ECOLOGY OF POPULATIONS AND COMMUNITIES

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Summary

Originating from general biology, modern ecology became an interdisciplinary science, which studies interactions of ecological systems of different hierarchical level (from a separate organism to global biota) with each other and with their inorganic environments. Biological subsystems with inorganic ones form ecological systems. Within these systems, biological components are like engines that use solar energy for keeping apart of thermodynamic equilibrium through work on turnover of matter. Ecological systems are organized hierarchically: systems of lower orders are subsystems of systems of higher orders. Within the hierarchy of ecological systems, populations have a distinctive position, being units of two dimensions of the structure of life on Earth: ecological and phylogenic. The discipline that deals with populations is population ecology. The main problem of population ecology is that of population dynamics. There are several models of population dynamics. Though very rough and incomplete, these models form a basis for better understanding of population dynamics, including changes not only in numbers or abundance of individuals, but also in population structures. Among these, spatial distribution, age composition, and sex ratios are the most important. The two latter structures together with characteristics of reproduction are studied by population demography. However, though very useful, a purely demographic approach has many limitations. Interacting populations of different species make a system of community or biocenosis. The main types of interactions of populations within a community are competition, cooperation, and exploitation. The first two interactions in general represent positive feedback loops, while exploitation is a kind of negative feedback loop. The problem of competition is related to the concept of ecological niche (the place of a species with respect to environmental factors, both biotic and abiotic) and the principle of competitive exclusion, which states that two species occupying the same ecological niche would never coexist. However, it is still debatable whether this principle has its own significance or is just a tautology. Exploitation is responsible for energy and matter flows through a community. With respect to this flow, populations are classified as producers, consumers, and reducers. Producers (green plants) use solar energy directly for synthesizing organic matter, consumers use living organic matter for further transformation of energy, while reducers utilize dead organic mass. These groups are defined as trophic levels. Flows of energy and matter make food chains coming from producers to consumers and reducers. Food chains have crossings, forming a food web. The flows of energy drive the turnovers of chemical elements, which are called biogeochemical cycles.

1. Introduction

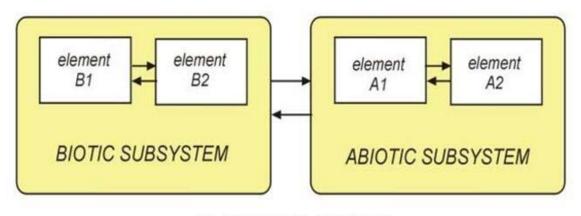
The word "ecology" has the same root as "economics." The former is translated from Greek as "knowledge about ones own house" and the latter as "housekeeping." It seems obvious that to keep the house properly it is better to know about it. However, historically economics as a science was established earlier than ecology. The "house" that is the focus of economics is more an artificial one, with surrounding nature being regarded as just a resource for this, while ecology studies the natural "house" of humankind—its environment on Earth.

Ecology as a science originated from general biology. The term has been in use since the 1880s when Haeckel introduced it into scientific terminology for the first time. The main efforts of botanists and zoologists before this time were concentrated around the problem of classification of different biological objects. Haeckel was the first biologist to realize the importance of studying interactions between different organisms and their environments.

He defined the subject of ecology as studying an animal within its own "house," that is, in its natural environment. In other words, ecology initially dealt with the interactions of an organism with its environment. Ecology has progressed a long way since that time, and now it has become an interdisciplinary science, dealing with the interactions of living (biological) systems of different hierarchical levels—from an organism to the global biota—with their environments. Among the modern ecological sciences, population ecology has its own place, being one of the most basic ecological disciplines.

2. Ecological Systems as a Subject of Ecology

The unity of a biological system of a particular hierarchical level with its environment (which includes both abiotic and biological systems, different from the given one) makes an ecological system. Hence, an ecological system is one that consists of at least two interacting subsystems—biotic and abiotic. Each of these are, in turn, a unity of some subsystems of lower hierarchical level. For example, a human organism is a system of different functional systems of organs and tissues (such as blood system, digestive system, nervous system, etc.). The principal scheme of an ecological system is presented in Figure 1.



ECOLOGICAL SYSTEM

Figure 1. The scheme of an ecological system

Since humans are alive, then in a general sense systems organized around them are also ecological ones. Therefore, from the viewpoint of an ecologist all the social and economic systems should in fact be subjected to the same general laws and regularities as all to other ecological systems.

