important methodologies for the study of the food chain and led ultimately to systems ecology.

Another element pertinent to the development of systems ecology were certain mathematical techniques. Their possibilities and constraints, in particular with respect to computers, shaped some of the essential presuppositions of systems ecology. Computers became available to ecologists during the 1960s. They soon raised high expectations, not least with respect to the possibility of a scientific management of ecosystems through the production of simulation models of ecosystems.

The institutional setting of radiation ecology, within AEC-directed programmes, provided an important impetus to fuse these elements together. 'All of a sudden you were bedfellows with physicists and chemists', as Odum said looking back at the heyday of radiation ecology.14 Through daily contact with these physicists, the radiation ecologists felt obliged to adopt whatever mathematical and physical methodology was available to win the esteem of their colleagues.

Yet the development from radiation ecology to systems ecology was by no means wholly determined by the institutional context provided by the AEC. Such a view would leave little room for the innovative actions of several of the key actors whose work is described here. Rather we could say, somewhat paradoxically, that this particular institutional context was instrumental in creating an atmosphere in which a confidence to bring about a 'new ecology' could flourish.

What I hope to demonstrate in the following pages is that the practical orientation of radiation ecology was retained in systems ecology on a more

14 Interview with Eugene Odum (11 October 1985).
abstract level. Radioactive isotopes had caused environmental problems that were addressed by radiation ecology in their specificity. Systems ecology transformed this practical orientation into a generalized managerial approach to the natural environment.

The first programmes of radioecology

After the end of World War II, the Atomic Energy Commission refused during many years to take problems of radioactive waste and fallout seriously. The 1954 Bikini thermonuclear bomb test changed that. The contamination of the Marshall Islands, their inhabitants, and in particular of a Japanese fishing boat, caused world wide concern and it forced the AEC to engage in biological research on a relatively large scale. The AEC Division of Biology and Medicine hired an ecologist, John Wolfe, in 1955, as a consultant. In 1958 he was appointed permanently, and within the DBM an Environmental Sciences Branch was created around him. Wolfe's appointment was instrumental in developing radioecological programmes at many universities. Already by 1954, budgets for ecological research rose sharply at both Oak Ridge and Georgia. By the end of the 1950s, 'radioecology' was being practiced at several National Laboratories and at up to fifty universities, sponsored by the AEC. Almost everywhere, radioecological research was directed to the ecological effects of specific isotopes, or the dose-response relationships between levels of radiation and organisms.

Yet, radioecological studies had preceded Bikini, even though there had been no central policy of engaging in ecological research. At the Hanford Works (now: Pacific Northwest Laboratory), ecological radiation studies started in 1946, and at Oak Ridge National Laboratory in 1950. If ecologists were in effect hired or given an opportunity to do research, it was the

17 Radioecology, op. cit. (2), p. 6. By fiscal year 1970, the budget of the Environmental Sciences Branch was $18.9 million, divided into $6 million for terrestrial and fresh water ecology, $4 million for marine sciences, and $8.9 million for atmospheric radioactivity and fallout.
18 At Emory University and Colorado State University comparatively large radioecological centers came into being. Both focussed on dose–effect relationships. See Stannard, op. cit. (16).
19 Research at Hanford originally started in cooperation with the Applied Fisheries Laboratory (later the Laboratory of Radiation Ecology) of the University of Washington. The first radiation studies were done at this university in 1943, on the effects of radiation on salmon and trout. These studies were largely physiological. From 1946 on, environmental surveys were undertaken in the Pacific and Columbia River, now also by scientists hired on the staff of General Electric, the operator of Hanford N.L. See Radioecology, op. cit. (2), pp. 4–5, and R. F. Foster, and J. J. Davis, 'The accumulation of radioactive substances in aquatic forms', Proceedings of the International Conference on the Peaceful Uses of Atomic Energy, (1956) 13, pp. 364–7, 364.
result of ad hoc decisions by the directors of the individual National Laboratories, sometimes responding only to initiatives taken by lower officials. Most ecological research, if not indeed all of it, originated from problems in the plants and reactors at the sites of the Laboratories themselves. The programmes at Hanford and Oak Ridge both found their origin in the toxic waste problems that the atomic installations had created for themselves: at Hanford significant amounts of radioactive isotopes were being released into the Columbia river; at Oak Ridge a small lake, the White Oak Lake, had been turned into a heavily contaminated waste depository during World War II. It ranked among the most contaminated areas in the world. Equally ad hoc was the decision of the AEC’s Biophysics Branch of the DBM to engage in ecological studies at the Savannah River Plant Reservation in South Carolina, where a new nuclear plant was being established in the early 1950s. There was no National Laboratory involved here and the research was commissioned to the University of Georgia.

The ecologists at Hanford achieved the first real breakthrough in radiation ecology. At the International Conference for the Peaceful Uses of Atomic Energy held in Geneva in 1956, two papers reported that several species accumulated radioactive isotopes in surprisingly high quantities.

The plutonium-producing plants at Hanford were cooled directly by water from the Columbia River, which was released to the river again. Even if under normal operating conditions no spills occurred, radioisotopes were formed through neutron activation of solids present in the cooling water. Moreover, the exchange surfaces became activated and radioactive material was released through corrosion. Radioactive levels of the effluent into the Columbia River, however, did not exceed the then permissible levels. But there was a potential environmental problem, since the water of the Columbia River was used as drinking water, and there were also salmon fisheries.

One of the isotopes present, albeit in smaller amounts than a number of

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20 A case in point is Karl Z. Morgan, Director of the Health Physics Division of Oak Ridge National Laboratory (see below). At Hanford, the initial impetus had come from Stafford Warren, medical director of the Medical Engineering District. See Stannard, op. cit. (16), p. 757.


22 The discovery of this concentration phenomenon along the food chain seems to have preceded the discovery of the very similar phenomenon of concentration of pesticides such as DDT and DDD. That DDT was passed on from one level of the food chain to another was noted as early as in 1949. However, the fact that these chemicals were concentrated in, for instance, the fatty tissues of birds, and that this was the cause of bird deaths, was not noted until the late fifties and published in the early sixties. See R. L. Rudd, Pesticides and the living landscape, Madison, Wisconsin, 1964, pp. 241–267.

others, was phosphorus-32, a biologically important element and fairly long-lived. R. F. Foster and J. J. Davis found high concentration factors of this isotope in various forms of aquatic life, e. g. 150,000 times in a small fish and 350,000 in caddis fly larvae as compared to the P-32 content of the water.\textsuperscript{24} W. C. Hanson and H. A. Kornberg, investigating terrestrial animals in the same area, found even higher concentration factors, up to 500,000 times in young swallows and 1,500,000 in the egg yolk of river ducks and geese. Apparently the levels were still such that no effect on the reproductive capability of the waterfowl was noted.\textsuperscript{25} But in principle it was established that water containing concentrations of contaminants well within the permissible limits for drinking water could give rise to hazardous levels of radioisotopes in the food organisms of man, as they were to note.\textsuperscript{26} But aside from noting the potential relevance of this finding to human health, they pointed out its ecological importance.\textsuperscript{27} Since it was obvious that the animals obtained the radioactivity from food,\textsuperscript{28} the studies that were designed to monitor levels of radioactivity also provided information on nutrient cycles, metabolic rates and ecological relationships.

The idea to use radionuclides in an experimental manner would be taken up by the ecologists at Oak Ridge and at Savannah River. But the team of Hanford and the neighbouring University of Washington at Seattle remained confined to doing environmental surveys. A possible reason is that the Hanford ecologists were financed from operating rather than research funds, the Hanford management (conducted by General Electric for the AEC on a contract basis) apparently unwilling to change this.\textsuperscript{29} Union Carbide, which ran the ORNL on a similar contract, did not enforce such constraints, while Odum at the University of Georgia could profit from the much more liberal climate of a university. Thus the Hanford ecologists remained oriented toward the needs of their plant, whereas the ecologists at Oak Ridge increasingly broadened their scope while striving for recognition by the academic ecological community.

**Eugene Odum and the University of Georgia**

In 1940, when Eugene Odum joined the Department of Zoology of the University of Georgia, he was the only ecologist on the Department’s staff.

