Ecology and Systems Thinking

An integrated approach to botany and zoology, a general theory of evolution, and the application of systems thinking

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History of Modern Earth and Life Sciences

Ecological thinking and systems approaches

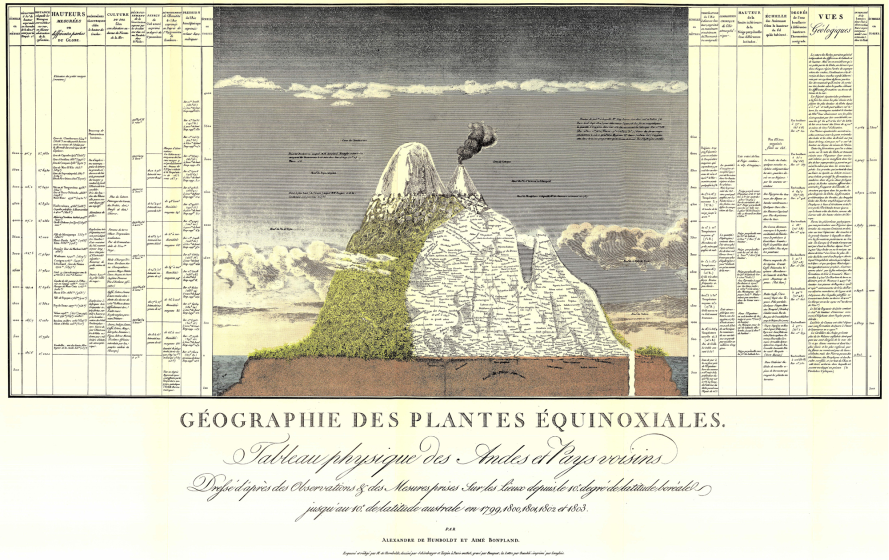
The discipline of ecology, which was formalized in the 20th century, became a major component of the naturalist approach to the life sciences. Like the theory of natural selection, ecological theory became highly abstract and mathematized in the middle of the 20th century, but the philosophical or conceptual basis was different. Whereas the modern theory of natural selection was a statistical approach based on quantification of the *fitness* of individuals – genes or organisms – the theoretical approaches to ecology involved the formalization of interacting systems.

The systems approach to ecology involved borrowings from the new mathematical disciplines of *cybernetics* and *general systems theory*, and it sought to incorporate physical and chemical processes that occurred in the environment in interaction with organisms. In this sense, the scope of naturalist studies as understood by ecologists was once again broadened to include physical and chemical processes and the atmosphere as well as minerals.

Plant geography

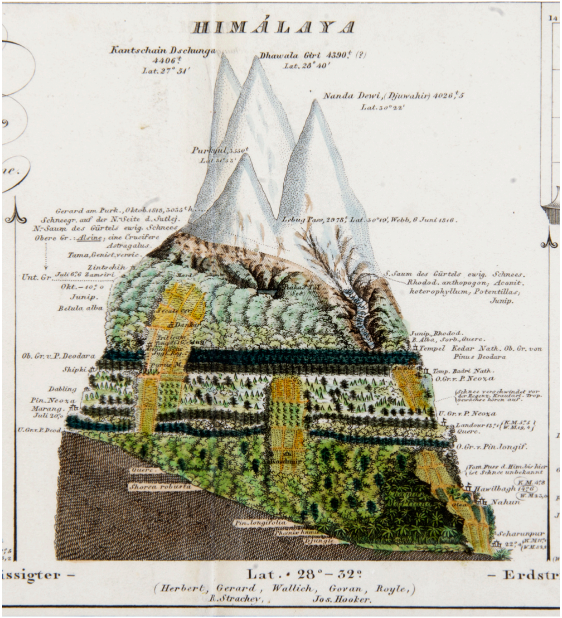
Alexander von Humboldt (1769–1859) was a Prussian polymath who was friends with Schiller and Goethe, a student of the geologist Werner, and brother of the famous statesman Wilhelm. He carried out extensive explorations, particularly in South America, and wrote about the natural history of the areas he explored.

