Functional Ecology 1997
11, 268–271

Forum

The ecosystem: an evolving concept viewed historically

The now widely used term ‘ecosystem’ has had quite a long history and at various times interest has been focused on different aspects of its meaning. Not infrequently the term has been imprecisely or even incorrectly employed. This account aims to outline the changing emphasis of the term and seeks to promote its more exact use.

The word ‘ecosystem’ was first used in print by A. G. Tansley (1935) in his well-known paper on vegetational concepts and terms. Tansley considered that organisms, when thinking is fundamental, cannot be separated from ‘the environment of the biome – the habitat factors in the widest sense … with which they form one physical system’ (p. 299). These ecosystems are regarded as the ‘basic units of nature’ and are of the ‘most various kinds and sizes’. He notes that although the organisms are thought of as the most important parts of these systems, the inorganic ‘factors’ are also parts and ‘there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and inorganic’ (p. 299). Tansley concludes that ‘the fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment is the ecosystem’ (1935; p. 306) and he also refers to the ecosystem as ‘a recognisable self-contained entity’ (1939, p. 228).

At the time of active debates about communities and their similarities to organisms, Tansley recognized the need for a non-community-based descriptor of a wide nature. Clements (1905, 1916) strongly propounded the holistic nature of communities as organisms and of the plant formation as a superorganism, progressing to a climax state. Tansley (1935, p. 289), while agreeing that ‘mature well-integrated plant communities … had enough of the characters of organisms to be considered as quasi-organisms’, wished to introduce a broad term to comprehend not only the organisms but also to focus on the complex interactions of biotic and abiotic factors.

Although the coining of the term ‘ecosystem’ has long been attributed to Tansley, and his 1935 paper gives no acknowledgement, this term was suggested to him in the early 1930s by A. R. Clapham when Tansley asked Clapham (then a young man in the Department of Botany at Oxford) if he could think of a suitable word to denote the physical and biological components of an environment considered in relation to each other as a unit (Willis 1994, p. 81). When Clapham suggested ‘ecosystem’, Tansley, after some consideration, wholly approved of it. About 1983, Clapham made this known to his son David (letter from D.H.C. to A.J.W. 1991), ‘with considerable pleasure’, by which time the term ‘ecosystem’ had come into everyday use. Strangely, for nearly two decades after its first appearance in print, the term was little employed in ecological literature, especially in Britain. This is reflected by the entries in the *Oxford English Dictionary*. Besides referring to Tansley (1935, 1939), the next reference is to *The Tropical Rain Forest* by P. W. Richards. Here, Richards (1952, p. 206), referring to the importance of soil in relation to vegetation, wrote ‘It is … preferable to regard soil, vegetation, animal life, climate and parent rock as components of a single system, the ecosystem … and the development of the soil as influenced by all the other components of this ecosystem’.

The basic concept of the ecosystem, although originally not clearly formulated, is by no means new. Major (1969, p. 11) refers to the ‘great antiquity of the idea of the ecosystem as well as to its universality among mankind’. Theophrastus was aware of the importance of climate in plant distribution and the ‘sympathetic relationships’ between the life cycles of plants and the season (Woodward 1987), but these early ideas were little developed for more than two millennia. However, in 1887, Forbes described a lake as a microcosm and realized its interactive nature. The close interaction between plants and their environment was well exemplified by Cowles (1899, p. 184) who referred to the ‘symbiotic nature’ of the growth of the dunes bordering Lake Michigan. Thienemann (1918) and Allee (1934) were also aware of the integration between the biota and environment.

Early developments

The well-known paper on the trophic–dynamic aspect of ecology by Lindeman (1942) was a major step forward, drawing particular attention to the transfer of energy from one part of an ecosystem to another. It also categorized organisms into fairly discrete trophic levels as producers, primary consumers and so on, each successively dependent on the preceding level as a source of energy. Lindeman (1942, p. 400) considered that ‘The ecosystem may be formally defined as the system composed of physical-chemical-biological processes active within a space–time unit of any magnitude’, and he regarded the concept of the ecosystem to be of ‘fundamental importance in interpreting the data of dynamic ecology’. But for Lindeman’s untimely death, this concept would probably have come into wider use in ecology more quickly, as Lindeman would no doubt have developed his ideas more fully.

