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Academician S.S. Shvarts in the History of Modern Ecology

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There are instances in the history of science that demonstrate great significance of talent and organizational abilities of individual researchers in the formation of different branches of science. Among ecologists, this fully applies to Stanislav Semenovich Shvarts, who contributed to progress in different spheres of theoretical and applied ecology. His ideas and concepts provided the basis for new trends in this field, such as evolutionary and chemical ecology ets.

Although the principal ideas of prominent scientists have a strong impact, their development, factual justification, propaganda, and practical application are impossible without the concerted activity of large scientific teams. This is the reason why Shvarts devoted much energy and time to creating the Ural Ecological School, which gained wide recognition from the scientific community. The journal *Ekologiya*, which Shvarts organized in 1970, was very important in this respect. Stanislav Semenovich was the first editor-in-chief of this journal, which is now wellknown in Russia and abroad, and headed its editorial board for the rest of his life.

Ecology is one of the most intensively developing biological sciences. At present, most professional ecologists understand ecology as a science dealing with populations. The focus of attention in ecological research shifted from the individual to the population owing largely to studies performed by Ch. Elton, E. MacFadyen, N.P. Naumov, and other scientists. Among these works, an important place belongs to a cycle of studies performed by Shvarts, who interpreted population as an elementary group of individuals that has all the properties necessary for independent existence and development during an infinitely long period of time and is capable of adaptive response to environmental changes (Shvarts, 1960, 1967a, 1969a, 1970a, 1972). He always emphasized that population should be regarded as an elementary biochorological structural unit of the species (Shvarts, 1967a, 1972). To designate animal aggregations that are temporarily segregated within a population but lack some of the properties ensuring the maintenance of their abundance in the principally unlimited sequence of generations, Shvarts proposed the use of the term "micropopulations." The ability for infinitely long independent existence and development is the only objective criterion for principally distinguishing between populations (forms of species existence) from micropopulations.

Population-genetic studies provided the basis for formulating a very significant statement according to which the population is an integral system: changes in individual genotypes affect the general gene pool of the population, as well as modification of the gene pool leading to changes in roles of individual genotypes in system development. Hence, the population may be logically regarded as an elementary unit of the evolutionary process. The same conclusions, but from the ecological standpoint, were drawn by Shvarts from the results of studies showing that the adaptive features of animals are not limited to adaptive responses (hereditary and phenotypic) of individual organisms but also depend on the properties of a population as a whole (Shvarts, 1967b).

Discussing problems related to population research, Shvarts (1967a) emphasized that the term "population," borrowed by biologists from demographs, came into use in scientific biological (in particular, genetic) literature significantly earlier than when population ecology emerged as an individual scientific field. Previously, however, many ecologists studied populations without using this term. A great amount of work had to be done before it became clear that the species settles in its environment in the form of populations, rather than as an aggregate of mutually unrelated individuals, and the properties of populations are not limited to the sum of properties of their individual members. Only then it became possible to consider the population as a real form of species life that has specific features ensuring its independent existence and development under concrete environmental conditions. Thus, the concept of population provided the necessary theoretical basis for studying the most significant ecological problems and created prerequisites for the scientifically sound rational management of natural biological resources.

Studies on the topographic structure of the populations showed that their spatial organization is determined by not only specific features of the landscape, but also by complex, poorly studied relationships between individuals and their aggregations. The intensity and pattern of intraspecific contacts proved to be largely responsible for the rate of reproduction and the mode of area utilization. Some mechanisms of infor-

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mation transfer used in the population for maintaining its optimal structure were revealed. In this context, well-known facts were interpreted in a new way. Thus, it became clear that the singing of birds and frogs, ritual fighting and playing behavior of many animal species, and other similar activities pertain to the system of information about the state of population as a whole. Ethology, the science dealing with animal behavior in the community, adopted new objective methods of research and began to acquire new significance.

