THE SCIENCE OF ECOLOGY FOR A SUSTAINABLE WORLD

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Contents

Summary

Ecology is the study of the interrelationships between living organisms and their environment. The term “ecology” was introduced by Ernst Haeckel, at the end of the nineteenth century. Since that time spectacular advances have been made. Much has been learned about the relationship between organisms and environmental factors, and about the processes that regulate the abundance and distribution of species. Progress is due to advances in several ecological sub-disciplines such as the ecology of individuals, eco-physiology, population biology, community ecology, macro-ecology, global ecology, and the developing inter-disciplinary research including social sciences and economics. Ecology has several practical applications in forestry, agriculture, nature conservation, restoration of disturbed landscapes, and politics. At present ecology is a key science that can contribute to solve the big global problems of humankind. In introducing the theme of ecology in the *Encyclopedia of Life Support Systems* rather than making a survey on the main trajectories of ecological research, which will be done at the topic and article levels, our major aim here is to illustrate the historical development of ecology and the nature of ecological thought, highlighting current critical issues and outlining future perspectives.

1. Introduction: Ecology as a Scientific Discipline

1.3. A Historical Perspective

Ecology is a word that first saw the light in the second half of the nineteenth century. It was first described by Ernst Haeckel, in 1869, as the "total relations of the animal to both its organic and its inorganic environment." Implicit in Haeckel's definition is that ecology has roots in natural history; accordingly, one can easily trace back the history of ecology to the beginning of human history on planet earth.

From earliest times humans interacted with their environment mainly through fishing, hunting, and food gathering, and these activities required an understanding of animal habits and plant production in relation to seasonal rhythm, climate fluctuations, and other physical constraints. The establishment of agriculture required that knowledge about plants and animals, in relation to the physical environment, became enlarged, to allow domestication. During the course of these evolutionary changes, humans experienced the pressure of other organisms as users of the same resources, such as locusts, mice, and rats. The problem of controlling these species captured the interest of Aristotle, who wrote about this issue in his *Historia Animalium.* His observation that rain, rather than predators or human effort, could control mice infestation, is an early observation about the complex interactions that link organisms to their environment. The attitude of the Greeks was that of considering nature as designed to benefit and preserve each species, as one can argue by reading Herodotus and Plato. Each species has a special place in the harmony of nature, and extinction did not occur because nothing could disrupt the balance of nature. Eventually outbreaks could occur, but due to divine interventions, usually as punishment. In 325 B.C., however, Greek scholar Theophrastus wrote the first ecological study about the relationship between organisms, and between organisms and their environment.

Although a rigorous and coherent framework for ecology did not see the light until the twentieth century, many studies, in various form, contributed to shape it, by increasing the understanding of the relationships between organisms and their environment. Natural scientists, and demographers in particular, played a decisive role in this respect. John Graunt (UK, 1620–1674) described human population in quantitative terms. He developed his approach to human population by measuring birth rate, death rate, sex ratio, and age structure, and making use of such parameters to predict the evolution of human population in London. The extension of the quantitative approach to non-human populations traces back to Antony van Leeuwenhoek (the Netherlands, 1632–1723) who, as well as many other relevant contributions in different fields of biology, focused his attention on the reproduction of arthropods. By studying carrion flies, grain beetles, and human lice he provided a way to calculate theoretical rates of increase of animal populations.

A hundred years before Darwin, Georges-Louis Leclerc Buffon (France, 1707–1788), in his *Historie Naturelle*, a forty-four volume encyclopedia describing everything known about the natural world, proposed that the environment acted directly on organisms through what he called "organic particles," whose physical counterpart, however, he never discovered. He dealt with problems of population regulation; in particular he

proposed that population outbreaks could be prevented by predators. The interactions between organisms and their environment was carefully considered by Thomas Malthus (UK, 1766–1834), who focused on constraints imposed to a geometrically increasing population by the arithmetic rate of increase in food production. Despite earlier contributions on the subject (Machiavelli, 1525; Buffon, 1751) it was Malthus who brought this idea to general attention. The work of Malthus inspired many important scientists, and interest in the mathematical aspects of demography increased after him.
The assumed belief that an increasing population followed a geometric progression was questioned by Adolphe Quetelet (1796–1874), a Belgian statistician, and by his student Pierre Verhulst (Belgium, 1804–1849). Quetelet believed that there are forces which tend to prevent this population growth and that they increase with the square of the rate at which the population grows. In 1846, Verhulst showed that such forces grow in proportion to the ratio of the excess population to the total population. The non-linear differential equation describing the growth of a biological population, which Verhulst deduced and studied, is now named after him. It is also called a logistic or S-shaped curve.