All living (and, consequently, ecological) systems possess the following important characteristics:

- 1. Living systems are dynamic; i.e. they always change in time and/or space.
- 2. Living systems are open; i.e. they exchange matter, energy, and information with other living systems and their inorganic environments.
- 3. Living systems are capable of self-replication. In other words they can produce copies of themselves made from the matter and using energy both taken from their environment.
- 4. Living systems grow, develop (self-organize), and then become senescent. Aging is a typical feature of any living system.
- 5. Living systems are always very complex. This means that the number of possible structures of a system is big, and it consists of a great number of elements, each of these is also a complex.
- 6. The responses of living systems to external factors as well as interactions between components of living systems are not linear. This nonlinearity means that one cause could have different consequences and/or different causes would have similar consequences under the different states of a system and/or its environment.
- 7. Living systems have memory; i.e. their development and evolution are dependent on their states in the past.

Existence of living systems is determined by the first and second laws of thermodynamics. The first law states that energy does not appear from nothing, nor does it disappear. This provides a basis for estimations of energy balance. For example, if the flow of energy that comes into a system (e.g. food taken by an animal per day) exceeds outgoing energy flow (excretion and respiration) then the amount of energy within a

system increases (the animal starts to grow more rapidly and/or becomes fatter).

The second law is perhaps even more important for an understanding of ecological systems. Since energy is a measure of ability to work, then different forms of energy exist depending on what kind of work is done-electric, osmotic, biochemical, mechanical, etc. However, there is an ultimate form of energy-heat-that cannot be used for any work, i.e. that cannot be transformed into any other type of energy. The second law of thermodynamics states that transformation of energy from one form to another is always accompanied by losses of part of it that comes into this ultimate form. If there is no external source of free energy then a system will evolve to the state of thermodynamic equilibrium (thermal chaos). Therefore, the outgoing flow of energy is inevitably present in open dynamic systems and, consequently, these cannot persist for a long time if these losses of energy are not compensated by the incoming flow of free energy. The more complex and organized a system is, the more work it does to keep itself a part of thermodynamic equilibrium, and the more energy income is needed for compensation of energy losses due to irreversible processes. Consequently, the rate of loss of free energy from an open system in the steady state (when the inflow of free energy is equal to its losses due to inevitable irreversible processes) could serve as a measure of its complexity and organization. The Russian scientist Bauer was the first to proclaim the principle of "thermodynamic unequilibrium" of living systems as early as 1937. He stated that "all and only living systems work constantly against thermodynamic equilibrium that is demanded by chemical and physical laws." Later (in 1945) Schrödinger provided scientific arguments for this principle.

The inevitability of losses of free energy in biological systems leads to a constant process of disintegration of organic structures which is accompanied by release of energy stored in biochemical bonds in the form of heat. The existence of living systems is only possible due to continual replacement of constantly disintegrating organic structures by newly synthesized ones with the use of incoming free energy. Therefore, the state of living systems is always dynamic.

Because of their constant work against thermodynamic equilibrium, biological subsystems play the most active role within ecological systems, serving as "engines" of the constant turnover of matter in the course of immeasurable biochemical reactions of synthesis and disintegration of organic matter. The products of this disintegration come to inorganic environmental systems, being then used for resynthesizing lost organic structures. Clearly, this huge work needs some extrinsic source of free energy. The sun is the only external source of energy known for our planet, which is powerful enough. Certain biological systems (primary producers, represented mainly by green plants) "capture" the energy of sunlight in the process of photosynthesis and then store it in the form of biochemical bonds of organic matter synthesized from inorganic components taken from the environment. Carbon dioxide, water, and nitrates are the most important of these. On the other hand, the vital inorganic substance oxygen is generated in the process of photosynthesis. Then the energy of chemical bonds is converted into other forms of energy (heat, movements, etc.) by means of biochemical and physiological processes. One of the most fundamental processes is respiration, which provides material for creating different types of organic molecules after decomposing other types. According to the second law of thermodynamics, part of the energy stored in these molecules (in the form of chemical bonds) is totally lost. This means that in the process of respiration, complex organic molecules are disintegrated into simple inorganic components (carbon dioxide, water). Therefore, the intensity of respiration manifests the intensity of irreversible processes within a living system. On the other hand, respiration is a source of carbon dioxide, which then is used for resynthesizing organic matter by primary producers.