Many modern zoologists believe that the development of ethology may provide a key to the solution of the most important ecological problems. This became obvious when the scientists turned from the analysis of populations to the analysis of intrapopulation aggregations. For many animal species, a group mode of life (schools, herds, family groups) is essential for a normal existence. This phenomenon, which has been known for a long time, received a principally new interpretation in modern ecology. It became known that any group of individuals has a perfect system of hierarchical interrelations, which aids in the most efficient utilization of available resources. Studies on mechanisms maintaining this system, among which an important role belongs to "signal codes" and neuroendocrine responses, offer new possibilities of gaining deeper knowledge of the most complex ecological processes and even establishing control over them. It was found that significant differences in this respect may be revealed both between the species and between the intraspecific forms. This finding may be regarded as an important achievement of modern ecology. The success of these studies shows the way to dialectical synthesis of individual biological regularities revealed in the course of ecological research. This synthesis is a distinctive feature of modern ecology.

Another important field of population ecology deals with intrapopulation variation. Populations proved to be heterogenous in virtually all biologically important parameters. This heterogeneity is determined by specific genetic features of individuals, on the one hand, and biological features of age groups and generations, on the other, and allows the population to efficiently adapt itself to environmental fluctuations by modifying its genetic and ecological structure. This research trend connected ecology with population genetics and promoted the intensification of studies in the sphere of evolutionary ecology.

Previously, ecology has also been very important for the development of evolutionary theory, and its significance especially increased in resent times, when it became clear that the initial stages of the evolutionary process actually concern the population level. Hence, studies on the pathways of transformations occurring in populations during their adaptation to the changing environment are not only interesting in the ecological context, but also form the basis for the direct analysis of the evolutionary process.

Evolutionary ecology, aimed at analyzing principles and trends in the evolutionary process, began to develop into an individual scientific field. In this respect, the objectives of ecology are close to those of theoretical systematics, which studies the relative role of clinal variation and intraspecific differentiation of forms in the course of dispersal over the species range, mechanisms limiting panmixia and providing for the reversibility of intraspecific transformations, etc.

Scientific interests of Shvarts were remarkably broad. His studies dealt with almost all the problems of modern ecology, to a greater or lesser extent. However, as N.N. Danilov noted in the foreword to one of Shvarts' books, from the first steps in science to the last days of his life Shvarts was interested primarily in the problems of evolutionary ecology, i.e., ecological mechanisms of population transformation and speciation.

The publication of Shvarts' book *Evolutionary Ecology of Animals* (1969) marked an important stage in the development of research on the problems of evolutionary ecology. This book, which summed up the results of 25-year studies and generalized numerous data and ideas accumulated by biologists working in this sphere of science, was widely acknowledged and has long since become a bibliographical rarity. It was translated and published in the United States. Soon after this publication, Shvarts began to think about revising the book with emphasis on the more detailed discussion of issues that have not been elaborated earlier. With this purpose, he collected literature, made notes, thought over the plan, and wrote down his ideas concerning the new edition. Shortly before falling ill, Shvarts began to prepare a new variant of the book, which he decided to name *Ecological Principles of Evolution.* Unfortunately, severe illness did not allow him to finish this work. The manuscript was prepared for publication by N.N. Danilov. The book was published in 1980.

Leading ecologists highly appreciated Shvarts' studies in the sphere of evolutionary ecology. For example, Chernov (1996) wrote: "According to S.S. Shvarts, evolutionary ecology is largely evolutionary population ecology, i.e., the study of ecological mechanisms and factors of the microevolutionary process that takes place in populations. His followers adhere to approximately the same interpretation of the essence and tasks of evolutionary ecology. Thus, A.G. Vasil'ev and V.N. Bol'shakov refer almost the entire scope of evolutionary ecology to the sphere of population ecology. The understanding of evolutionary ecology by Shvarts corresponded to the developmental stage of the theory of evolution in the 1960s, when it became evident that this theory should be complemented by ecological ideas. Evolutionary ecology as he understood it entirely fits into the synthetic theory of evolution. After Shvarts, the problems of development of this scientific field have not been discussed at such a high conceptual level, although numerous studies on the mechanisms responsible for transformation of the genetic and adaptive structure of populations and the ways of developing the adaptive strategies actually corresponded to its meaning and tasks of this research as Shvarts understood them.

