



The ecosystem: research and practice in North America

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Abstract. Since the early 1940s, the ecosystem approach has been developed in a variety of forms by North American ecologists. Lindeman established its foundation, with his focus on functional components and energy transfers between trophic levels; this view was developed further by several ecologists, including G. Evelyn Hutchinson, and H. T. and E. P. Odum. Ecosystem ecology eventually became closely associated with powerful American institutions, such as the Atomic Energy Commission, receiving ample support; in association with the International Biological Program it became known as "big ecology". More recently, ecosystem ecology has exhibited strengthened interest in spatial patterns, the role of species in ecosystems, and global change. This history has encompassed various ontological, methodological, ethical and political claims regarding the place of this approach in the discipline of ecology and in environmental governance.

1 Early ecosystem ecology

Ecologists in North America drew on numerous strands of ecological research elsewhere in formulating their initial perspectives on ecosystem ecology. Among these, British ecology was most prominent, including Charles Elton's conceptions of the niche, trophic levels, and food chains and cycles (Elton, 1927), and Arthur Tansley's definition of the ecosystem in terms of the interactions of plants and animals with each other and their abiotic environment (Tansley, 1935). As North American ecologists subsequently developed it, the ecosystem approach has incorporated claims regarding the ecosystem as ontological reality, as a methodological approach, and as an ethical and political perspective.

In 1942 Raymond Lindeman established the foundation of ecosystem ecology. His paper, "The Trophic-Dynamic Aspect of Ecology", appeared a few months after his death at the age of 27 (Lindeman, 1942; Hagen, 1992). In it he discussed concepts long of interest to ecologists, including succession and the trophic structure of communities. However, he integrated these concepts using energy to relate successional changes to the productivity of trophic levels and the efficiency of energy transfer between them. He thus showed how to relate long-term ecosystem change to shortterm events in energy flow and transformation such as food consumption and respiration.

Prior to Lindeman, ecologists had generally viewed nature in terms of species within an abiotic environment. He suggested instead that an ecosystem be viewed in terms of functional components. By reducing the complexity of food chains and ecological change to energy flows, he made ecosystems amenable to quantitative physicochemical analysis. This was a step towards a single unified ecology, and a step away from the view of ecology as grounded in appreciation of the uniqueness of each species. In addition, by stressing the rapid transfer of nutrients between living and nonliving ecosystem components, he undermined the distinction between these components. Thus, the chief ontological implication of Lindeman's concept was that ecosystems, as systems of flows and transformations of energy, encompassed not just living organisms, but all physical matter in the locality of interest.

Lindeman wrote his paper while a post-doctoral student with G. Evelyn Hutchinson of Yale University, who had been considering similar themes (Hutchinson, 1940). Through his reading of Victor Goldschmidt's works on geochemistry and Vladimir Vernadsky's explication of his biosphere concept, his own limnological studies of Linsley Pond, and his commitment to equilibrium, Hutchinson developed a theoretical understanding of the "metabolism" of ecosystems. In a 1948 paper he described the movement and accumulation of carbon in the biosphere and phosphorus in lakes. Organisms, he noted, influenced the movement of these elements; in turn, their productivity was partly determined by the availability of these substances. He also developed mathematical equations depicting the growth and interactions of populations. Underlying the behavior of both elements and populations were circular-causal paths, or feedback loops, damping oscillations, maintaining equilibrium, thereby ensuring the system's persistence (Hutchinson, 1948).

Hutchinson derived the feedback concept from developments in the study and management of complex systems. During World War II operations researchers had demonstrated that complex technology, such as missile guidance systems, could employ feedback loops to ensure optimum performance. After the war the study of self-regulation through feedback, or cybernetics, was transferred to peacetime research, motivated by the expectation that living and nonliving complex systems, including ecosystems, could be understood in terms of these general principles (Bowker, 1993; Taylor, 1988).

Hutchinson's students had considerable impact on ecosystem ecology. One was Howard T. Odum. In 1950 he completed his dissertation on the biogeochemistry of strontium. Its global distribution, he concluded, had long remained constant; this exemplified the self-regulation and stability of the "strontium ecosystem" (Odum, 1951). In subsequent research, Odum measured energy flow between trophic levels in a series of mineral springs in Florida (Odum, 1957). He drew energy flow diagrams, and converted these into electrical circuit diagrams, using a symbolic language to portray energy flow.