Scientific research carried out in the late eighteenth and early nineteenth century seriously challenged Plato's idea of harmony governing nature; major contributions in this respect came from the discovery that species become extinct, and the recognition of the role of competition by population pressure. All these ideas culminated in what can be considered the maximum expression of the way organisms and environment interact, that is, the evolutionary theory. The basic principles of evolutionary theory, enunciated by Charles Darwin (UK, 1809–1882), can be summarized as follows:

- Evolution is something that occurs.
- Evolutionary change are gradual, requiring thousands to millions of years.
- Natural selection acts as the primary mechanism for evolution.
- The millions of species alive today arose from a single original life form through a branching process called "specialization."

Darwin's theory of evolutionary selection holds that variation within species occurs randomly and that the survival or extinction of each organism is determined by the ability to adapt to the environment. Darwin set these theories forth in his book, called *On the Origin of the Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life* (1859), known simply as *The Origin of the Species*.

Although Darwin had the merit of condensing many ideas and observations in one coherent framework, many other thinkers contributed to develop the core idea of evolutionary theory, that is, the interaction between organisms and their environment. Herbert Spencer (UK, 1820–1903) thought that all phenomena could be explained in terms of a lengthy process of evolution in things. Spencer's "principle of continuity" stated that homogeneous organisms are unstable, they develop from simple to more complex and heterogeneous forms, and that such evolution constitutes a norm of progress. This description of evolution provided a complete and "predetermined" structure for the kind of variation noted by Darwin.

The evolutionary theory represents a milestone also for ecological thought, and for all the concepts that form the background of ecology. Many of the early developments in basic ecology came from applied fields, in particular agriculture and medicine. In agriculture the problem of regulating the abundance of crop pest populations first captured attention in 1762, when the “mynah bird” was successfully introduced to the island of Mauritius (from India) to control red locusts. Since then effort to identify controlling factors for pest population improved the knowledge of species interaction, in particular predation and parasitism. In the field of medicine, contributions to ecology have come from the study of infectious diseases, in particular malaria. Noticeable in this respect has been the contribution by Ronald Ross (India 1857–1932). He commenced the study of malaria in 1892 and a few years later confirmed the hypothesis that mosquitoes are connected with the propagation of the disease by demonstrating the life-cycle of the parasites of malaria in mosquitoes. He made many contributions to the epidemiology of malaria and to methods for surveying and assessment; perhaps his greatest contribution was the development of mathematical models in epidemiology.

Through his research Ross provided a substantial input to the development of ecology as a science: first, the idea that complicated ecological mechanisms are at the base of disease propagation and that such mechanisms must be understood for an effective approach to cure; and second, the possibility of investigating ecological phenomena by using mathematical models. In considering the process of propagation, Ross came to the conclusion that he was dealing with a peculiar case of a struggle for existence between the malaria plasmodium and humans, with the participation of mosquitoes. For this case Ross formulated mathematically an equation of the struggle for existence, which closely approached in its conception those more general relations proposed in 1926 by the Italian mathematician Vito Volterra (Italy, 1860–1940), to describe the mechanism through which the struggle for existence takes place.

While Ross was working on the propagation of malaria, the American mathematician Alfred James Lotka (USA, 1880–1949) examined theoretically certain chemical reactions by using equations of the same type proposed by Ross. He became interested in population interactions, and focused on the relationship between hosts and parasites. Without being acquainted with these researches, Volterra proposed similar equations to describe the interactions between predators and prey. He attempted to describe the dynamics of fish species in the Adriatic Sea, a problem first illustrated by the zoologist D’Ancona, who inspected the fish markets for several years and claimed that the diminished intensity of fishing during the war-period (1915–20) caused a comparative increase of the number of predatory fish. The importance of Volterra’s methods as a new and powerful tool in the analysis of biological populations was soon recognized. Thus, three distinguished investigators came to the very same theoretical equations almost at the same time but by entirely different ways. The Lotka-Volterra model is still the basis of many models used in the analysis of population dynamics. Lotka contributed to ecology also by incorporating thermodynamics into the study of nature, inspiring the fundamental work of Arthur Lindeman.

In parallel with the theoretical advancements by Ross, Volterra, and Lotka, the microbiologist Georgyi Frantsevitch Gause (Soviet Union, 1910–1986) experimentally explored the phenomenon of competition, and published what has become known as the “principle of competitive exclusion” based on experimental work done with microorganisms in culture. Gause used mixed cultures of yeast species in his experiments, and also Paramecium cultures. Many of the data published from these experiments, in addition to results obtained from experiments on predation, have been used by other ecologists in the formation and testing of stochastic models of the interaction of populations. Simply put, Gause's principle states that no two species with the same requirement can coexist on the same limiting resource.