\textsuperscript{24} Foster and Davis, op. cit. (19).
\textsuperscript{25} Hanson and Kornberg, op. cit. (21).
\textsuperscript{27} Foster and Davis, op. cit. (19); J. J. Davis and R. F. Foster, 'Bioaccumulation of radioactive isotopes through aquatic food chains', *Ecology*, (1958) 39, pp. 530–35.
\textsuperscript{28} Direct absorption from water in fish contributed only 1.5% of the radioactivity, Davis and Foster, op. cit. (22).
\textsuperscript{29} Stannard, op. cit. (16), p. 770.
At his retirement in 1983, Odum was still at the Department. He was also Director of the Institute of Ecology at the University of Georgia, with about 100 faculty members, 100 graduate students, and 50 support staff. The Institute has a world-wide reputation as a center of ecosystem ecology. Since Odum can be considered its chief architect, it seems justified to start the history of the development of ecology at the University of Georgia with a look at Odum’s career.

‘One of the best ways to begin the study of ecology is to go out and study a small pond.’ Odum’s example of an ecosystem is introduced in the style of a natural historian. Eugene Pleasants Odum was born on 17 September 1913. Odum received his undergraduate education at the University of North Carolina at Chapel Hill. He wanted to pursue his graduate studies with Victor Shelford at the University of Illinois at Champaign. Charles Kendeigh, a former student and collaborator of Shelford, became the advisor of his doctoral thesis, on geographical and physiological aspects of the ecology of birds. After he obtained his PhD in 1939, Odum assisted Shelford on his field trips through the United States. He came to know Shelford well, and, along with sharing his naturalist’s enthusiasm, sympathised also with Shelford’s intellectual project, which was to combine plant and animal ecology in order to understand the functioning of ecosystems (or biomes, as they were called in his terminology). Shelford and Frederic Clements tried to accomplish this goal in their joint publication of 1939, *Bio-ecology*. In the eyes of contemporaries, the book remained largely classificatory, however, and was by many, including Odum, considered a failure.

Odum got his next most important intellectual stimulus from Hutchinson, after he was appointed to a position at the Department of Zoology of the University of Georgia in 1940. Odum’s younger brother, Howard Thomas Odum, at the end of the 1940s was a graduate student of Hutchinson’s at Yale. Through him Odum was asked to give a seminar. At the time Raymond Lindeman’s paper on trophic-dynamics was one of the most talked-about topics. Odum acquainted himself also with Hutchinson’s writings, much of which reflected the same interest. Eugene Odum’s interests were clearly similar to those of Hutchinson’s students who were primarily concerned with the movement of nutrients and biogeochemical cycles.

Odum’s *Fundamentals of ecology*, published in 1953, can be seen as an attempt to integrate these various intellectual influences, around the central concept of the ecosystem. The book was written primarily to secure ecology a place among the so-called core curricula of his own Department at the

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31 Odum, interview.
University of Georgia.\textsuperscript{34} But its instantaneous success was nationwide. The next year, it went through two more printings. It has continued to be reprinted, as well as translated into many languages. A new edition appeared in 1959, followed by a third edition in 1971. For several generations of students, ‘the Odum’ was the textbook.\textsuperscript{35}

\textbf{Odum’s ‘Fundamentals of ecology’}

\textit{Fundamentals of ecology} is centered around Lindeman’s (and Hutchinson’s) concept of trophic-dynamics. Trophic-dynamics is essentially a reinterpretation of the feeding relationships (and the cycling of elements such as phosphorus and nitrogen that they involve) existing in a given ecosystem. Food chains, in terms of the species involved, can be extremely complex.\textsuperscript{36} Charles Elton, the British ecologist, had found an underlying pattern in the form of trophic levels and expressed them very elegantly by a \textit{pyramid of numbers} (Fig. 1), in which it is shown that the number of animals in small size classes is much greater than the number of animals in larger size classes (that may feed upon them), and these in turn significantly greater than the still bigger animals that may prey upon these, and so on.\textsuperscript{37} Lindeman performed a reduction operation on these pyramids of numbers, transforming them into pyramids of biomass corresponding to discrete trophic levels (producers, primary and secondary consumers, and so on). Thus ‘the principle of the Eltonian Pyramid (was) redefined in terms of productivity.’\textsuperscript{38} As Hutchinson pointed out, the advantage of Lindeman’s approach ‘lay in reduction of all the interrelated biological events to energetic terms’,\textsuperscript{39} which could be quantified by measurements of the productivity at the various trophic levels.

Odum dismissed the original Eltonian pyramid of numbers out of hand to entirely embrace the pyramids of biomass and energy (Fig. 2).\textsuperscript{40} He con-

\textsuperscript{36} Elton was the first to use the words ‘food chain’ and ‘food cycle’, but he himself attributed the concepts to a 1913 publication by Victor Shelford. See D. L. Cox, ‘Charles Elton and the emergence of modern ecology’, PhD thesis, Washington University, 1979, p. 88.
\textsuperscript{37} C. S. Elton, \textit{Animal ecology}, London, 1927. See also Cox, op. cit. (36), pp. 94–9.
\textsuperscript{40} Odum said notably: ‘The pyramid of numbers is not very fundamental or instructive . . . . The pyramid of biomass is of more fundamental interest.’ (\textit{Fundamentals}, 1st ed., op. cit.
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Fig. 1: Eltonian pyramid of numbers according to animal size as drawn by Eliot Williams, 'An ecological study of the floor fauna of the Panama rain forest', *Bulletin of the Chicago Academy of Sciences*, (1941) 6, pp. 63–124, 109.

![Eltonian pyramid of numbers](image)


![Pyramid of biomass](image)

structed some pyramids on the basis of Lindeman's data. Odum reflected Hutchinson's influence in other respects as well. Clements and Shelford had regarded communities or ecosystems as supraorganisms. Odum's thought is informed by the metaphor of the homeostatic machine, by cybernetics.

Hutchinson had most clearly expressed his thoughts about the cybernetic nature of ecosystems in his paper 'Circular causal systems in ecology', where he undertook to demonstrate the validity of Norbert Wiener's cybernetic conceptions for the study of ecosystems. 'It is well known from mathematical theory' (i.e. cybernetics), he stated, 'that circular paths often exist which tend to be self-correcting within certain limits, but which break down, producing violent oscillations, when some variable in the system transgresses limiting values. . . . It is, therefore, usual to find in natural

(p. 74). Elton was understandably not very happy about these remarks, as he made he clear in his review of Odum; see Cox, op. cit. (36), p. 98.

41 See Kwa, op. cit. (7).
circular systems various mechanisms acting to damp oscillations... These self-correcting circular paths also occurred in ecosystems: 'The resulting stability, which appears to characterize most ecological systems, while it permits their persistence, makes investigation difficult.' These self-correcting circular paths also occurred in ecosystems: 'The resulting stability, which appears to characterize most ecological systems, while it permits their persistence, makes investigation difficult.'

He then identified two different circular causal ecological systems, one of which concerns us here: the biogeochemical cycling of substances through the ecosystem. Hutchinson had already contributed greatly to the elucidation of the cycling of essential biological elements through nature. He now conferred on these cycles the property of being regulatory mechanisms, ensuring the stability of the ecological systems for which they were relevant. H. T. Odum, Hutchinson's student, would complete his PhD thesis in 1950 on the biogeochemical cycling of strontium.

In several respects Fundamentals remains the work of a naturalist, who always looks for the application of abstract principles to concrete ecosystems, and wants to operationalize them in the field. But the book conveyed much more than a naturalist's enthusiasm. We may see this textbook as a careful assimilation of the major new trends in the ecology of the 1940s. As such, it was not only a powerful textbook, but became the manifesto of a movement to modernize research as well. This summarizes its two achievements: (1) the book motivated the research programme at the UGa and also at ORNL to which Odum was asked to be a consultant; and (2) it created a larger audience for the ecosystem approach, ecosystem management and preservation, albeit on a programmatical level. The second edition of 1959 incorporated many of the radio-ecological results, and articulated the systems approach to ecosystems more clearly.