Odum in *Fundamentals of Ecology* (1953 and later editions) considered the ecosystem as the basic fundamental unit in ecology. Functionally, two components were recognized – autotrophic and heterotrophic – and four constituents – abiotic, producers, consumers and decomposers. Odum believed that the main function of the concept in ecological thought was to emphasize obligatory relationships, interdependence and causal relationships. Evans (1956), referring to food chains, physical processes and regulatory mechanisms, also regarded the ecosystem as a basic unit as important to ecology 'as the species is to taxonomy'. Odum gave a further boost to the ecosystem approach in 1957, writing (p. 531) 'After about 15 years of experimentation in the teaching of ecology, I have come to the conclusion that the ecosystem approach is by far the most effective for a basic "principles" course'. He considered that two ecosystems, a small lake and a recently abandoned agricultural field, illustrated beautifully many of the most fundamental ecological principles, e.g. trophic structure, productivity, succession and limiting factors, and provided a means of stressing principles basic to good management. Whittaker (1962) also commended the ecosystem approach, writing (p. 104) 'The stand and its habitat form together a functional whole, the ecosystem, or nature-complex, in which matter and energy are transformed between environment and organisms'. He also noted (p. 125) that 'The ecosystem conception suggests a multi-factorial or landscape approach to classification'.

Russian views

The landscape approach was one long favoured in Russia, developed by Dokuchaev (1898) and subsequently by Sukachev (Sukachev & Dylis 1968). The inter-relations considered by Dokuchaev were echoed in the word 'geobotany', and expressed in terms of landscape under 'geocoenose' and subsequently 'biogeocoenose' to emphasize the major role played by organisms. The biogeocoenose (or biogeocoenosis) was defined (Sukachev & Dylis 1968, p. 26) as

> a combination on a specific area of the earth's surface of homogeneous natural phenomena (atmosphere, mineral strata, vegetable, animal and microbic life, soil and water conditions) possessing its own specific type of interaction of these components and a definite type of interchange of their matter and energy among themselves and with other natural phenomena, and representing an internally contradictory dialectical unity, being in constant movement and development.

While closely similar to the ecosystem, the term biogeocoenosis has been claimed to have a more definite meaning, and to be preferred by some authors, especially Russian. The biggest difference in the concepts relates to scale; whereas biogeocoenosis refers to a single defined system of limited extent, the ecosystem may range from an anthill to the entire biosphere of the globe. Despite the undefined extent of ecosystem, this term is the one that has prevailed in ecological literature since about 1960 and come into general parlance. Many other terms (see, e.g., Sukachev & Dylis 1968; Major 1969) of fairly similar meaning have been proposed, including microcosm, biosystema, holocoen, epigen, ecotope and bioecos, but are currently little used instead of 'ecosystem'. There seems no advantage in a multiplicity of terms. The word 'facies' has also been used for ecosystem (Major 1969) but is employed in several other quite different senses.

