

**An Entangled Bank: A Brief history of Ecosystem Ecology**

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**The beginnings of ecology – the 1800s:** Much of the early work on ecology was conducted in England.

*Charles Darwin* (1809–62) – proposed the idea of survival of the fittest; viewed nature as battlefield on which individuals ceaselessly struggled in the "war of nature," but the battlefield was also a stable complex of interacting parts. He appeared to be suggesting an ambiguous relationship between competition and stability.

*Thomas H. Huxley* (1825–1895) – viewed the individual organism, or even the cell, as kind of population or community. A struggle for existence occurred within the stable multicellular organism.

*Herbert Spencer* (1820–1903) – a social scientist – developed a mechanical/organic model. Telegraph lines were compared to nerves, railroads to arteries, currency to red blood cells.

*Stephen A. Forbes* (1844–1930) – Indiana University – suggested that lakes were social microcosms; well ordered aquatic communities evolved and maintained by competition and natural selection. The term community became a fundamental ecological concept during the 20th century by suggesting a close analogy between human affairs and biological processes.

**Ecology in the early 1900s:** By 1900 the major themes of ecological discourse were established: change and uniformity, instability and equilibrium, competition and cooperation, integration and individuality. Plants and animals together formed a kind of superorganism.

*Henry C. Cowles* (1869–1939) – University of Chicago – studied long-term process of vegetational change (succession on sand dunes of Lake Michigan). Competition played a role in succession, but unlike Forbes' lakes, competition on dunes was less a matter of struggle among individuals than a struggle between individuals and their physical environment.

*Frederic Clements* (1874–1945) – Carnegie Institute of Washington: introduced a physiological perspective to ecology. He suggested that the community was a kind of simple organism. The community was an organic entity made up of interacting parts, much as an organic entity was made up of interacting cells. This was not a new idea but

what was unusual was that it was tied to a physiological perspective; the study of processes. Clements reputation rests primarily on his contribution to the study of succession (Clements 1916). No aspect was more controversial than his ideas on climax; especially the Clementsian "monoclimax" concept. The idea that within a given climatic region succession always ends in a single type of community; he did realize, however, that natural disturbances (such as fires) could modify climax patterns so a landscape could be a mosaic of climax and subclimax vegetation. Most of Clementian ecology has not stood the test of time but he had a powerful influence on the development of ecology.

*Henry A. Gleason* (1882–1964) – University of Michigan and New York Botanical Garden. He developed the individualistic concept of the plant community. To him succession was not a meaningful concept. The distribution of plants in a given area was the result of fortuitous immigration and environmental selection (never collected data to test this).

*Robert Whittaker* (1920–1987) – Cornell. He demonstrated that communities lacked clearly defined boundaries and suggested that climaxes are relative and there are degrees of climaxes.

*Charles Elton* (1900–) – an animal ecologist from Oxford interested in populations. He – developed the idea of food cycles or web and predator, prey relationships and the pyramid of numbers. He further developed the idea of the ecological niche originally developed by Joseph Grinnell in 1917. He diagrammed the food cycle of Bear Island (See Figure 1) and presented the food cycle as a regulatory mechanism for maintaining equilibrium within a community. His contribution are recorded in *Animal Ecology* (Elton 1927).

*G. Evelyn Hutchinson* (1903–) – Yale University – started by studying biogeochemistry of a Connecticut lake (Linsley Pond). A mathematical-limnologist who studied the idea of logistic growth along with the central ideas of cybernetics – the system, self-regulation, feedback oscillation and time lag.

### **Introduction of the term ecosystem**

*Arthur Tansley* (1871–1955) – A British plant ecologist who introduced the term ecosystem. He originally suggested that ecologists refer to plant communities not as organisms (like Clements), but as quasi-organisms. Towards the end of his career, however, he proposed the more neutral term ecosystem.

*Raymond Lindeman* – Yale. A mathematical-limnologist. He developed the – general theory of energy flow in ecosystems "trophic-dynamic viewpoint" He asked why the number of trophic levels in a food chain is limited to 4 or 5. At the 4th or 5th level the amount of energy is insufficient to sustain another populations of predators and productivity decreased at each step. He also noted that trophic levels did not exactly correspond to populations or species, since a given species may function as both a carnivore and herbivore.

Ecology and the Atomic Age (1945–1959): The split between zoologists (interested more in trophic levels and populations) and botanists (interested more in plant competition and succession) was a prominent feature of pre-World War II ecology.

Bacteria, fungi and the lower forms of life were barely considered. For ecologists after World War II the ecosystem concept promised a means for unifying what previously been a discipline sharply divided along the boundary between zoology and botany. The atomic age after 1945 was a double edged sword; capable of wreaking environmental havoc but also providing new tools, techniques (radioactive tracers) and research opportunities.