The 'stability principle'

One of the principles of ecosystems that Odum proposed tentatively, and that literally inspired several generations of students of ecology, was the relationship between diversity and stability of ecosystems. The research on food chains at Savannah River, and the tagging of plants and animals that it involved, would also serve to make possible investigations on this relation-

43 Hutchinson, op. cit. (42), p. 221.
44 Hutchinson, op. cit. (42), p. 221.
46 Odum, Fundamentals, 1st edn, op. cit. (30), pp. 18-23.
ship. Already in the first edition of *Fundamentals* Odum had hinted at the possibility that diverse ecosystems were less likely to feature wildly fluctuating populations, in contrast to poor ecosystems such as tundras which are known for their regular outbreaks of, for instance, lemmings. Following a suggestion by the Spanish ecologist Raimón Margalef, Odum had proposed the hypothesis that in a diverse ecosystem with many species and many kinds of relations between them, these links would act as checks and balance against disturbances in population numbers, amounts of food minerals and possibly other system parameters as well. In a word: the more species present, the more possible negative feedbacks will be established.

The mere presence of species would not, of course, automatically give rise to such balancing relationships. However, by elucidating food webs in all their intricacy, in a quantitative way, one would be able to 'deal with diversity in terms of network variables rather than merely in terms of number of species and individuals present'. Although Odum clearly included in his relationship population interactions such as predation and competition, its outlook was definitively synchronic and functional, rather than evolutionary and long-term.

Odum's relationship between diversity and stability provided a hypothetical mechanism to what he had named 'the stability principle', the idea that, obeying the second law of thermodynamics, every natural system would evolve to a state of stable adjustment. The development of regulating mechanisms would bring successional and to some extent also evolutionary change to a halt.

We may also reconstruct the diversity/stability relationship as Odum's contribution to one of the major theoretical problems of ecology during the 1950s. Odum set out to solve on a 'systems level', a problem that had been posed within the ecology of populations. The central question had been: how are populations regulated? The debate had culminated in the Cold

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49 Odum, personal communication. R. Margalef's earliest theoretical work on the subject is 'La teoria de la informacion en ecologia', *Memorias de la Real Academia de Ciencias y Artes, Barcelona*, (1957) 32, pp. 373–449. This reference in Spanish is cited several times by the Odum brothers.
50 E. P. Odum, *Ecology*, New York, 1963. 'Without much scientific evidence', he added as a qualifier in this textbook (pp. 34, 93). In the 2nd edn of 1975 he expressed his reservation in the relationship even more strongly.
51 Wiegert et al., op. cit. (47).
Spring Harbor Symposium of 1957. At the time, two radically opposing answers were given. In one camp, the importance was defended of density dependent mechanisms in the regulation of population size, i.e., factors inhibiting or reversing the growth of a population would become more important with increasing population size and vice versa. This would make factors such as competition and predation the most relevant. Others argued for the predominant importance of density independent factors, primarily climatic factors that would check population growth and size irrespective of its then prevalent values. Thus the question can also be put as: is the abundance of a certain population of animals checked by depletion of resources and by other animals or by the weather?

The 1957 debate took the form of an empirical controversy: whether interrelated cycles of predator and prey really existed (which would argue for checks by animals), or whether there was a close correspondence between fluctuations in climate and population fluctuations (which would argue for checks by the weather). The former position was the orthodox one, stemming from classical population dynamics. As one of the adherants of the latter position observed, the disciples of the density-dependent position ‘vastly outnumber(ed)’ those of other theories, which were ‘rejected by common consent’. American ecologists were strongly involved in this international controversy, and usually took the ‘orthodox’ position. Before the controversy really developed, Allee and his collaborators had held it. A couple of years after the Symposium, two of Hutchinson’s former graduate students, Frederick E. Smith and L. Slobodkin, in a joint paper with Nelson Hairston, expressed their conviction that ‘the hypothesis of control by the weather leads to false or untenable implications’, and they upheld the theory

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55 As phrased by someone who argued that the terminology of density dependence and independence was misleading: A. Milne, ‘Theories of natural control of insect populations’, Cold Spring Harbor symposia, (1957) 22, pp. 253–71.

56 In 1924, the British ecologist Charles Elton advanced the theory that fluctuations in animal numbers found an ultimate cause in climatic variations. He proposed a 10- to 11-year cycle, corresponding to the sunspot cycle. We might infer from this a single causal chain, leading from the sunspots to vegetational growth, and further to the prey species and finally to the predator species. On this account, fluctuations in the number of predators would be caused by fluctuations in the number of prey, but not vice versa (see Cox, op. cit. (36), pp. 54–6). However, when Elton had acquainted himself with the idea of the generation of oscillations through internal causes, he adopted it (see Kingsland, op. cit. (53), pp. 129–30, and Cox, op. cit. (36), p. 62).


58 Orlando Park wrote notably: ‘In general terms, a community at the level of self-maintenance is a self-regulating assemblage in which the populations of plants and animals hold each other in a state of biological equilibrium . . . the several species populations hold each other in a system of checks and balances . . .’ (W. C. Allee et al., Principles of animal ecology, Philadelphia, 1949, pp. 507–8).
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of resource-limitation in the ‘classical density-dependent fashion’. The paper was written in an authoritative fashion. It received much favorable attention and may have contributed to the affirmation of orthodoxy, at least for a time. But that did not settle the controversy. It was argued some time later by ecologist Gordon Orians that this debate revolved not so much about an issue to be decided solely on empirical grounds, but depended rather upon one’s perspective: an evolutionary approach would incline more to the density-dependent, a functional one more to the density-independent perspective. At the heart of the controversy were the different concepts of causation implied in these two perspectives. The debate was thus related to a larger question: was there (or should there be) a relationship between ecology and evolutionary theory? The dominance of the ‘density-dependent’ position could then be interpreted as the dominance of the evolutionary perspective in ecology, with the corresponding relative unimportance of a functionally oriented, synchronic approach.

Eugene Odum put the density-dependent and density-independent mechanisms in conjunction. He assigned the former the function of a steam engine’s ‘governor’. The latter, he proposed, could ‘cause a shifting of upper asymptotic or carrying capacity levels’. If we would recast this in the metaphor of the regulation of the steam engine, the density independent mechanisms, or climatic factors, would determine the value of the set pressure which the governor would then maintain. An ecosystem thus appears as a machine, full of stabilizing mechanisms and driven by the climate.

Succession studies at Savannah River

In 1951 it became clear to the AEC that the new atomic weapons plant to be built on the Savannah River in South Carolina would become an even bigger operation than was first thought. Costs for the entire project were estimated at more than a billion dollars. The whole area along the river below Augusta, Georgia, would be transformed.

At the time of the construction of the reactors and laboratories at Oak Ridge, during World War II, there had been no opportunity to study their impact on the environment. The newly established Division of Biology and Medicine of the Atomic Energy Commission did not want this mistake to be

60 The paper was so well known in the 1960s that it received the status of an acronym (‘HSS’). See McIntosh, op. cit. (1), p. 244.
repeated at the Savannah River installations. In the spring of 1951, the Universities of South Carolina and Georgia were invited to submit proposals for 'pre-installation' inventories. As it turned out, the DBM granted not more than $10,000 per year to each university, over three years. Georgia and South Carolina were asked to divide up inventories of terrestrial flora and fauna and the general ecology of the area among themselves. The result was in fact an Environmental Impact Statement long before the practice was legally required.

Odum would congratulate himself ever after for the way he made use of that original offer. The University of South Carolina 'wasted' the grant by using it for the summer salaries of their own staff, and dropped out of the project at the termination of the initial contract period. Odum decided it was solely to be spent on graduate students who could be given research assistantships. Since a research assistant would cost $2000 a year, Odum could afford three of them, and could buy some equipment such as trucks as well. The University of Georgia had approved a PhD programme in biology a few years before. Odum already had one graduate student, and he could thus considerably enlarge the graduate programme through the arrangement with the AEC. In a quick procedure, the DBM approved Odum's grant proposal in late June, and Odum immediately went out to several other universities to interview candidates whom colleagues had recommended.