While Howard Odum drew analogies between ecosystems and physical systems, his brother Eugene, in contrast, related order and stability in ecosystems to physiological mechanisms of homeostasis. Eugene was probably more influential: at the University of Georgia, and in his textbook, *Fundamentals of Ecology*, he alerted ecologists to the potential of ecosystem ecology (Odum, 1971). The result was a growing number of ecosystem studies, including Ramon Margalef's (1958) application of information theory to ecosystems, Bernard Patten's (1959) work in cybernetic theory, and John Teal's (1962) study of energy flow in a salt marsh (Golley, 1993).

By 1960 a growing number of ecologists interpreted nature in terms of ecosystems within which energy and nutrients are exchanged, consumed, and transformed, and that possess feedback loops ensuring equilibrium. Such an interpretation had several implications. One was that ecological systems were not, in principle, distinguishable from physical systems: both obeyed common mechanical principles. Both also tended to remain at a point of stable equilibrium, to return to this point when perturbed, and the regulatory processes responsible could be understood and possibly manipulated to ensure optimum behavior.

This had political implications. After the war, the contribution of industry and science to victory, the hazards of societal instability, and the promise of cybernetics, encouraged a burst of "technocratic optimism" (Taylor, 1988). Howard Odum promoted his ecosystem theory as a potential basis for technocratic management. Human-nature ecosystems, he argued, could be designed and managed by an "ecological engineer" to ensure optimum efficiency and well-being. These notions of ecosystem efficiency and control also became associated with space exploration. The challenge of creating a livable environment within a spacecraft could be conceived as akin to that of designing a functioning artificial ecosystem - a similarity expressed in the science of "cabin ecology" (Anker, 2005). The ecosystem concept was also compatible with the widely invoked metaphor of "Spaceship Earth", which combined notions of a finite and fragile global system with confidence in the capacity of science and technology to understand, and manage, this system (Fuller, 1970; Höhler, 2008).

However, many ecologists disagreed with the implications of these perspectives, preferring to see knowledge of ecosystems as a basis for their preservation, not their control. Eugene Odum's research on coastal salt marshes, for example, contributed to a movement for their protection. In the 1970s the need to safeguard intact ecosystems was often invoked in arguments for wilderness protection. However, wilderness advocates did not work directly with ecologists in making these arguments, nor did they draw on the most recent work in ecosystem ecology; instead, they generally relied on simple assumptions regarding the stability and constancy of undisturbed ecosystems (Turner, 2012).

2 Big science and big ecology

In the 1960s large-scale funding stimulated development of ecosystem ecology. Until 1974 the Atomic Energy Commission (AEC) was the largest supporter of ecosystem research. It fostered innovations such as the use of systems analysis, radionuclides and other tools that helped shape ecosystem research. At the Oak Ridge National Laboratory, for example, ecologists used computerized simulation models to predict the movement of radionuclides (Bocking, 1997).

The AEC had several motives in supporting ecosystem ecology. It provided a quantitative physicochemical perspective on nature that physical scientists could respect. Ecosystem ecologists promoted AEC research tools, such as radionuclides. They also often defined nature as analogous to the complex engineered systems that were the AEC's primary concern. Overall, ecosystem ecologists contributed to the AEC ideal of a technological, nuclear-powered basis for American society.

In the late 1960s the American government allocated approximately \$40 million for ecosystem studies, through the International Biological Program (IBP). Through AEC and

IBP support, ecosystem ecology became known as "big ecology": large, hierarchical research teams based on corporate or military models of organization, focused on the study of entire ecosystems, developing computer models able to simulate and predict ecosystem behavior (Blair, 1975; Bocking, 1997; Kwa, 1987). It was believed that ecosystem ecology could provide the scientific basis for a response to increasing environmental concerns. Ecosystem ecology was also consistent with one view of the appropriate role of government: consistent with the technocratic ideal presented by Howard Odum, it promised a basis for replacing piecemeal, uncoordinated decisions that neglected the broader public interest, with comprehensive, rational policies (Hays, 1985; Hurst, 1977). By the late 1960s this view had gained a certain currency within the American political system. It was, however, soon displaced by an embrace of processes more typical of a pluralistic political system, including the negotiation, compromise and brokerage of competing individual interests, often in adversarial contexts. The comprehensive perspective of ecosystem ecology was less readily applicable to these processes. As a result, much of applied ecology, including the emerging field of conservation biology, turned away from this field, focusing instead on the study and modeling of populations and communities. One way in which ecosystem science did maintain its relevance was by providing a basis for evaluating the economic value of ecosystem services and, thus, for the commodification of ecosystems themselves (Robertson, 2006).