Brothers *Eugene Odum* (1913–) – University of Georgia, and *Howard Odum* (1924–) – University of Florida – studied energy flow in ecosystems. In 1951 Gene started a study of old-field succession at Savannah River Nuclear Facility in Georgia. In 1954 they undertook a detailed study of Eniwetok Atoll in the Marshall Islands the site of nuclear testing. There were concerns about the environmental impacts of atomic energy. They studied the energy budget of coral reefs with the idea that if the productivity did not equal respiration the community was not self sustaining. The Atomic Energy commission began funding ecological research at Savannah River and Oak Ridge, Tennessee after this. At Oak Ridge radiation ecology was studied. Radioactive tracers provided a means for quantifying the movement of materials and energy through the ecosystem. The Odums developed considerable ecosystem theory. Gene believed that the evolution of homeostasis and consequent stability of ecosystems occurred through a combination of group selection and evolution. Howard attempted to provide a thermodynamic explanation for ecosystem stability; stable ecosystems were in thermodynamic steady state, where photosynthesis was almost completely balanced by respiration.

**Ecosystems ecology in the 1960's:** Emergence of "systems ecologists". The primary foci of ecosystem ecology began to emerge in the 1960s: biogeochemical cycling, energy flow and succession. It was obvious that ecosystems could be quite variable in size; they might be a pond, aquarium or the entire biosphere. To be an ecosystem ecologist in the early 1960s required one to think in terms of systems.

The principal systems ecologists were *George Van Dyne*, *Jerry Olson*, *Bernard Patten*, *Ramon Margalef*, *Lawrence Slobodkin*, *Kenneth Watt*, and *Howard Odum*. They believed that the diverse physical and biological entities in ecosystems could be treated as systems using the concepts of cybernetics and computer simulation. Analog computers were also used with electric circuits, currents and resistances.

Holism versus reductionism and molecular biology. Howard Odum introduced the idea of the "macroscope" of ecosystems science was introduced. In contrast to the microscope that allowed the scientist to observe hidden detail, the "macroscope" served as a "detail eliminator" – not concerned with individual species. The idea of "man the manipulator" was a common thread running through the literature of ecosystem ecology and the concept of the ecosystem became the basic principle underlying conservation.

Biogeochemical cycles were fundamental processes in ecosystems even for toxic substances such as DDT. Energy flow seemed to hold the key for understanding the structure and function of ecosystems. The study of community metabolism is one means of making a functional analysis of an ecosystem.

Gene Odum developed the idea of the *strategy of ecosystem development*, i.e., there was increased control of the physical environment with succession such that an ecosystem achieved maximum protection from its perturbations. During succession diversity should increase as species become specialized for particular functional roles. Therefore the number of species should be greatest in mature, climax ecosystems.

Specialization promoted symbiosis as species became more dependent on each other. The growth of decomposer populations and detritus based food chains would increase the efficiency of nutrient cycling. As a result the leakage of nutrients from the system would decrease. During succession the amount of biomass would increase until it reached a maximum at climax; however, the rate of production in relation to the rate of respiration would decrease. Virtually all production would be channeled into self maintenance, rather than growth.

The idea of a strategy of ecosystem development was obviously a metaphor, but it seemed to suggest that ecosystems had "goals." By the end of the 1960s most evolutionary biologists believed that natural selection operated on individuals, not collections of individuals. Even metaphorically, ecosystems could not have strategies. This set up a conflict among ecologists; ecosystem scientists and evolutionary ecologists whose primary interests were in studying species and populations. The population ecologists began to develop theories of their own such as the theory of island biogeography.

### **The late 1960s and early 1970s: Big Ecology and the IBP**

From 1968 to 1974 the U.S. participated in the International Biological Program (IBP) whose major objective was to determine "the biological basis of productivity and human welfare" (Mitchell et al. 1976— *this is a great reference for understanding the rationale, successes, and failure of the IBP; I also recommend Loucks 1986*). The umbrella organization was the International Union of Biological Sciences (IUBS) and the IBP program was widely embraced in Europe. The U.S. program was funded to the tune of about \$60 million mostly from the National Science Foundation. The big programs were grassland, deciduous forest, desert, coniferous forest and tundra biome programs. The tropical biome program never got off the ground but a large ecosystem study of tropical forests was conducted at El Verde in Puerto Rico in the 1960s (Odum and Pigeon 1970). There were several smaller programs such as Aerobiology.