During 1951 and 1952 approximately 6000 inhabitants were moved out of the area of the Savannah River Plant, abandoning their houses and leaving their fields (approximately one third of an area of 250,000 acres) untilled. Odum established a temporary field laboratory in one of the country houses that were left vacant. The major study that Odum assigned to his students was to follow the development of old field succession or secondary succession. Since crop fields of various kinds and on various soils were left bare, a gradual but ongoing change of vegetation (with corresponding fauna) would take place — theoretically until a so-called climax stage would be reached. Six hundred fields were designated study areas, and these were exempted from reforestation with pine. To map the successional changes, in vegetation as well as in bird populations, training as a naturalist was a prerequisite. Odum

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65 E. P. Odum, 'Brief history of the University of Georgia's ecological studies at the Savannah River Plant prior to establishment of the On-Site Savannah River Ecology Laboratory, 1951-1962', unpublished manuscript, 1985, 22 p.
66 Odum, op. cit. (65); interview with Odum.
67 'An ecological study of land-use, succession, and indicator invertebrate and warm-blooded vertebrate populations of the Savannah River Operations Area'.
68 The three graduate students were William H. Cross (MS, Florida State University), Leslie B. Davenport (The College of Charleston) and Edward J. Kuenzler. Kuenzler graduated at the University of Florida, where H. T. Odum was Assistant Professor. In 1952, a fourth graduate student, Robert Pearson, a bird biologist, was added to this first 'crew'. He had taken his Master's degree with Kendeigh at the University of Illinois.
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had selected his students partly on this basis. After three years, they were replaced by a new team of five graduate students, who continued the measurements.69

Odum summed up the results of this first line of research at Savannah River in a way true to the intentions set forth in *Fundamentals*. Previous studies of secondary succession had focussed completely on species change in vegetation.70 In contrast, Odum related these changes to ‘functional’ aspects of the developing ecosystem under study, i.e. the ‘energy flow’ through its trophic levels. The results as reported were admittedly incomplete, and were confined to measurements of the productivity of the standing crop through seven consecutive years. Its main finding was that following the abandonment of agriculture, a relatively quick steady state in terms of primary production was achieved, though the process of change in species composition and species dominance had by no means come to an end.71 The suggestion that the occurrence of steady states had to be looked for at these ‘higher levels of integration’, or emerging ecosystem properties, was to remain a dominant theme in systems ecology through the years of the International Biological Programme.

Radioecological studies at Savannah River

From 1954 on, the DBM increased the budgets for ecological research at the Savannah River site significantly. Odum hired Robert A. Norris, a former student of his to be a full time ‘resident’ at the Savannah River research site. The AEC also assigned Odum a more professional laboratory. Support at the AEC headquarters in Washington for ecological research continued to increase. John Wolfe, head of the new Environmental Sciences Branch, was very supportive of the ecological research at Savannah River. He was keen on developing radiation ecology programmes at universities, and, in comparison, seems to have been more supportive of Odum’s programme than of Auerbach’s at Oak Ridge.72

Wolfe backed Odum’s proposal for a permanent on-site laboratory at the Savannah River Plant. In 1960, the AEC approved, and the next year the laboratory was made available.73 The Savannah River Ecology Laboratory thus came into existence, a University of Georgia institution that was completely dependent on ‘soft money’. At the time, the SREL had an annual budget of $60,000, but it quickly increased.


70 An example is the work of H. J. Oosting during the 1940s, cited in Odum, op. cit. (69).


72 Interviews with Auerbach (16 October 1985) and Odum.

73 Odum, op. cit. (65).
Already in 1951 Odum had expressed interest, as had the team of South Carolina, in the use of radioactive tracers and in experimenting with radiation effects in their ecological studies. But they had no expertise in these methods, and the first grant did not give them room to develop it. Others had preceded them in the use of radioactive tracers in ecology, notably Hutchinson. But Hutchinson did not have the AEC behind him, a support that would be crucial in this field.

Norris and a graduate student started the first radiation effects studies in 1955. In 1957, the first radioactive tracer experiments were carried out, initiating a second major research line on food chains. Odum took a leave of absence during the academic year of 1957–58, to increase his competence in radiation ecology. He was by then already thoroughly familiar with the Oak Ridge programme, having been asked to serve on its advisory board by Stanley Auerbach. On an NSF fellowship he spent four months at UCLA, studying desert ecology and the effects of radiation near the testing grounds in Nevada. He spent another four months at the Hanford Works. During this period, Odum wrote a new chapter on radiation ecology for the second edition of his Fundamentals, which appeared in 1959.

In the early years of radiation ecology, the ecologists at ORNL had been mostly limited to problems (and isotopes) with some direct relevance to the problem of radioactive waste. Odum, in comparison, was much more free to make his own research choices and steer radio-ecological methods in the direction of food chain analysis earlier than Auerbach did. They had to sort out for themselves many problems related to the radioactive tagging of plants and animals, even though other researchers had preceded them. Hutchinson had simply administered a sample of radiophosphorus to a lake by dumping a small quantity into the water, and with the help of Geiger counters and a graduate student traced its uptake by the vegetation and plankton.

Experiments started at Savannah River in the spring of 1957. Tagging techniques proved most useful (by injecting the stems of plants with P-32). Measuring of the uptake of radioisotopes was performed with Geiger counters. By plotting radioactive uptake against time, Odum and his colleagues were able to show the place that various insects occupied in the food chain, such as the predatory activities of certain spiders who fed on

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74 Odum, op. cit (61).
77 He stayed with Charles Elton in Oxford during the remainder of the year. (Odum, interview).
79 Hutchinson and Bowen, op. cit. (75).
leafhoppers and beetles (which in turn obtained their radioactivity from plants).  

In many respects, the methods were simple and crude, and later would be much improved. The application of radioactive tags to plants was standardized in 1962, and a new method, applicable on a larger scale, was introduced in 1967. In the early years, insects were collected by making ten rapid sweeps through the vegetation with a sweep net (others made fifty sweeps to obtain greater accuracy). In 1967, the use of a commercially made motor driven suction insect collector was reported. The Geiger counter is not a very efficient counting device — it would be replaced by a Tracerlab thin window, gas flow, automatic beta counting system or by a well-type scintillation detector. Still later, stable isotopes could be used with mass spectrometers, while measurements of concentrations of compounds would be performed with gas chromatography.

How did the radiological studies contribute to Odum's stated goal of developing a 'holistic' point of view with respect to the functional characteristics of whole ecosystems? In 1956, on the occasion of the International Conference of Peaceful Uses of Atomic Energy, he had pointed out that studies of the effects of radiation should not be directed merely to individual organisms. The impact on the 'total' system should also be assayed, and tolerance levels for entire ecological systems determined. In order to reach that goal, he distinguished three approaches to finding 'methods for the measurement of total community structure and function': measurement of productivity, trophic structure and species structure.

As we have seen, the research that Odum developed at Savannah river met these demands reasonably well. Occasionally, Odum was rather quick to claim the existence of homeostatic mechanisms. Be this as it may, Odum...
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did develop testable hypotheses concerning the structure of ecosystems as related to the theoretical properties of ecosystems, such as his general theory on succession, and the famous relationship between diversity and stability of ecosystems.

Yet it is interesting to note that research at the University of Georgia diverged in a number of directions, not least toward physiological studies of individual organisms and populations. In a sense, these originated from an extension of the research on energy transmittal from one trophic level to another. The physiological studies are still being pursued. One relatively early example of these studies, carried out in the late 1950s, was the investigation of excretion rates of various radioactive tracers. The tracers were examined with regard to their appropriateness for the measurement of metabolic rates of animals such as arthropods and fish. It was now possible to quantify the extent to which the energy contained in food consumed by the species in a particular trophic level was ‘lost’ through processes such as respiration, so that only a limited amount of the energy was assimilated and in turn became available for higher trophic levels. The effects of various environmental factors on these physiological processes were also examined.\(^ {88}\) There was thus no overriding effort to direct as much research as possible to the single level of the ecosystem.

It should be pointed out that Odum had a very liberal attitude with regard to the research that his fellow workers originated. His style of directing the programme consisted, in his own words, in pointing to some opportunities and leaving the rest to the newly hired person.\(^ {89}\) As a result, the programme at Georgia could indeed diverge, to the point that research projects with a ‘reductionistic’ perspective were welcomed as a natural complement or precursor of the ‘holistic’ research that Odum had in mind. But Odum more than made up for this divergence by his way of conferring his enthusiasm for discovering the principles on which the functioning of ecosystems were founded. In a way, his style of directing the programme was that of a charismatic role model rather than that of a manager-entrepreneur.