The recognition that populations interact led to investigation of aggregates of populations, and their structure and dynamics as related to physico-chemical conditions. Edward Forbes (UK, 1815–1854) was the first to investigate the distribution of marine organisms at various depths in the sea. He defined the areas associated with the bathymetrical distribution of marine life, and pointed out that, as we descend into depths below fifty fathoms, plant life tends to fade away and that aquatic organisms become more and more modified. Forbes recognized the dynamic aspect of interrelations between populations and their environment, establishing the foundations of community ecology.

Similar ideas were developed by Karl Möbius (Germany, 1825–1908), he introduced the concept of the "biocoenose" or biotic community, which appeared in an 1877 monograph on oyster-culture. In his 1887 influential article "The Lake as Microcosm" Stephen Forbes (USA, 1844–1930) presented one of the first statements of the ecological concept of biological community. He suggested that specific regularities depend on the scale of observation: what at the individual level might seem disordered and chaotic becomes necessary to maintain regularity and stability at the level of populations and community. Forbes believed that there was a steady balance of nature as a result of opposing forces and that each species maintains a community of interests with other species. He concluded that limiting study to a single species is misleading.

Ernst Haeckel (Germany, 1834–1919) was influenced by Darwin's *The Origin of the Species* in such a way that he first proposed the use of a word to indicate the study of the relationship of organisms with their environment, and coined the term "ecology." This word did not acquire much of its current meaning, however, until it was adopted several decades later by the Danish botanist Eugenius Warming (1841–1924). In his pioneering text on plant ecology of 1895, this scientist defined ecology as the study of "the manifold and complex relations subsisting between the plants and animals that form one community." Warming emphasized the environmental context in which plant communities are formed, and the role of factors such as temperature, moisture, and soil composition in determining their expansion or decline. In Warming's description, plant communities are always in a state of change, with some species overtaking and replacing others as relationships between plants shift and as conditions outside the community are altered over time.

Eugenius Warming's thought deeply influenced the work of Henry Chandler Cowles (USA, 1869–1939), who developed a theory of dynamic vegetational succession based on physiography, emphasizing the importance of landforms as factors shaping the community of plants. Forbes's idea of biological community was picked up and elaborated on by Frederic E. Clements (USA, 1874–1945), a pioneer of dynamic ecology and a father of modern ecology. He argued that plant aggregations were generally in a state of constant flux in which species are continuously replaced by other species in a process called succession, which converges to a final equilibrium community called climax, which he supposed to be the most stable and the most diverse for a given set of environmental conditions. Clements and his many followers held a holistic view of plant formations. They believed that plant communities were themselves super-organisms, and that the stages of succession were analogous to the stages in development in individuals. They believed that the individual plants in a community (or formation) were quite similar to the cells in the human body.

Clements's ideas, although very popular, were not without critics. Henry A. Gleason (USA, 1882–1975) in his *The Individualistic Concept of the Plant Association*, opposed the idea that plant associations should be given the status of super-organisms; instead, he considered plant communities as fortuitous associations of species whose adaptation and requirements enable them to live together under particular conditions. The controversy that originated from the works of Clements and Gleason has been one of the most debated issues in the history of science, because behind them lay two opposing views about the functioning of nature and the way to investigate it. The British ecologist Arthur Tansley (UK, 1871–1955) felt that the idea of plant community as an organism was useful, but just as a metaphor. His personal dissatisfaction with the current approach in studying nature and its functioning led him to introduce the term "ecosystem" to describe a community of plants and animals and the abiotic (non-living) environment in which it was situated. Tansley however did not offer a specific definition for his concept. For him ecosystems were "mentally isolated" systems "of the most various kinds and sizes" that "overlap, interlock and interact." He felt that the term "system," which he borrowed from physics, was a more appropriate way to talk about the relationships between organisms in a biological community.

Since the Second World War, ecosystem ecology has become the predominant research paradigm, and replaced Clements's ideas about climax community. Victor Shelford (USA, 1877–1968) was able to extend ecological concepts furthest into new areas of biological research. A zoologist who was strongly influenced by Cowles's work, Shelford applied the concepts of ecology initially to the life histories and habits of tiger beetles. He shared many common interests and theoretical perspectives with Clements. In their collaboration they discussed the importance of animal–plant interactions within the area that Clements was the first to designate as the biome, "an organized unit comprising all the species of plants and animals at home in a particular habitat." Shelford and Clements worked together to create a unified synthesis of scientific work on plant and animal ecology. Their approach marked a significant point in the transition of scientific research and theory from the examination of plant ecology and animal ecology to the study of bio-ecology.