However, "big ecology" was not the only possible approach to ecosystem study. Beginning in 1963 F. Herbert Bormann and Gene Likens, with colleagues and students at the Hubbard Brook Ecosystem Study, began study of the biogeochemistry of a forest. They focused on the relation of the ecosystem to its surroundings, measuring the flow of nutrients into and out of watersheds. The varying capability of the watershed to retain nutrients, they argued, could provide insights into ecosystem functions. Further insights were derived from ecosystem experiments in which they deforested a watershed, measured its nutrient exports, and used the results to assess its capability to maintain stability and respond to disturbance (Bormann and Likens, 1979; Bocking, 1997). Experimental studies that involve the manipulation of entire ecosystems have since been undertaken at numerous other locations, including the Experimental Lakes Area in northern Ontario, particularly to understand problems such as eutrophication and acid rain. More recently, new ecological perspectives, as well as demands to understand the impacts of human activities, have led some ecologists to develop fieldbased experimental practices that, rather than manipulating entire ecosystems, instead take advantage of local environmental features to generate knowledge that can meet the standards of credibility of laboratory science, even in the "real world" of changing and imperfectly understood ecosystems (Kohler, 2012).

The continuing demand for scientific advice that is relevant to policy has also encouraged efforts focused on assembling existing knowledge about ecosystems. The largest such project, the Millennium Ecosystem Assessment (MEA), conducted between 2001 and 2005, was an effort by more than 1360 ecologists and other scientists to assess the state of the world's ecosystems. Unlike earlier international ecosystem projects, such as the IBP, the MEA did not include original research. Instead, its aim was to synthesize knowledge and generate results that would be relevant to policy and management. Accordingly, the MEA emphasized measures of the state of ecosystem services – that is, the contributions of nature to human well-being, such as through the supply of clean water, food, or climate regulation (MEA, 2005).

3 Research themes

Since the late 1970s several themes have been evident in North American ecosystem research. One is a continuing interest in energy flows and biogeochemical cycling. Environmental problems have often been defined in such terms, and in recent years urban theorists have applied an ecosystem approach to cities (Decker et al., 2000). However, after the IBP's limited success in modeling ecosystems, a perception also emerged that to conceptualize ecosystems only in terms of energy and matter was inadequate. More attention to the critical role of species, and to the spatial complexity of landscapes (including the mingling of natural and human history that has occurred in most localities), would be necessary. Interest in species and their roles in ecosystems has also been encouraged by developments in neighboring disciplines, including conservation biology, as well as by political interest in the status of species (particularly those considered invasive or endangered), and by the emergence of ecosystem management, conceptualized as a more holistic approach to managing natural resources and their use by humans (Bocking, 2004).

Another theme has been a shift to larger scale phenomena, especially apparent in studies of global change. Since the late 1980s study of the globe as a single system, through such initiatives as the International Geosphere-Biosphere Programme, has provided ecologists with both opportunities and obligations to scale up their work. New research tools, including satellite remote sensing data (often provided by NASA, which has played a role in encouraging adoption of new research technologies analogous to the role once played by the AEC), were applied to ecosystem studies at both global and smaller scales (Kwa, 2005). Many scientists studying local phenomena have also linked these to changes at global scales, especially climate.

However, these and other new directions in ecosystem research have also posed challenges. For example, technologies for remote sensing and tracking have raised questions regarding the extent to which it is technology, and not scientific priorities, that determines research problems; another question has been the implications of invasive technology (such as radio collars) on conceptions of wildlife and wilderness (Benson, 2010). These technologies, and the related ambition to link studies conducted at a variety of scales, also raise conceptual and practical challenges. The places where research is done are both practice- and question-specific; accordingly, when different techniques, guided by different research questions, are used to locate ecological phenomena (such as species populations), it becomes impossible to map unambiguously the locations of these phenomena (Shavit and Griesemer, 2009). Similarly, the definition of an ecosystem at a particular place is unavoidably ambiguous: ecologists with different theoretical and practical commitments, and applying different study techniques, will be studying different ecosystems, even if their studies are located in the same place. It becomes all the more difficult, therefore, to construct useful generalizations regarding the behavior of any particular ecosystem.

And finally, perspectives on the dynamics of ecosystems have been revised. No longer seen as an orderly system in equilibrium, nature is instead a patchwork, characterized by pervasive disturbance and instability. Ecosystems experience patterns of change over time: cycles of slow accumulation of biological capital, punctuated by its sudden release and reorganization. Forces that stabilize the ecosystem (such as forest growth) maintain its productivity and nutrient cycles, while destabilizing forces (say, a forest fire) maintain diversity and resilience. Constancy has been replaced by change, chaos, and non-equilibrium conditions (Botkin, 1993; Holling, 1986; Worster, 1994).

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