On the institutional level the creation of the Institute of Ecology prevented Odum’s activities from falling victim to the vicissitudes of the university’s departmental organisation. Odum and his colleagues with faculty positions at the University of Georgia lobbied successfully for an Institute, independent from any department. In 1963, the Board of Regents approved the establishment of the Institute of Radiation Ecology. (The following year, slows down, another may speed up in a compensatory manner.’ Odum, op. cit (50), p. 4. A researcher with a way of thinking different from Odum might have ascribed this phenomenon to the law of great numbers operating in an aggregate, rather than assuming some system property.

\(^ {88}\) Odum and Golley, op. cit. (84).

\(^ {89}\) Odum, interview.
the name was changed to Institute of Ecology.) In 1966 the University provided funds to employ an executive director and secretary. In the same year, the Institute obtained an NIH training grant in ecology, which was used to attract new graduate students and to hire more members of the staff. In 1970, the Graduate School approved the Institute's programme leading to a PhD in ecology.90

The Institute of Ecology was a very versatile organisation. Odum and his fellow ecologists could bring in a new person without the necessary approval of one of the departments. If a tenured university position should be desired for someone, it was not just to the Zoology Department they could turn, but to departments such as Entomology or Forestry as well. The ample sources of 'soft money' were used to enhance their academic freedom considerably.

Radioecological studies at Oak Ridge National Laboratory

Oak Ridge National Laboratory started a collaborative project with the Tennessee Valley Authority in 1950. Scientists from the latter agency conducted ecological surveys under the direction of Louis Krumholz, determining the contamination of fish with radionuclides in White Oak Lake.91 The project was discontinued in 1954, apparently at the instigation of Alvin Weinberg, director of research of ORNL.92 Krumholz's project had been initiated by the director of the Health Physics Division, Karl Z. Morgan. He and his associate Edward Struxness remained interested in adding ecology to the research performed at their laboratory, biomedical and biochemical investigations of the problems radioactive waste posed to human health. In the same year that Krumholz had to stop his project, ecologist Stanley Auerbach joined the staff of the Health Physics Division.93

Stanley Auerbach had received his education from some of the best known American naturalists and animal ecologists. He had taken his Master's in Zoology with Victor Shelford at the University of Illinois in 1947, at the age of 26. He had worked mainly on the taxonomy and ecology of arthropods, and he pursued that interest when, at the suggestion of Shelford, he turned to Orlando Park at Northwestern University to work on his PhD.94 He completed his dissertation in 1949, and on the basis of it published an extensive description of the centipedes of the Chicago area in

91 Whicker and Schultz, op. cit. (2), p. 5.
92 Interview with Stanley Auerbach, 16 October 1985.
93 Struxness, leader of Waste Disposal Research and Engineering of the Health Physics Division at ORNL, had first asked Orlando Park, Professor of Ecology at Northwestern University, to be consultant to the Division. Park acquainted himself with radiobiological problems and he suggested hiring his latest graduate student, Stanley Auerbach.
94 Auerbach, interview.
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*Ecological monographs,* while his naturalist inclinations are even more clear from a key to those centipedes. 95

At Oak Ridge, Auerbach set up an experimental project, in the laboratory and in the field, exposing arthropods to radiation and establishing simple dose–response relationships. In the field studies, radiation sources were brought close to the natural habitat of the arthropods. He made attempts to explain findings that were not in accordance with expected dose–response relationships as a complex combination of reduced predation, parasitism, or competition, thus taking species with whom the centipedes interacted into account. He thus aimed at developing an ‘ecosystem’ concept of the soil, the habitat of the centipedes. 96 Later, Auerbach would comment that this ‘proved to be an intellectual challenge well beyond [their] capabilities’. 97

In 1956, D. A. (Dac) Crossley, an insect ecologist, was added to the staff and joined Auerbach with his experiments. 98 Auerbach’s not yet recognizable empire-in-the-making grew steadily in size, but his institutional environment also became more complex. John Wolfe let Auerbach know that the opinion in Washington was that his arthropod approach was ‘too fundamental’. At Oak Ridge, independently of Wolfe, Alvin Weinberg was taking a detailed interest in what all his associates were doing. During laboratory meetings, Weinberg ‘grilled’ Auerbach with questions concerning the relevance of his research, questions that Auerbach found hard to answer. 99 But Weinberg had reasons of his own not to dismiss an ecology programme at his Laboratory. His policy was one of diversification of research activities, 100 and ecology could conceivably play a role in that, albeit a small one.

Around 1956, the White Oak Lake was drained, producing one of the most contaminated lands in the world, with high amounts of strontium-90 and caesium-137. Auerbach and Crossley concentrated their research on this area. In focussing their attention on the succession of plants and movement of radionuclides through plants and insects, they became in part plant ecologists. In the summer of 1957 they created an experimental agricultural plot where they grew corn, and performed measurements on the uptake and behaviour of strontium-90 and caesium-137 in corn, and subsequent transferral of these radioactive isotopes to insects. 101 Weinberg was very

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97 Auerbach, interview.

98 D. A. Crossley (1927) received his education at Texas Technological College and the University of Kansas. Among his fellow students at Kansas was Paul Ehrlich (Interview with Crossley, 10 October 1985).

99 Auerbach, interview.


101 See S. I. Auerbach and D. A. Crossley, ‘Strontium-90 and cesium-137 uptake by vegeta-
happy with the direction that the research had taken, and the ecological programme at Oak Ridge was saved.\textsuperscript{102}

Both Auerbach and Crossley were strongly interested in a further development of the ecosystem concept in their research, whatever its meaning would be, even if they did not have the background necessary to do it wholly by themselves. Auerbach's interest in ecosystem concepts dated from his graduate student days. Like his advisor Orlando Park, he had been very impressed by the paper on ‘trophic-dynamics’ by Raymond Lindeman.\textsuperscript{103} Crossley, on his part, sympathized very much with Eugene Odum's ecosystem approach in his \textit{Fundamentals of ecology}, a book that Crossley had greeted with enthusiasm.\textsuperscript{104} But they needed help to guide them in their intuitive search for an ecosystem approach. Auerbach would accomplish this for his group thanks to the help of Eugene Odum and Jerry Olson, the former in his capacity of consultant in the early stage of the group, the latter hired in 1958 as a research ecologist.

Odum was nominated to the advisory committee of the Health Physics Division. His nomination also served to enhance the scientific credibility of the ecology programme at the Division in the eyes of Alvin Weinberg.\textsuperscript{105} '[Odum] came up every six months or so and told us in great detail what to do and what not to do', Crossley said, looking back twenty years later.\textsuperscript{106} Auerbach and Crossley regarded Odum's approach as novel and particularly suited to radio-ecological problems:

Ecology at that time was in this country very largely physiological ecology. . . . Eugene's approach resurrected the ecosystem concept. It was different and very timely, because we were concerned in 1956 with radioactive fallout, where is it going to go, what is it going to do. We were just beginning to be concerned with pesticides in the environment. These things were problems that could not be approached by the ecology of that time, [which] was evolutionary based ecology.\textsuperscript{107}

But if Odum took the lead in establishing ecosystem ecology in the United States, he would not translate its concepts in mathematical terms. In contrast the reputation of Oak Ridge would ultimately rest on the production of simulation models of ecosystems, for which the use of mathematics
in ecology was an essential prerequisite. For this, Jerry Olson, who joined Oak Ridge National Laboratory in 1958, would lay the foundations. The models found their fullest expression during the American contribution to the International Biological Programme (1968–1974). By that time, Oak Ridge was established within the community of academic ecology, a position to which it was led most purposively by Stanley Auerbach.

The institutional development of the Oak Ridge programme

As has been noted above, Stanley Auerbach at Oak Ridge National Laboratories faced a much more constrained situation than Odum in institutional respects. ORNL was not an academic environment, even if an arrangement between ORNL and a group of Tennessee universities, notably the University of Tennessee, brought Auerbach and several of his collaborators an academic status.108

In addition to the ORNL’s general characteristic of being a mission oriented science laboratory, there was the peculiar circumstance that the ecology group resided in the Health Physics Division, not in the Biology Division. As a consequence, Auerbach, Crossley and the rest were in daily interaction with physicists, not biologists. This circumstance influenced the perspective that Auerbach took in the development of his group’s work.109

Within the Health Physics Division, Auerbach obtained some independence for his group of ecologists with the creation on a Radiation Ecology Section in 1959, of which he became Chief.