Shelford's work influenced the thought of the British ecologist Charles Elton (1900–1992). If Clements and Gleason can be considered as fathers of plant ecology, certainly Elton should be given the same position for animal ecology. He was more interested in the structure of biological communities than in their dynamics. The basics of Elton's synthesis were first laid out in his book *Animal Ecology* (1927). Three important parts to Elton's theory must be remembered. First is the idea of "food chains" and "food webs." In nearly every community, plants use photosynthesis to convert sunlight to food, thereby providing the first link in the food chain. The other links in the chain (of which there are usually no more than two or three and almost never more than four) include herbivorous (plant-eating) animals and their predators (carnivores or meat eaters). The second important insight in Elton's trophic theory related to the relative size of organisms in food chains. Elton noticed that in most food chains the size of the organism generally increases as you move up it. For example, wolves might be smaller than their prey, but they tend to hunt in packs, which compensates for their smaller size. Third, Elton discovered the so-called pyramid of numbers. He found that the populations of the smaller organisms at the bottom of food chains tended to be much larger than the populations of the larger organisms at the top of food chains.

If Elton introduced the concept of a food chain, Raymond Lindeman (USA, 1915–1942) provided a mechanistic explanation of food web patterns based on energy flow. He first coined the concept of "trophic level," and extended Elton's idea of ecological pyramid by including energy (in addition to Elton's numbers and biomass). The energy pyramid is related to the efficiency of energy transfer among trophic levels. His work formalized the idea that energy fluxes occurred among trophic levels and as one moved up trophic levels energy was lost from the system. We now state that only about 10 to 20 percent of the energy available at one level makes it to the next level. At the highest levels (terminal consumers) very little of the energy that was available in the producers is left. Lindeman defined energy content of trophic levels from field data. Lindeman's pioneering work on the linkages among nutrient cycling, productivity, energy flow, and nutritional efficiency laid the foundations for modern ecosystem ecology.

Inspired by the work of Lindeman, Eugene Odum (USA, born 1913) proposed that because energy is a common currency for plants and animals it can be used for describing ecosystem structure and function. Odum also envisioned that as the ecosystem persisted it would develop new capabilities in a process termed maturation or succession. Since Odum, a new branch of ecology called "new ecology or systems ecology" has emerged. It is only after Odum that ecosystems have been recognized as units that regulate the flow of energy, increase efficiency of energy transfers among biotic compartments, and regulate the circulation of material between the abiotic environment and the living things acting within it.

The development of ecology as a science has been characterized by four main trajectories: individual ecology, population ecology, community ecology, and ecosystem ecology. Different approaches have been used for investigation and often they created hot controversies through which ecological thought has taken shape. However, until the 1960s ecology was not considered an important science. Increasing human population, exploitation of natural resources and degradation of the environment have awakened people to the importance of studying such problems scientifically and this has given further momentum to ecological research. Nevertheless, ecology has never been considered as a fundamental science, being itself based on mathematics, physics, chemistry and natural science. In recent years, however, the influence of ecology on everyday life has become so profound that certain concepts arising from it have achieved widespread currency, and ecological thought permeates human activities as much as other disciplines have done. Thus it seems that ecology has acquired the necessary maturity to be considered one of the fundamental sciences.

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Biographical Sketches

Antonio Bodini is a researcher in the Department of Environmental Sciences, University of Parma. He graduated in Biological Sciences and successfully completed his Ph.D. in Environmental Sciences by discussing a thesis on the applications of qualitative modeling in ecology. He spent two years in the Department of Population Sciences, Harvard University (Boston) working as a postdoctoral fellow with Professor Richard Levins on the use of qualitative modeling in ecology. In summer 1997 he worked as visiting scientist at the Chesapeake Biological Laboratory (University of Maryland) on the applications of network analysis to ecosystem ecology. Ecosystem ecology is his main field of research. In this framework his interests focus also on the applications of ecosystem analysis to environmental impact assessment. In the context of sustainable development he has been exploring the possibility to extend ecosystem network analysis to urban ecosystems, in which flows are expressed in terms of unusual currencies such as water, wastes, inorganic nutrients, etc. His interests are also in the field of mathematical ecology, ecological economics, and political ecology. He presently teaches environmental impact assessment to undergraduate students in the Science Faculty at the University of Parma.

Stefan Klotz is head of the Department of Community Ecology at the UFZ-Center of Environmental Research Leipzig/Halle Ltd, Germany. He graduated in Biological and Chemical Sciences and successfully completed his Ph.D. in Ecology by a thesis dealing with Plant Ecology and Biogeography of urban regions. Plant Ecology, Community Ecology, and Biogeography are the main fields of his research. In this framework his interests focus also on succession, plant-animal interactions, and especially on biological invasions. In the context of global change he has been exploring the possibility of extending plant ecological and biogeographical analysis to artificial landscapes, in which extinctions and immigrations are very important and dynamic processes. He is involved in inter-disciplinary research projects on the influence of landscape structure and land use intensity on biodiversity patterns, on the role of disturbances on species composition, and on ecological processes behind immigrations of alien species. He presently teaches Nature Conservation and Biogeography to undergraduate students in the Faculty of Agriculture in Halle and the Faculty of Geography in Leipzig.