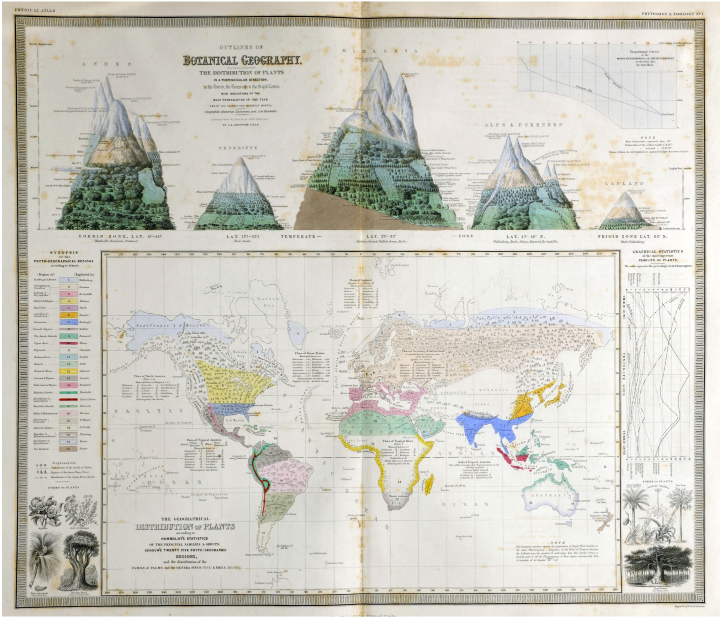
In his work, he emphasized the *geographical distributions* of plants and animals, introducing the concept of the geographies of flora and fauna. He was particularly interested in the relationship between plants and their physical and geological environment. He made extensive studies of the ways that the groupings of plants change as altitude changes in the foothills and lower reaches of a mountain range – demonstrating relationships between climate and plant communities. He also made more global studies of the distributions of plants by latitude and longitude.



Humboldt, *Essai sur la géographie des plantes* (1805)

A detail of Humboldt's graphic of the Himalayas.





Johnston, “Outlines of Botanical Geography,” 1848

The lake as a microcosm

In 1887, Stephen Forbes (1844–1930), an American naturalist who worked at the University of Illinois, wrote a paper called "The Lake as a Microcosm," which was reprinted in 1925 and was influential for the whole first half of the 20th century.

In this paper, he created a vivid image of the aquatic environment and the organisms interacting in it. He argued, first, that there was a *community* of interests, even among predator and prey; each systematically acting to maintain the optimal size of the population of the other. And, second, that this well-regulated community had evolved and was ordered by "the beneficent power of natural selection." He asserted that the "fearful slaughter" brought about by a "scramble for food," in fact, produced *social harmony* and *progress*. His paper was full of various mechanical, organic, military, political, and economic *metaphors*. Although his paper was highly anthropomorphic and teleological in its approach, it gave a lively description of interactions of the various organisms in the lake.

A detailed study of an ecological system

In 1901, François-Alphonse Forel (1841–1912), a Swiss professor of anatomy and physiology, published *Le Léman : Monographie limnologique*, a massive, 3-volume study of a single lake. He had developed a number of instruments to measure, for example, the shades of the water and the oscillations of the lake level.

This work founded the discipline of *limnology* – the study of lakes. In a section called "The Circulation of the Organic Matter," he described many of the functions of what we call an *ecosystem*.

Forel, *Le Léman : Monographie Limnologique* (1901)

"While small and large organisms, which devour each other in the lake waters, make the living matter through more and more complex and higher successive incarnations, microbes represent the reverse function… The function of the microbian agents of putrefaction closes the transmutations cycle of organic matter, by making it back to its primitive form, or staring point."

Plant communities

Eugenius Warming (1841–1924), a Danish botanist, published a work on plant ecology in 1895, which was translated as *Oecology of Plants* (1909). He described how both the physical conditions of an area determined the types of plants, but also how the network of interacting plants was characteristic of a particular environment. These plants formed a biological *community*, each dependent in various ways on the others.