It might be said that Auerbach, in building his group, deployed two seemingly conflicting strategies. One was to adapt to the constraints of his environment, in cognitive and institutional respects. This is shown, for instance, by his eagerness to develop a mathematically oriented ecology. The physicists, his superiors and his close colleagues, expected no less.

A second strategy of Auerbach became apparent in his ambition for academic recognition. It was very clearly shown by his desire to play a role in the Ecological Society of America. In 1964, he became Secretary of the ESA (when Eugene Odum became its President-elect); he remained Secretary until 1969. Auerbach had taken the Secretaryship ‘for the very deliberate reason that it would provide an entree for (him) into the Ecological Society, and also to get Oak Ridge identified as an ecological center’, reasoning that the ESA members would receive mailings seven times a year with Oak Ridge on the letterhead.110 Being ex officio member of ESA committees such as the

108 The universities involved form the ‘Oak Ridge Associated Universities’. Stanley Auerbach received an appointment as Lecturer at the University of Tennessee at Knoxville in 1960, and as Adjunct Research Professor in 1965; D. A. Crossley as Lecturer in 1965 and as Associate Professor in 1966.
109 Auerbach, interview.
110 Ibid.
Public Affairs committee, Auerbach tried to interest Senators and Representatives and their staff in ecology. Several of those contacts proved most useful when the lobbying for the IBP started. Little things helped him to function efficiently. Auerbach could freely make long-distance calls, which most of his academic colleagues at the time could not. During this time, he established a reputation among ecologists in the United States of being a good administrator.

Most important for realizing his ambition of academic recognition was of course the building of a sound research group, visible to the scientific community. Auerbach succeeded, after 1960 turning himself more and more into the administrator of his own expanding program. Around 1966, he had a group of 14 scientists. In 1968 he was designated as Director of the Eastern Deciduous Biome Project of the American part of the International Biological Programme, thus becoming Principal Investigator of a very large NSF-funded research project, in which several ecological academic research centers of high reputation also participated, along with his own group. Auerbach was elected President of the ESA in 1970.

It seems fair to say that Auerbach's success consisted in reconciling the conflicting demands of adapting to the norms and values specific to the ORNL and the Health Physics Division, and realizing academic recognition, the latter most forcefully demonstrated by the fact that a large NSF project was administered through the ORNL. But true to the 'big science' culture of the National Laboratories, Auerbach did not import the more liberal features of a traditional academic work organisation into the ecology group. Hierarchic forms of work organisation became even more apparent when Auerbach's group received a separate status as Ecological Sciences Division within the ORNL in 1970: while Auerbach was thus promoted from Section Chief to Division Director, some of his collaborators could now be promoted to Section Chief. Unlike Odum, he acted as a real scientific director for the whole group, setting out research lines for all of its members. As a result, the Oak Ridge programme had a much more focussed character than the Georgia program. Its focus did evolve, however, in important new directions.

Around 1957 then, we might speak of some convergence between the ecological programmes at Oak Ridge and the work at Savannah River. Both used radioactive tracers to measure the flow of materials through the food chain. Both groups did so in an experimental and quantitative manner, although the Oak Ridge group was constrained with respect to the choice of radioactive isotopes: strontium-90 and caesium-137 were investigated primarily for their relevance to the problems of fallout and radioactive waste. But the Oak Ridge group took the lead in the use of quantitative data for the
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mathematization of ecosystem processes and the construction of ecosystem models. 112

In 1957 Auerbach attended the annual AIBS meetings in Connecticut, where he listened to a contribution by an as yet little known plant ecologist, Jerry Olson. In his lecture, Olson presented the use of a pair of differential equations to account for the gain and loss of nutrients in an ecosystem. Auerbach discovered a certain similarity between Olson's subject and the research of his own group on the flow of radioactive isotopes through ecosystems, and he felt that Olson's approach might be just the right way to develop the mathematical description of ecosystem flow processes. The following year, Olson was offered a position at the Health Physics Division. 113 Karl Z. Morgan, the director of the Health Physics Division, was also pleased with Olson's equations, discovering a remarkable similarity between them and the kinds that the physicists in his Department employed. 114

Olson initiated a second stage in the mathematization of ecosystems around 1960. Together with the ecologists Bernard C. Patten, 115 who joined the staff in 1963, and also with George Van Dyne 116 who was hired the following year, Olson developed simple ecosystem models that could be simulated on analog and digital computers.

Jerry Olson (born in 1928) received his education at the University of Chicago. After taking undergraduate degrees in liberal arts and geology, he completed his education in 1951 with a PhD in botany with the plant ecologist Charles Olmsted as supervisor. He interrupted his studies at the University of Chicago for a semester at the University of California at Berkeley, where he studied soil science with Hans Jenny. From 1952 until 1958 he worked at the Connecticut Agricultural Experiment Station in New Haven. Olson did not have any formal connection with Yale University, but he regularly attended the seminars of Hutchinson. Olson regards Olmsted and Jenny, and to a somewhat lesser extent Hutchinson, as his most influential teachers. 117

The first research line that Olson developed at Oak Ridge was a continuation of his previous empirical research on soil formation and the part played

112 The use of mathematics for the theoretical investigation of ecological systems was, of course, by no means new in ecology. These previous studies were usually confined to simple systems, such as predator-prey systems, and formed part (as they still do) of population dynamics. See Kingsland, op. cit. (53) and McIntosh, op. cit. (1), pp. 171–92.

113 Interviews with Jerry Olson (16 October 1985) and Stanley Auerbach. Olson was the fifth person to be hired in the ecology group of the Division.

114 Ibid.

115 Bernard C. Patten (1928) received his education at Cornell University, the University of Michigan and Rutgers University (PhD in Botany in 1959).

116 Van Dyne (1922) received his education at Colorado A & M College, South Dakota State University and the University of California at Davis (PhD in nutrition).

117 Olson, interview.
in it by the breakdown of organic litter. But from now on he had the advantage of having radioactive tracer methods at his disposal.\textsuperscript{118}

Secondly, Olson elaborated his theoretical treatment of litter decay. In 1959, Olson gave a paper at the Ecological Society of America Symposium on 'Energy flow in ecosystems', at the University of Pennsylvania. The Symposium was organised by E. P. and H. T. Odum. The paper was published in 1963, in *Ecology*.\textsuperscript{119} (The editors of *Current contents* classified the paper as a 'citation classic', noting that it received over 200 citations by 1985.)\textsuperscript{120}

In comparison with his earlier work, the article in *Ecology* shows a remarkable shift in vocabulary. Olson discusses the subject of litter decay in terms of *production*, *energy*, and *trophic levels*, none of which were mentioned in previous articles. References to R. Lindeman and E. P. Odum now also appear.\textsuperscript{121}

An important new line of theoretical investigation was started around 1960, when Olson turned to the analog computer to simulate ecosystem processes such as litter decay. At first, Olson may have turned to the analog computer as a simple computational device to keep account of net change in radioactivity in terms of gains and losses. But in his earliest publication on the subject, the analog computer is used for much more than that, notably for situations in which the analytic solving of differential equations would be too difficult. Instead of only one 'compartment' (i.e. the soil) of which gains and losses are determined, computations are performed on several coupled compartments at once.\textsuperscript{122} Olson was among the first to use an analog computer to investigate ecological problems, and probably the first to use it for simulating ecosystem processes. Shortly before him, H. T. Odum had simulated ecosystem behaviour with an electrical circuit.

In Odum's analogue circuits, the flow of electrons corresponded directly with the flow of carbon through the ecosystem. Branching electrical wires represented different flows of food in a real ecosystem, while variable resistances likewise represented populations of producers and consumers (Figs. 3–4). Milliammeters in each circuit permitted 'rapid visual examination of the electrical flow which represents the flow of carbon . . . '.\textsuperscript{123} The manipulation of the analogue (resembling an ecosystem on which Odum had empirical data) enabled him to produce a number of 'hints' as to how


\textsuperscript{120} *Current contents* (in press).

\textsuperscript{121} Olson, op. cit. (119), pp. 322, 328.