There are some other forms of work (wind, streams of water, waves, etc.) in inorganic parts of ecological systems that also comes from solar energy. Most of the energy moving social systems also comes from the sun, through coal, oil, or hydropower. All the cycles of matter on Earth are driven by the flow of energy coming from the sun and the greater part of these turnovers (biogeochemical cycles) is the result of work of natural ecological systems. These systems rely on abundant, diffuse, and available sources of energy, while social and economic systems rely on more scarce, concentrated and, consequently, expensive ones. Moreover, these concentrated sources of energy (oil, coal, and gas) are products of the work of biological systems in the past, which have been accumulated as so-called reserve funds of the biosphere.

There is more and more evidence that on the earth these are living beings in all their diversity which provide the surprisingly constant physical and chemical conditions of our planet (composition of the atmosphere and ocean, surface temperature, etc.). In some sense this constancy is similar to homeostasis of an organism, and such similarity has prompted some views of the biosphere as a super-organism with its own regulating and stabilizing mechanisms.

3. Hierarchy of Ecological Systems

Modern ecology as a science can be subdivided into several parts according to the hierarchy of ecological systems based on the hierarchy of biological ones, which makes the active, i.e. functionally most important, part of corresponding ecological systems. However, not all levels of biological systems could serve as a subsystem within ecological systems. For instance, a separate intracellular structure (e.g. a nucleus) does not directly interact with the inorganic environment; their environment is totally biological. Any functional system of organs within an organism also does not interact with the inorganic environment as a separate entity.

The first structural level of biological systems that directly interact with the surrounding environment (both organic and inorganic) is the level of an organism. This level is the subject of ecological physiology and studies "organism–environment" systems. This discipline is distinguished from pure physiology. Ecological physiology (which is also often called "factorial ecology") always considers an organism as a whole together with its relationships with environmental factors, whereas physiology deals mostly with different functional systems (respiratory system, digestive system, nervous system, etc.) within an organism.

However, in nature organisms never exist separately. They always form groups with interactions between different organisms within them as well as with other components of the environment (both organic and inorganic). These interactions are studied in

population ecology. The most general definition of a population is a group of organisms belonging to the same species that occupy a certain area and are to a certain extent isolated from other groups.

Interacting populations of different species make up the biological subsystem of the higher level of community or biocenosis. This subsystem forms an ecosystem (in a narrow sense) or biogeocenosis together with inorganic environmental systems present in the territory occupied by these interacting populations. The ecological science that deals with such systems is called biogeocenology.

All the ecosystems of our planet form the biota of the earth. This huge biological system is a subsystem of the global ecosystem—biosphere. This ecological system, belonging to the highest structural level, is a superior life-supporting system. The biosphere is the subject of the youngest of the ecological sciences—global ecology.

The above structural scheme of ecological systems, though very rough, is presented in Figure 2. This scheme shows that systems of sub-organismic level are the subject of several biological sciences, but not ecology. In addition, it indicates that there are at least two approaches for classification of living systems at the super-organism level: ecological and phylogenetic or systematic. These two approaches display different aspects of biological systems of the earth. The first (ecological) approach emphasizes the functional organization of life, while the second (systematic or phylogenetic) deals more with evolution and genetic distances between different living beings.

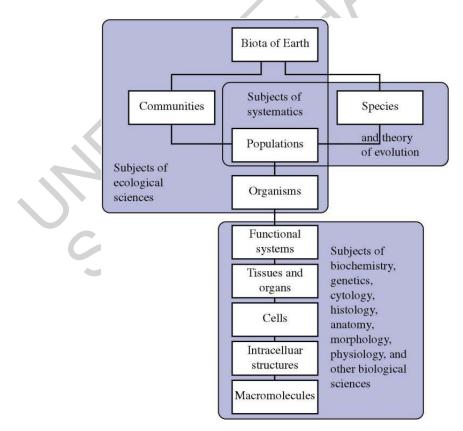


Figure 2. Structural levels of biological systems and corresponding scientific areas

4. Population Systems as a Crossroad of Ecology and Evolution Theory

Population ecology is one of the most important of the ecological disciplines reviewed in the previous section. As presented in Figure 2, the global biota is formed by the whole set of different communities of living beings. On the other hand, each of the living organisms belongs to a certain biological species. In fact, the statement that the global biota is formed by the whole set of biological species is equally true.