Henry Cowles (1869–1939), an American botanist who taught at University of Chicago, studied the life history of the sand dunes on the shores of Lake Michigan, paying particular attention to the *succession* of plant species as the dunes came into being and were eroded. This shifted focus towards the *temporal* aspect of the plant community. He asserted that the process ends in an equilibrium, which he called the *climax*. Although Cowles did not publish much, he was an influential teacher.

The Carnegie Institution of Washington

The Carnegie Institution was endowed by Andrew Carnegie, starting from 1901. Initially, the Institution functioned by giving individual grants to authors, scientists and scholars. For example, in the earth and life sciences they funded the paleontologist Oliver Hay, the botanist Luther Burbank, and the geneticist Thomas Morgan.

Under the directorship of Robert Woodward, the Institution began to fund long-term projects, involving a number of individuals and sometimes multiple sites, in a number of fields such as astronomy, earth and planetary science, ecology, genetics, eugenics and plant science.

Because the Institution is located in Washington DC, it has often been influential in US science policy. During WWII, Vannevar Bush, the head of the Institution, set up the new National Defense Research Committee (later the Office of Scientific Research and Development) to mobilize and coordinate the nation's scientific war effort, and directed it from the Institution's offices.

The organismic conception of plant communities

Frederic Clements (1874–1945), an American plant ecologist who spent most of his career as a researcher at the Carnegie Institution, was a prolific researcher and author who put forward the strong claim that plant communities behave like an *organism*, governed by developmental patterns of regularity as strong as those of physiology.

Clements, *Research Methods in Ecology* (1905)

"The plant formation is an organic unit. It exhibits activities or changes which result in development, structure, and reproduction… According to this point of view, the formation is a complex organism, which possesses functions and structure, and passes through a cycle of development similar to that of the plant."

Although this was an old idea, which had been articulated many times before, Clements produced extensive, detailed studies that he believed would support this view of plant communities.

Succession and climax communities

Clements believed that the processes of *adaptation*, *speciation* and *succession* were closely interrelated. Because he was a Lamarckian, he understood changes in the environment to directly cause changes in the organism – his adaptation and speciation. As the organisms struggled against the conditions of life, they moved inevitably towards a *climax community*.

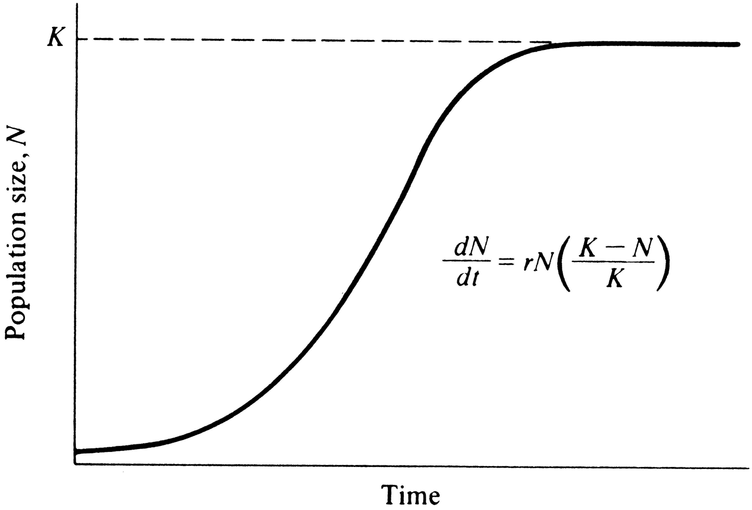
Clements and his colleagues developed surveys of plant communities undergoing succession by clearing an experimental area of all vegetation, and then periodically counting and recording every single plant growing in it as the plant community reestablished itself until it reached its climax population. The most controversial aspect of this work was his claim that succession will always end with a single type of community.

Lamarckian approaches to ecology became increasingly marginalized throughout the course of Clements' career.