\textsuperscript{122} J. S. Olson, 'Analog computer models for movement of nuclides through ecosystems', in *Radioecology*, op. cit. (80), pp. 121–5.

\textsuperscript{123} Olson, op. cit. (122), p. 5.
ecosystems would work, in qualitative as well as in quantitative ways. Thus the analogue circuits served him as an ‘electrical computer’.\textsuperscript{124} The perceived analogy between real ecosystems and electrical networks was so important to Odum, that he continued to make use of it.\textsuperscript{125}

In comparison, there are important similarities between the way Olson translated a hypothetical scheme of boxes and arrows representing functional relationships in an ecosystem into an analog computer circuit, and Odum’s operations leading to electrical circuits. The diagrams resemble each other and can be transformed into each other (Figs. 3–5). The ecosystem diagrams that they represent (consisting of various compartments such as herbivores and decomposers) are essentially a new transformation of Lindeman’s pyramids of trophic levels, now drawn as a number of interconnected boxes.\textsuperscript{126}

\textsuperscript{124} Olson, op. cit. (122), p. 7
\textsuperscript{126} The first such diagram may have appeared in H. T. Odum, ‘Primary production in flowing waters’, \textit{Limnology and oceanography}, (1956) 1, pp. 102–17. It is redrawn in E. P.
Fig. 4: 'Electrical analogue circuit for a steady state ecosystem like the one in Fig. [3]' H. T. Odum, 'Ecological potential', 4.

An important similarity between both kinds of models is the fact that they both depend on 'input'. The nature of this input is perhaps most clearly evident in Odum’s electrical circuit: the power derived from the charged batteries is analogous to the input of sunlight in the ecosystem.\footnote{Olson's 'photosynthetic rate functions' are their equivalent.} The nature of this 'input' would prove to be of far-reaching consequence for the implicit philosophy of these and later system ecological models. The implication was that the 'driver' of the ecosystem was a non-biotic, climatic factor, and thus put what we may in fact remember as the 'density-independent' factors of the 1950s in ultimate control of ecosystems.

Yet there are differences. One is that Olson introduced positive feedback as well as negative feedback functions in his diagrams, which allowed him to account for situations other than the steady state. Later, Odum would make up for this. The most important difference, however, concerns the nature of the model. Odum measured currents, representing flows. Olson measured voltages, representing flow rates. Rates are expressed by differential equations. In contrast, Odum used the much simpler arithmetic of Ohm’s Law.

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The electrical circuit provided Odum with a direct material analogy, with 'energy' as the common denominator of ecosystem flows and electric currents. In addition, the circuit helped him to make computations. To Olson, like Odum, the analog computer was not primarily a computational device. His diagrams also implied analogies between ecosystems and non-ecological systems. But because these analogies were abstracted in equations, the computational aspect gained more prominence.

Systems ecology at Oak Ridge (1963–1968)

It seemed as if the process of litter decay on which Olson originally worked was too small a problem for the large capacity of the National Laboratory Analog Computer Facility at Oak Ridge. Flows between nine interrelated compartments could be charted, and computations performed on them. These nine compartments represented a partial ecosystem. Olson's original research interest can be deduced from the fact that five of these compartments were soil related, e.g., 'roots' and 'organic litter on top of soil'.

Subsequent ecosystem models gradually lost the emphasis on soils and litter decay.

In a paper he gave at the 1963 Jubilee Symposium of the British Ecological Society, while on a Guggenheim fellowship in England, Olson set forth some theoretical questions that he thought could be addressed by ecosystem modeling. He firmly put the steady state of ecosystems in the center of his considerations:

More important for questions of stability of the community and ecosystem is whether the widespread deflections from the steady state automatically tend to become corrected, and if so, how rapidly . . . . Many models would imply negative feedbacks and a restoring tendency. The further point deducible from models but not from verbal formulation and climax theory is some estimate of time-lags in the response of the ecosystem after a perturbation.

In fact, Olson formulated here what would become the orthodoxy of systems ecology during the International Biological Programme, namely that ecosystems function in, mathematically speaking, a single domain of attraction. If perturbations made ecosystems deflect from their steady state situation, they would self-correct, i.e., move back toward the stable equilibrium point of the domain of attraction.

The new systems orientation also inaugurated an upscaling of the empirical studies and with them, of the use of radioactive nuclides. In 1962,

128 Olson, op. cit. (122), p. 124.
130 Olson, op. cit (129), p. 112.
Auerbach and Olson took part in an experiment in which they tagged thirty tulip poplars on a forest portion of 20 x 25 m with caesium-137, the results of which were published in *Nature*. The experiment was set up to determine cycles and rates of cycling of caesium in this forest ecosystem and apply the results to Olson's analog computer model of mineral cycling. One of the conclusions was that much more data was needed. This conclusion is not as trivial as it may seem. The expensive IBP projects that started in 1968 were partly conceived as crash programmes to obtain the vast amount of data needed for ecosystem simulation models. In a subsequent publication a validation of the model by comparing model simulations on a digital computer with real data showed that in order to achieve an approximation of the model's behaviour with the real forest system the incorporation of many more refinements, such as seasonal fluctuations would be required. Olson noted with satisfaction that the analogy between the ecological model and physical-chemical and physiological systems seemed to work out.

Systems ecology as it was developing at Oak Ridge obtained a much broader audience when a course — the first of its kind — was offered at the nearby University of Tennessee at Knoxville. The course was given by Olson, Patten and Van Dyne for a number of consecutive years. Their part-time (20%) faculty appointments were paid for by the Ford Foundation. Apart from students who could take the course for credit, the course was also attended by other ORNL ecologists, post-doctoral fellows and visitors, for whom National Science Foundation support was available.

Olson, Patten and Van Dyne contributed in various ways to the course. Olson’s method of model construction was followed. The imposition of a strong cybernetic framework on the subject matter might be considered a contribution of Patten's. George Van Dyne’s contribution to the course may be characterized in part by the development of the general management relevance of the models. Coming from a background in range management, Olson already was lecturer at the University of Tennessee since 1960. In 1964 he became Professor of Botany. Patten and Van Dyne became Associate Professors in Botany in 1964.

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134 Jerry Olson already was lecturer at the University of Tennessee since 1960. In 1964 he became Professor of Botany. Patten and Van Dyne became Associate Professors in Botany in 1964.
he was strongly interested in the optimization of the performances of systems. The course served to create visibility for Oak Ridge National Laboratory as a center for the simulation modeling of ecosystems.

Olson's models became the major influence on the future work of the Oak Ridge ecologists. Crossley, for instance, started learning the mathematics of systems ecology. During the IBP, Crossley would head a separate systems ecological program at the University of Georgia. Patten and Van Dyne after 1963 increasingly used digital computers. Like Crossley, Patten moved to the University of Georgia, Van Dyne to Colorado State University. They all continued ecosystem modeling. During the International Biological Programme, in which the three institutions participated, ecosystem models formed the core of the IBP research projects.

The state of systems ecology around 1967

To what extent then did systems ecology exist in 1967, the year in which Congress decided to endorse an American contribution to the International Biological Programme with the specific intention to promote systems ecological research? A comparison with other system-like ecological activities in the USA at the time will help us to appreciate the extent to which the programs at ORNL and the UGa were forming the beginnings of a new ecological subdiscipline, i.e. systems ecology.

If we disregard for the moment the fact that any computation carried out on a 'system' as simple as for instance two species could be called 'systems ecology', and seek instead to capture the meaning of the term 'systems ecology' assigned to it during and immediately after the IBP, we may come to the following definition: (1) it is ecosystem ecology, i.e., it assumes large entities such as landscapes or biomes to be functionally integrated wholes and it attempts to uncover their structure and behaviour; (2) it attempts to represent such ecosystems by models that lend themselves to simulation and analysis with the help of computational devices, and by doing so to develop or test assumptions concerning the structure and functions of ecosystems; and (3) it attempts to make ecosystems amenable to management, i.e. to put their functioning under the control of man and to optimize its yield or output. Models of the latter kind are called 'total ecosystem models'. By consequence, any model not representing a whole ecosystem is a submodel or a partial model, and, within the context of the systems ecology of the 1960s and 1970s, presupposes such a comprehensive model, even if that

137 G. M. Van Dyne, Ecosystems, systems ecology, and systems ecologists, Oak Ridge, 1966.
138 'At the kitchen table, on Sunday afternoons.' (D. A. Crossley, interview).
140 On Van Dyne's project at CSU, see C. L. Kwa, 'The modeling of the grasslands', Historical studies of the physical and biological sciences, in press.
141 See Kwa, op. cit. (7).
model does not in fact exist. The expectation of the early systems ecologists was that the models eventually would mimic the real ecosystem in all its relevant aspects.