Recent developments

Since about 1960 there has been a very substantial burgeoning of literature related to the ecosystem concept and the use of the term ecosystem, especially in America and Europe (see, e.g., Neel & Olson 1962; Van Dyne 1969, 1980; May 1973; Shugart & O'Neill 1979; McIntosh 1985; Jørgensen 1992). The contributions of many Americans and others to the development of ecosystem ecology are fully discussed by Hagen (1992) who described Eugene Odum as 'the dean of ecosystem ecologists' (p. 20). A major development was of 'systems ecology' (Odum 1964) concerning 'the structure and function of levels of organization beyond that of the individual and species'. Odum (1964) considered the ecosystem to be the basic unit of ecologists and he favoured a holistic, rather than a reductionist, approach. 'Functional' attributes of the ecosystem were stressed; indeed Odum (1968) concluded that 'eco-energetics is the core of ecosystem analysis'. Systems ecology, based on the ecosystem concept, was promoted by Patten (1966) and also by Van Dyne (1966) who considered systems ecology to be 'the study of the development, dynamics and disruption of ecosystems'. Applied mathematics and the use of computers in systems analysis have progressively led to the change in ecology from a 'soft' to a 'hard' science (Watt 1966; Patten 1971). This was foreshadowed by the modelling of ecological systems (Neel & Olson 1962) by the use of equations and simulations of ecosystems on computers. Many types of model are now available to synthesize details concerning components and processes, dynamic models using differential equations being particularly appropriate in the analysis of ecosystems (Mauersberger & Straskraba 1987; Jørgensen 1988). The development of systems analysis was promoted in the early 1960s onwards by the International Biological Programme, involving what has been termed 'big biology', elucidating the functioning of a wide range of ecosystems in many countries (see, e.g., Clapham, Lucas & Pirie 1976). Experimental manipulation of ecosystems has been described as 'a very powerful analytical approach' (Likens 1985), provided that there is a meaningful

reference or control (much has been learnt, for example, from long-term studies at Hubbard Brook).

On the occasion of the 75th Anniversary of the founding of the British Ecological Society, a survey of members was made concerning what were regarded as the 50 most important concepts in ecology. Of these 50, the ecosystem proved to be a highly outstanding first (Cherrett 1989). Other concepts very high on the list included energy flow, conservation of resources and materials cycling, all closely related to the ecosystem concept. As this concept can accommodate both the holistic and reductionist approach, these findings are not unexpected.

It may be cogently argued that ecosystem studies have changed from a descriptive to a predictive emphasis (Waring 1989). Systems theory, control theory and simulation modelling have all helped to elucidate the control points for fluxes of matter and energy and to estimate difficult-to-measure fluxes. The laws of thermodynamics have been increasingly invoked as a basis of ecosystem theory (Watt 1968) and recently a new 'law' propounded (Jørgensen 1992) that a system receiving a through-flow of high-quality energy will use it to move away from thermodynamic equilibrium; the organization that obtains the highest storage of high-quality energy will win. Jørgensen (1992) considers that an ecosystem theory incorporating both the analytical and synthetical approach is urgently needed, especially in relation to pressing global problems, and contends that different approaches have basically much in common.

Conclusion

The ecosystem concept has provided a productive basis for the understanding of natural systems with a high degree of organization. Concern for 'environmental health' (Rapport, Gaudet & Calow 1995) involving sustainable development has high-lighted the need for integrative science to safeguard ecosystems at risk. Studies of such ecosystems can be profitably designed to involve a wide geographical scale and also an extended time-scale. The robustness of the concept is evident from its ability to be extended across scales. However, it is important that the scale should be specified; for example, the utility of the progressive efficiency, the ratio of assimilation by two adjacent trophic levels (E_p), used as a measure of ecosystem maturity, is limited because E_p can be scale dependent (Strayer 1991). The definition of *ecosystem* could be refined as *a unit comprising a community (or communities) of organisms and their physical and chemical environment, at any scale, desirably specified, in which there are continuous fluxes of matter and energy in an interactive open system.* Stricter use of the term ecosystem is needed. It has often been misapplied, for example when simply population or community has been intended, and the scale of the ecosystem has frequently not been indicated (although many authors imply this to be large). Its future value may lie, at least in part, in providing a framework for predictive studies, using relatively new methodologies such as remote sensing and isotope analyses in the elucidation of the complex interactions in the natural environment.

Acknowledgements

I am very grateful to Professors P. Calow, C. H. Gimingham, J. A. Lee and F. I. Woodward for their warm encouragement and comments.

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