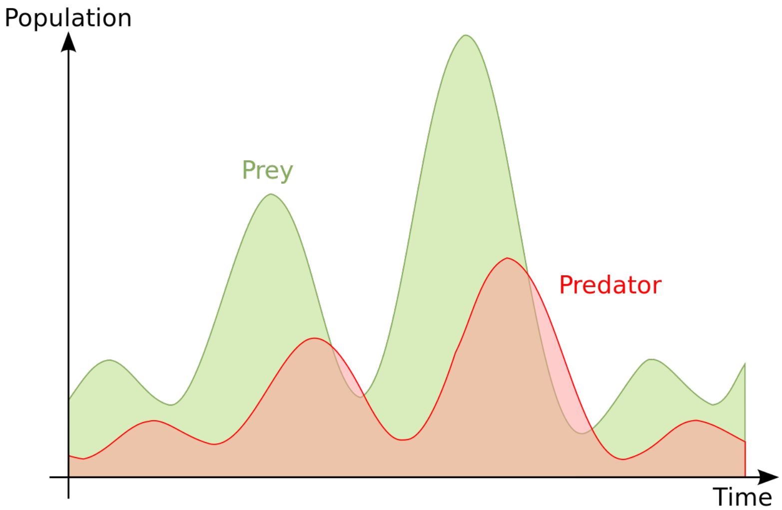
Population dynamics

During this period, a number of mathematicians and physicists carried out purely mathematical investigations of the ways that populations grow and decline based on pressures having to do with food supply and predation.

- In 1920, the zoologist Raymond Pearl (1879–1940) rediscovered the work of one of Quetelet's students, the Belgian mathematician Verhulst, on the equation of population growth and leveling off in a saturated environment.
- In 1925, the Polish-American physicist Alfred Lotka (1880–1949) published a system of differential equations that describes the changing relationship between a predator and prey.
- Lotka's model was further developed by the Italian mathematician Vito Volterra (1860–1940) in order to develop policies around fishing the Adriatic Sea.
- The Lotka–Volterra model was experimentally verified by the Russian biologist Georgii Gause (1910–1986).



The Verhulst-Pearl equation, N = population size, K = carrying capacity (food supply, etc.), r = a constant of proportionality



Graph of Lotka-Volterra equations, two differential equations that are computed iteratively each using the output of the other

Animal ecology

In 1927, the British zoologist Charles Elton (1900–1991) published *Animal Ecology*, in which he applied ecological ideas to studying animal communities – arguing that the fundamental issue of animal ecology is that of *food supply*.

He produced a theoretical model that could be applied to various different environments, in which different species of animals would fit into places made up of *herbivores*, *carnivores*, and *scavengers*. But more specifically, at each level animals were specialists – usually based on size – which gave rise to an optimal food range, or *niche*.

Because of these specialties, each ecological environment would have definite feeding patterns, following along these niches, which would produce *food chains*. He pointed out that as nutrients moved up a food chain, the animals got larger, but fewer, in what he called a *pyramid of numbers*. On the other hand, there were also parasitic chains and decomposer chains, made up of much smaller organisms.

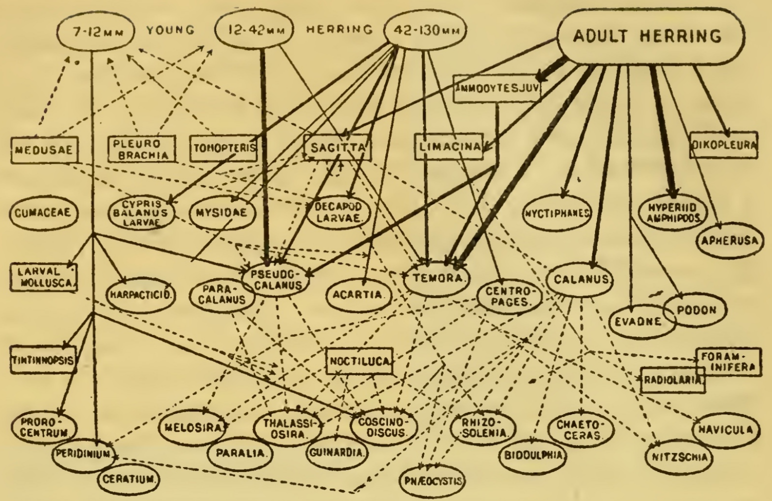


FIG. 3.—Diagram showing the general food relations of the herring to other members of the North Sea plankton community. Note the effect of herring size at different ages upon its food. (From Hardy.[102])