Therefore, as mentioned, the global biota can be structured in two different ways ecological and systematic (phylogenetic). Within ecosystems, it is not the whole biological species that interacts with others, but certain populations of these. That is why populations are the common elements of both structures—ecological and systematic.

Since populations of one species are to some extent isolated from each other, they possess genetic specificity. Genetic changes also occur not within a single organism, but at the population level. The main factors of evolution through natural selection (isolation, mutation process, recombination, and fluctuations of numbers) act at this very structural level. Therefore, it is at the population level where ecology is integrated to a large extent with the theory of evolution (see Figure 2).

Besides this principal feature of population level, there are other factors indicating the importance of population ecology, since the interactions between different biological species occur at the population level rather than at the level of a separate organism.

For example, a predator either kills its prey or does not—the interaction between predator and prey at the level of an organism is too simple for revealing any regularity. At the level of populations, however, predators act as a factor of prey's mortality (they kill some proportion of the prey's population which could be different under different conditions).

The basic elements of a population as a system are individuals, that is, separate organisms. However, in some species it is not easy to separate individuals from each other. This happens where vegetative reproduction predominates over sexual reproduction (perennial herbs are one example). That is why the theory of population ecology was based first of all on studying animals.

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Biographical Sketches

Vladimir N. Bolshakov is professor of zoology at the Urals State University and the director of the Institute of Plant and Animal Ecology, Ural Division of the Russian Academy of Sciences in Yekaterinburg, Russia. He is one of the leading scientists in the field of population and evolutionary ecology and protection of animals. He graduated from the Urals State University and since that time he has got scientific degrees of Candidate of Sciences, and Doctor of Sciences. He has made a significant contribution to the elaboration of fundamental problems of ecology, in the theory of intraspecific diversity and ecological adaptations. He has studied different forms of intraspecific diversity, structures of animal populations, their dynamics and stability under the influence of different anthropogenic factors. He has also examined some theoretical problems of productivity, stability, and protection of mountainous and northern ecosystems, as well as the theory and practice of ecological forecasting and ecological expertise. He has published more than 340 scientific works, with 20 books. He supervised 40 doctoral students in the field of ecology. V. N. Bolshakov conducts some courses at the Urals State University, with more than 50 undergraduate students being taught every year. He took part in numerous scientific expeditions to different regions of Russia and other countries. He is an editor-in chief of the first Russian academic journal in the field of ecology-the Russian Journal of Ecology. He also is a member of several editorial boards of Russian academic journals (Russian Journal of Zoology, Science in Russia, and others), as well as an international journal on mountain ecology-Pirineos (Spain). He is a chairman of the Russian National Committee on the UNESCO MAB Programme and a President of the Russian Theriological Society. His awards include a Gold Medal of the Russian Academy of Sciences and International Award of Karpinski (Germany). He is an active member of the Russian Academy of Sciences in the field of ecology.

Feodor V. Kryazhimskii is a professor of ecology at the Urals State University and head of Laboratory of Population Ecology and Functional Biocenology at the Institute of Plant and Animal Ecology, Urals Division of the Russian Academy of Sciences in Yekaterinburg, Russia. He graduated from the Urals State University in 1973 and since that time has got scientific degrees of Candidate of Sciences and Doctor of Sciences in the field of ecology. He is a leading specialist in the field of population ecology, functional biocenology, and ecological energetics. He took part in different expeditions to polar regions of Russia, studying interactions between population characteristics and extrinsic factors. He has published

more than 100 papers and 5 books. He also conducted courses at the Urals State University. He has lectured as a visiting lecturer at Oxford University (Great Britain), University of Oslo (Norway), and Free University of Brussels (Belgium). Now he conducts courses in Human Ecology, System Ecology, and General Ecology at the Faculty of Biology and the Faculty of Mechanics and Mathematics of the Urals State University. Every year more than 200 undergraduate students are taught. He supervised 3 doctoral students in the field of ecology. For five years he was a General Secretary of the Editorial Board of the *Russian Journal of Ecology*.