The structure of the IBP research was very organized. First taxonomists would collect and identify the constituent species in an ecosystem. Ecologists trained in autecology and natural history would identify the food chains and group species into trophic levels. The system ecologists would gather data on energy and material flow through the trophic levels and large systems models would be created to study the outcome of various disturbances or experimental modifications of the system. But the total system modeling effort was considered to be a failure because of the sheer complexity of the systems.

Some researchers considered the IBP a total failure because it produced no revolutionary change in the way ecosystems were studied and developed no new ecological theories. But there were some legacies; increased funding for ecological research, introduction to ecologists to computer simulation modeling, increased international cooperation, and trained many graduate students (Mitchell et al. 1976). Results of the grassland program are summarized in Breymeyer and Van Dyne (1980) and the Coniferous Forest Biome program is summarized in Edmonds (1982). Another legacy of the Coniferous Forest Biome was a better understanding of the structure and functioning of old-growth forests, including the importance of belowground processes and the role of coarse woody debris.

### Hubbard Brook: Alternative to Big Ecology

A watersheds program was developed at Hubbard Brook, New Hampshire by *Gene Likens* (1935–) and *F. Herbert Bormann* (1922–) ecologists at Dartmouth. The watersheds were located on the National Forest land. The approach was different than the IBP. The program started small and focussed on biogeochemistry using a more individualistic approach. Seven small watershed were used with degrees of manipulation including clearcutting and herbiciding. They also studied community structure and function, natural history and used computer simulation.

The centerpiece of the study was the Biomass Accumulation Model; four stages were recognized following clear-cutting: reorganization (1–2 decades) – in this stage the ecosystem lost total biomass, net primary productivity (NPP) declined, as did transpiration and nutrient uptake. Nutrient export increased; aggradation (100 yrs +) where the system gradually regained homeostatic capacity. Biomass increased and reached a peak at the end of this phase; transition phase – in this stage biomass declined slightly because of death of large old trees; steady state – here the total biomass fluctuates around a mean. They used the JABOWA (developed by *Janak, Botkin and Wallis*) model for computer simulation. Diversity and ecosystem stability were not as closely related as Odum believed and the relationship between photosynthesis and respiration was more complicated than suggested by Odum. During the reorganization and transition phases respiration actually exceeded photosynthesis. Thus the ecosystem was drawing on energy reserves in nonliving biomass in the soil. Bormann and Likens emphasized the important role of chance fluctuations and local disturbances in determining ecosystem structure and function. The steady state was not stereotypical Clementian climax rather it was a "shifting mosaic steady state made up of irregular patches of vegetation of various ages. They combined the ideas of both Clements and Gleason. Results of this program are summarized in Bormann and Likens (1979).

### **The 1980s: Gaia and beyond?**

James Lovelock's (1987) Gaia hypothesis – the biosphere is controlled by living organisms. Microorganism are the primary living agents of biogeochemical cycling. The biosphere is self-regulating and this self-regulation is analogous to homeostatic mechanisms in organisms and cybernetic controls in automated machines.

Non equilibrium ecology: Homeostasis or negative feedback do not imply perfect balance and critics have attacked what that see as an over emphasis upon constancy, balance and gradual change in tradition ecosystem ecology. In its place they would erect a new ecology that emphasizes indeterminism, instability and constant change. ecosystem may be perpetually out of balance, i.e., nonequilibrium ecology. References on this topic are Pickett and White (1985), Kolasa and Pickett (1991) and Reynolds (2001).

There is still gap between evolutionary ecology and ecosystem ecology. Populations do interact with each other and the surrounding physical environment. Understanding the web of nature is all its complexity is as central to evolutionary biology today as it as in Darwin's day.

The LTER program. Starting in 1979 The NSF, Division of Biotic Systems and REsources has undertaken the support of research on long-term ecological phenomena at a national network of sites. An initial set of 6 sites were funded in and in the 1980s additional sites were added and some were dropped bringing the total to 17. In 1991 the Antarctic site was added bringing the total to 18. *Jerry Franklin* – University of Washington was the original coordinator of this program which is continuing in the 1990s.

Acid Rain Programs. To determine what relationships exist between atmospheric deposition and forest health two major ecosystem studies were initiated in the 1980s. These were the National Acid Precipitation Assessment Program (NAPAP) and the Electric Power Research Institute (EPRI) Forest Effects Study. Results of the western U.S. NAPAP research are summarized in Olson et al. (1992) and the EPRI Study is summarized in Johnson and Lindberg (1992).

### **The 1990s: Is the Past Prologue of the Future?**

- Landscape ecology
- Global Change Ecology
- Complex adaptive systems
- Activity of IGBP (see <http://GCTE.org/>)
- Others?

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