Elton, *Animal Ecology* (1927)

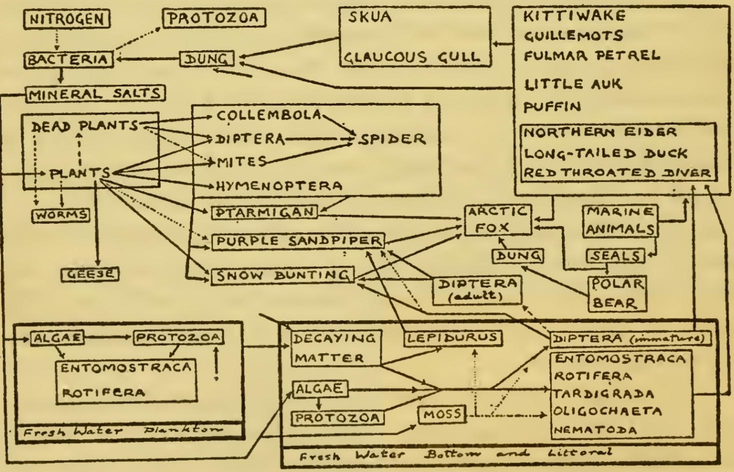


FIG. 4.—Food-cycle among the animals on Bear Island, a barren spot in the arctic zone, south of Spitsbergen. (The dotted lines represent probable food relations not yet proved.) The best way to read the diagram is to start at "marine animals" and follow the arrows. (From Summerhayes and Elton.[25])

Elton, *Animal Ecology* (1927)

The ecosystem concept

Authur Tansley (1871–1955), a British botanist, strongly disagreed with the organistic approach of Clements, and sought to explain succession and climax as based on *contingent*, or historical, processes, not a real development-like ontogeny.

Tansley argued that holism was a form of intellectual defeatism – stating that the fact that we cannot now explain many *emergent properties* cannot be an argument that it is impossible to do so. In place of the *organism*, he introduced the idea of the *ecosystem*.

Tansley, "The Use and Abuse of Vegetational Concepts…," 1935

"The more fundamental conception is, as it seems to me, the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what the environment of the biome – the habitat factors in the widest sense… These ecosystems, as we may call them, are of the most various kinds and sizes."

The biosphere concept

Vladimir Vernadsky (1863–1945) was a Ukranian-Russian geologist who developed the concept of the *biosphere*, introduced by the Austrian geologist Eduard Suess in 1911. In his *The Biosphere*, 1926 (in Russian), Vernadsky pointed out that the biosphere was a very thin layer composed of the upper regions of the oceans and the earth's surface and the lower regions of the atmosphere. (We now know that there are organisms in the deep ocean, and that microorganisms, the archaea, that live somewhat deeper everywhere.)

The biosphere exhibits a constant process of *cycling* the chemical elements that involves both living organisms and inorganic components. Vernadsky proposed that the major gases of the atmosphere – oxygen, nitrogen, and carbon dioxide – were all produced by organic processes. This emphasis on a *biogeochemistry* was a major innovation that had implications for how biologists considered the boundary between organic and non-organic elements in ecological studies.

Cybernetics

Cybernetics was defined by the American mathematician Norbert Wiener (1894–1964) as “the scientific study of control and communication in the animal and the machine.” It was understood to be a transdisciplinary approach to the study of systems and how they interact with each other – be they natural or mechanical. The hope was that it would become a sort of overarching theory or set of methods that would unify disparate fields, such as electrical network theory, mechanical engineering, logic modeling, evolutionary biology, ecology, neuroscience, anthropology, and psychology.

Although cybernetics never really came together as a single field – there are relatively few departments of cybernetics – it was highly influential in the development of fields such as artificial intelligence, machine perception and learning, robotics and biomedical engineering. Cybernetics approaches were also used in many areas of the medical and life sciences.

The Macy Conferences

The Macy Conferences were academic meetings held in New York at the Josiah Macy Jr. Foundation, 1941–1960. Most of the conferences focused on cybernetics, as well as one on neuropharmacology (on the psychedelic drug LSD), and later “group processes.”