In addition, certain basic assumptions about the nature of ecosystems and modeling were shared by the early system ecologists: (1) Ecosystems are stable systems. After a perturbation they return to equilibrium. According to E. P. Odum’s thesis, they are the more successful in doing so when they are more diverse, that is when more stabilizing relationships of a cybernetic type can be assumed to exist. (2) True to the legacy of Lindeman, an emphasis is placed on nutrient cycling and the transfer of energy and biomass between compartments of functionally related species rather than on individual species. Diversity and stability are also usually defined in these terms. (3) The actual state of an ecosystem is determined by climatic variables, rather than by the dynamics between species in the ecosystem. The inclusion of these assumptions makes systems ecology a specific research program as much as a subdiscipline. If we take the above definition of systems ecology as a yardstick, systems ecology existed around 1967 as a research project, or even as a research ideal, rather than as an established research practice. It was expected that the IBP would bring this practice about.

What else existed on the American ecological scene that bore relevance to this systems ecology in statu nascendi? With respect of the modeling of whole ecosystems, Olson, Patten and Van Dyne (and H. T. Odum) were still pioneers. H. T. Odum’s study in Puerto Rico had many important similarities with the Oak Ridge approach. Later, while the IBP was already under way, an attempt to establish a Tropical Forest Biome project for which Odum was to serve as Biome Director, failed to obtain support. Thus Odum was deprived of a way to put his own variant of systems ecology much more to the test.\(^{142}\)

With regard to comprehensive ecosystem projects, the most important in terms of size and funding was the Hubbard Brook Ecosystem study, which is still being pursued. In 1963, Gene Likens (Yale University) and F. Herbert Bormann (Dartmouth College) set up an experimental project to determine the input–output relations of nutrient elements in a small watershed. But Likens and Bormann never aimed at producing ecosystem models, not even in verbal form.\(^{143}\) The nutrient budgets that they established represented, in

\(^{142}\) Several organizational and planning meetings of the Tropical Forest Biome project were held during 1969. The project was still listed as one of the Biome projects in Research programs constituting U. S. Participation in the International Biological Program, Report No. 4 of the US National Committee for the International Biological Program (Washington DC, National Academy of Sciences, 1971), pp. 35–36.

the eyes of the IBP ecologists, important but partial system properties of ecosystems.\textsuperscript{144} Prior to the IBP, the Hubbard Brook study was probably the biggest of its kind, and certainly the biggest ecological project sponsored by the NSF. Likens and Bormann missed the IBP boat, although the Hubbard Brook study was considered for inclusion in the IBP.\textsuperscript{145} Comparing the Hubbard Brook study with the IBP projects carried out at UGa and ORNL, we can note important similarities. For instance, the Hubbard Brook project had a certain precedence in transcending a traditional barrier in ecology between limnological (freshwater) and terrestrial studies, and it also inspired IBP ecologists by its methodology of extensive and continuous measurements.\textsuperscript{146} It also had features that the IBP projects had not, among others a strong practical orientation to the problem of erosion of watersheds. Perhaps the project of Likens and Bormann could have been labelled ‘systems ecology’, but eventually it was not.

In order to understand the significance of the ecological programs at the UGa and ORNL in a national context, we should not merely point out their theoretical importance, but also their sheer size. Research on whole ecosystems as performed at the Oak Ridge National Laboratory and the University of Georgia needed more manpower than was normally available at American universities. The ecology programme at the National Science Foundation was chiefly oriented toward individual research projects at universities, mainly in population dynamics and community ecology. In this context the importance of the Atomic Energy Commission as a patron of ‘big ecology’ must be understood. But even most of the AEC-funded projects were small and strictly confined to radiological aspects of ecology.\textsuperscript{147} In terms of size, the groups at the UGa and ORNL were virtually unique. The IBP enabled them to expand further, and they retained their new size after the IBP.

\textit{Systems ecology as a movement and the impact of the AEC}

We found a movement of ecologists that wanted to ‘revolutionize’ ecology in its entirety. This movement wanted to unify the various subdisciplines of ecology under a single perspective. It wanted to point the way toward a new rationalistic approach to the management of nature.

\textsuperscript{144} Interview with F. E. Smith (25 September 1985).

\textsuperscript{145} See \textit{Report of the working session on deciduous forest ecosystems : Design of research for the comprehensive study (Atlanta, Georgia, January 26–28, 1968)}, for the potential inclusion of the Hubbard Brook study as one of 18 sites (p. 31).

\textsuperscript{146} Crossley mentioned the Hubbard Brook study as a source of inspiration for the design of the Coweeta project (Crossley, interview).

\textsuperscript{147} In 69 of the 82 research papers read at the First National Symposium on Radioecology in 1961, support from the AEC was acknowledged. Apart from AEC-run laboratories and government agencies, 32 different universities were listed as home addresses of the contributors to this symposium. See \textit{Radioecology}, op. cit. (86).
The starting point was radiation ecology, which originated almost completely in a mission-oriented context. With the exception of Hutchinson's early experiment of dropping a small quantity of radioactive phosphorus in a lake, the monitoring and use of radioactive isotopes was induced by the needs of the AEC.

The first stage of the movement toward systems ecology, 'ecosystem ecology', can be dated at 1953 and is linked with the name of Eugene Odum. This stage marks the beginning of a severance of links with evolutionary biology; a comprehensive functional perspective led to transcendence of traditional barriers in ecology. Several concepts originally developed by Lindeman (and later to become key concepts of systems ecology), may have fallen on fertile ground because of their management applicability and the fact that it appeared to be possible to implement them by radiation ecological methods. They had become entrenched at the UGa and ORNL before systems ecology properly speaking had been developed. Olson started to use its vocabulary only after he had joined the ORNL.

The AEC appears to have constituted a selective environment at least, and perhaps a formative one in some respects. However, the case of Hanford shows that the role of the AEC should not be overestimated. At Hanford, the Laboratory management expressed its needs explicitly, which constrained their ecologists to surveying the environment of the atomic plants. At ORNL and the UGa, the ecosystem ecologists created space for themselves to carry out a programme that apparently was not incompatible with the interests of the AEC. Their programme may indeed have appeared to serve those interests because of its management orientation, but it was a management orientation of a very general scope and not one exclusively designed to solve safety problems with regard to radioactive isotopes. And insofar as the AEC did form a selective environment, systems ecology as it arose in the early 1960s was not its completely contingent product. The ecosystem ecologists did have notions with regard to the direction they wanted to go, however vague they were.

The second stage, or 'systems ecology' phase can be dated at 1959 and is linked with the name of Jerry Olson, among others. The modeling of total ecosystems and simulation on computers was then inaugurated. With 'ecosystem ecology', Odum reached beyond the too narrow constraints of a small university culture with its departmental barriers. With 'systems ecology', the ORNL ecologists reached beyond the too narrow constraints of mission-oriented research. The new concept helped them to transcend the culture of the AEC and the National Laboratories and to reach out to the academic ecology of the universities and the National Science Foundation.

But we would have an incomplete understanding of the radiation/systems ecologists if we were to understand their movement as a way of securing for themselves a niche for a mere new subdiscipline of ecology. First, 'ecosystem
ecology’ was not a fail-safe strategy to win them a comfortable position. Even if Eugene Odum had created a sympathetic audience almost singlehandedly, ecosystem ecology risked being too fundamental for the AEC and too applied for academic ecology. Second, the ecosystem/systems ecologists aimed higher than a new subdiscipline. The ecosystem/systems ecologists have consciously sought to put the management of natural resources on a rationalistic footing. The metaphor of the automatic machine, the cybernetic combustion engine, gave a direction to the development of systems ecology concepts and its aims of managerial application in ways that have not always been transparent to its practitioners. The development of systems ecology was a manifestation of great technological optimism with regard to the possibility of the management of natural systems, by no means confined to ecologists.