The cybernetics conferences were chaired by Warren McCulloch (1898–1969), an American neurophysiologist who was an early researcher on computer models of neural networks and AI. McCulloch made a point of stressing interdisciplinarity and tried to organize both the topics and the individual talks to cut across disciplinary approaches.

Although none of the topics addressed at the Macy conferences were explicitly ecological, a number of ecologists did present papers, and the general approach was influential in developing abstract models for treating the behavior of complex systems.

The Ratio Club

The Ratio Club was an informal dining club of British cyberneticists, organized by the neurophysiologist John Bates (1918–1993), that met some 34 times in a basement of the National Hospital for Nervous Diseases, 1949–1955, 1958. The format of the meetings was that everyone would listen to a talk over food and drinks, followed by a group discussion. The members of the club were a combination of fairly junior level researchers in neurobiology, engineering, mathematics and physics – including Alan Turing (1912–1954) – from a number of different types of institutions, such as departments, hospitals and research centers.

The focus of the Ratio Club was on physiology, neurophysiology and electronics and machine intelligence. Although the Club had no institutional continuity – and did not grant degrees – many of the members went on to become professors and major figures in British science.

Cybernetic models

G. Evelyn Hutchinson (1903–1991) was a Cambridge trained zoologist who spent most of his career working at Yale University and studying Lindley Pond, Connecticut, with his graduate students. Through his writing, and especially his teaching, he influenced a generation or two of American ecologists.

Hutchinson continued to develop Clements' ideas of *development*, but now in a more abstract manner. He incorporated the ideas of the cyberneticists and the physical biologists and focused on biogeochemical processes. He presented a talk on the concept of negative feedback in ecological systems at one of the Macy Conferences.

- He applied and extended the Lotka–Volterra model as a "governor" controlling population.
- He developed equations to describe the ocean as a regulator for CO^2 in the atmosphere.

Energy flows, matter circulates

In 1942, Raymond Lindemann (1915–1942, 27yo), as postdoc working in Hutchinson's lab, wrote "The trophic-dynamic aspect of ecology," which went on to become one of the most influential papers in the new science of ecology.

Based on 5 years studying Cedar Lake Bog, Minnesota, and Hutchinson's theoretical work, he pointed out that previous studies had focused on biotic communities, and hence ignored the inorganic elements, arguing that an ecosystem is a "system composed of physical-chemical-biological processes active within a space-time unit of any magnitude." The basic ideas were as follows:

- Energy is consumed and gradually lost, matter conserved.
- Organisms are made up of producers, consumers, and decomposers.
- Some energy is dissipated at each level: $\lambda_0 > \lambda_1 > \ldots > \lambda_n$.
- Organisms in a chain can be treated as abstract tropic levels.

Ecology in the atomic age

Postwar ecology gained a huge boost from two different quarters: 1) public concern about the environmental impact of atomic radiation, and 2) massive government spending in the atomic era.

With the proliferation of nuclear testing, the Marshall Islands became a center for extensive biological, geological, and oceanographic research. In 1954, The US Atomic Energy Commission funded a major study of the overall metabolism of an entire ecosystem, the Enewetok Atoll, to be carried out by brothers Eugene (1913–2002) and Howard Odum (1924–2002). This resulted in a major report on the ecosystem. The research of the Odums and a number of other teams of ecologists continued to be funded by The Atomic Energy Commission, the Office of Naval Research, and a number of other large governmental funding agencies.

The atomic age also provided ecologists with a new range of technologies in the form of radioactive tags that could be used to trace the detailed movements of nutrients through the food chain.

An hydrogen bomb test on Enewetok Atoll

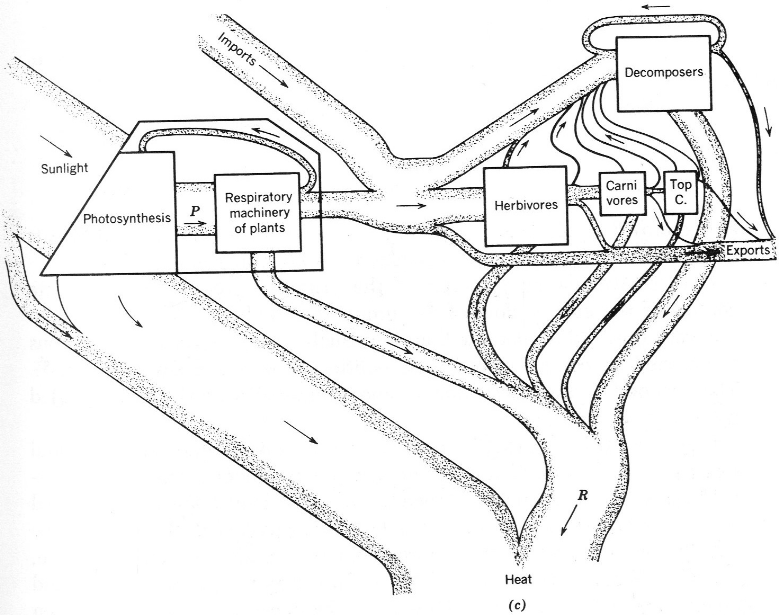
“The Tomb” on Enewetok Atoll

The new ecology: systems thinking, systems ecology

While E. Odum was a more traditional ecologist, with a focus on biological field studies, H. Odum, a student of Hutchinson, was a physical biologist, whose research specialty was mathematical and computer modeling. E. Odum's *Fundamentals of Ecology* (1953), with the chapter on energy written by H. Odum, became the standard textbook of the new ecology for the next generation.

- An antireductionist approach, which was complemented by quantitative measurements and mathematical models.
- The ecosystem, which is defined by the investigator, is open and in steady state (*homeostasis*).
- Energy flows through the system, while matter circulates. (These can be quantified and mathematized.)

H. Odum was explicit about the link between the new ecology and cybernetics. Although few cyberneticists moved into ecology, ecologists were reading their works.



H. Odum, *Environment, Power, and Society* (1971)

Ecology and the modern synthesis

As the new ecology became institutionalized in the 1940s and 50s, there was a growing sense that some of its core ideas were in conflict with certain fundamental principles of the modern evolutionary synthesis.

Prior to the modern synthesis, biologists often claimed that natural selection acted at a number of different levels: for the good of the individual, for the good of the species, and perhaps for the good of the ecosystem. Certainly many of the concepts developed in ecology seemed to imply that the system was working together in some way.

In the mid-1960s there was a debate about the role of *group selection* in evolution and the majority of evolutionary theorists came out against it. This called into question that idea that organisms could be playing a role within an ecosystem – for example, decomposers were simply freeing up nutrients as a fortuitous consequence of their primary function.

Big ecology and its discontents

"Big science" is a term used to describe a type of scientific practice developed during WWI and particularly WWII, involving a close interrelation between the military and industry, and an organizational structure that is closer to that of a military or a corporation than normal scientific organization.

In the Cold War period, ecology entered into a big-science stage. In 1868–1974, the US participated in the International Biological Program (IBP), with a focus on large scale ecosystem studies. Some 1800 scientists participated with funding in the rage of $40–60m USD.

From the beginning, however, there were criticisms, and the whole endeavor was never very successful. Although a number of large-scale, detailed studies were produced, they were theoretically fairly derivative and few new ideas were advanced. Also, because the individual researchers had little autonomy, few top level ecologists were produced.

Hubbard Brook

During the same time period, 1963–1976, a more traditional "small science" project at Hubbard Brook was considered to be more successful than the IBP projects. In fact, the Hubbard Brook was large-scale by previous standards – involving some 150 researchers and $2m USD – but it allowed individual researchers their traditional autonomy.

Under the direction of Gene Likens and Herbert Bormann, Hubbard Brook consisted of seven self-contained watersheds that were geologically watertight and because of their similarity allowed for experimentation with controls. By building weirs at the base of each watershed, the water and nutrients leaving the system could be measured, which made it possible to study biogeochemical cycling. This, combined with computer simulation, lead to the development of the Biomass Accumulation Model to describe succession in a forest.

A weir at Hubbard Brook

The Biomass Accumulation Model

The Biomass Accumulation Model developed at Hubbard Brook elucidates four stages of recovery for a forest after clear-cutting.

1. *Reorganization* (10–20 years): The system losses total biomass; productivity, transpiration and nutrient uptake decline.
2. *Aggradation* (100+ years): The system slowly regains homeostatic capacity; biomass increases steadily towards a peak; nutrient input and output come into ballance.
3. *Transition* (250–300 years): Total biomass declines slightly; old, massive trees die off and are replaced.
4. *Steady State* (indefinite): Biomass fluctuates around a mean.

This model was quickly adopted into ecology textbooks and became the basis for governmental and corporate planning.

The Gaia theory, returning to old metaphors

One of the most influential and controversial ecological theorists of the late 20th century was the British environmentalist James Lovelock (1919–), who developed the Gaia theory. Lovelock was trained as a chemist and medical researcher, and worked for years at NASA's Jet Propulsion Laboratory in planetary science. He also developed a number of key instruments for measuring the content of various chemicals in the atmosphere and water.

The Gaia theory proposes that the Earth is a cybernetic planetary system that tends to stay in homeostasis – that is, the temperature, state of oxidization, acidity and various aspects of the minerals and water are kept relatively stable through various control systems and feedback mechanisms maintained by processes occurring in the biosphere involving organic as well as inorganic entities.

Although this theory is disputed by scientific ecologists, the concept of the whole Earth as a self-regulating system has become influential in popular culture and among environmentalists.

“The Blue Marble,” 1972, Apollo 17

Breakdown of the consensus

In the 1970s and 80s, there was a breakdown in the consensus that ecosystems formed coherent units that were stable over time. This was an idea that had been voiced since the 1920s, but new empirical and theoretical work seemed to strengthen this position.

In the 60s and 70s, Margaret Davis (1913–) applied the study of plant pollen remains to the period since -25,000 in North America and showed that there had been massive changes in the types and distributions of forests. Daniel Botkin showed that there was no balance, or even a clear relationship between wolves and moose in Isle Royale park, Michigan, USA.

In the 70s, ecologists began to admit that their computer models were too simplistic. The next generation of more detailed, more mathematically rigorous, computer models did not result in stable states, but rather predicted constant change.

Change is constant

In the 1980s, mathematicians, computer scientists and physicists developed chaos theory and then complexity theory to model non-stable systems. The outcomes of these models could not be predicted, and they did *not* result in stable equilibria. Ecologists began to use these ideas to argue that there was no reason to believe that ecosystems would achieve *homeostasis*.

Daniel Botkin, *Discordant Harmonies* (1990)

"Until the past few years, the predominant theories in ecology either presumed or had as a necessary consequence a very strict concept of a highly structured, ordered, and regulated, steady-state ecological system. Scientists know now that this view is wrong at local and regional levels … that is, at levels of population and ecosystems. Change now appears to be intrinsic and natural at many scales of time and space in the biosphere."

Levels of resolution and the meaning of *function*

In systems ecology, organisms are reduced to their function in an overall system. This gives rise to the idea that groups of organisms play some *function-s* in the biosphere.

In evolutionary ecology, *function-e* refers to an adaptation that has evolved by natural selection to carry out a specific purpose, of benefit to the individual organism – or its genes. These two notions of function, however, are different – and possibly contradictory.

Initially, it was hoped that this difference in the idea of function might be overcome with the theory of group selection, but when it was shown that both altruism and cruelty could be selected for as advantageous to individual genes, it began to be doubted that this was the case.

Depending on the resolution that we take – on the organism, or on the system – we come up with a different idea of what it means to talk about *function*.

Overview

- We covered some aspects of proto-ecological thinking in the 19th century.
- We looked at early studies of lakes and the idea of the ecosystem as a community, or an organism.
- We discussed at the development of the ecosystems concept and its relation to cybernetics and systems thinking.
- We touched on the Gaia theory.
- We noted the breakdown of the consensus that ecosystems have homeostasis.
- We addressed some of the philosophical difficulties that arise in taking a strongly realist perspective on the concept of function in either ecosystems or evolution by natural selection.