On the whole, the interpretation of the contents of the evolutionary ecology by S.S. Shvarts is very similar to that in studies by S.A. Severtsov. It consists primarily in the analysis of evolutionary transformations and their effects on the process of evolution.

Returning to Shvarts' concepts of specific features characterizing the population level of integration in biological systems, it should be emphasized that he regarded populations primarily as functional and only secondarily as biochorological intraspecific units. Certainly, the functional unity appears because of the fact that individuals inhabit the same territory and may be regarded as its consequence, but this does not mean that the spatial species structure in this territory can serve as the main criterion for distinguishing individual populations. "The population functions as a unity, but this does not mean that it is the smallest biochorological unit. Most populations (but not all!) are naturally divided into micropopulations, which differ from the population in that they are not independent forms of the species existence, are incapable of long-term individual existence, and exist only as parts of the whole (Shvarts, 1969a, p. 15)."

The concept that the population level is an independent form of life integration, which exists along with the molecular, organism, and biogeocenotic levels, conditioned the development of methods for studying concrete populations. Populations differ from one another not as sharply as groups of higher rank, and sufficiently accurate methods are needed for their morphophysiological and ecological assessment. As the primary purpose of the ecological study is to reveal principles and factors of population dynamics, it is particularly expedient to use the methods allowing the researchers to assess the physiological state of individual populations, taking into account their age-related, sex-related, and seasonal-specific features. In this case, the analysis of the physiological features of populations is not an end in itself but only a means for studying population response to environmental changes. It is Shvarts who developed this approach and named it the method of morphophysiological indicators. Its essence is that the analysis of a complex of morphological and physiological parameters provides the basis for the conclusion about the biological specificity and viability of the population under study (Shvarts, 1958; Shvarts *et al.*, 1968). Although this method is seemingly simple, its use in ecological studies requires a thoughtful, differential approach. This is a prerequisite to obtaining results that reflect the actual relationship between the dynamics of the environmental conditions and changes in the interior specific features of populations.

Apparently, the most significant conclusion drawn from the results obtained by the method of morphophysiological indicators is that the average interior parameters of animal populations or intrapopulation groups do not arise randomly but are determined biologically. They are nonrandom for the very reason that they readily respond to environmental changes (needless to say the existence of differences between groups under comparison is determined on the basis of statistical data processing). However, the method of morphophysiological indicators may produce good results only when the average morphophysiological parameters of groups under study are determined correctly.

Reviewing the studies performed by the method of the morphophysiological indicators, it may be concluded that they allowed Shvarts and his followers to make a series of principally important generalizations concerning the problem of species in terrestrial vertebrates, evolutionary ecology, and the ways of animal adaptation to different conditions.

The accumulated data on the interior features specific for different species of terrestrial vertebrates convinced Shvarts that one of the most important ways of understanding specific features of the species as a principal category of the animal world is to gain knowledge of specific morphophysiological features of individual species (Shvarts, 1954, 1959a). The corresponding approach was based on the principle of comparing morphofunctional, ecophysiological, and biochemical features of closely related species and intraspecific groups in order to reveal the biological essence of species and subspecies (with emphasis on determining the essence of concepts, rather than elaborating practical criteria for distinguishing species and subspecies). Shvarts convincingly demonstrated the existence of principal differences in the pattern of adaptation in species, on the one hand, and in individual intraspecific forms, on the other. If intraspecific forms respond to similar living conditions in the same way, the response of different species, albeit closely related, is principally different. In other words, specific features of adaptation prove to be the most significant characteristic of the species, and specific relationships of the species with the environment serve as the initial point of its development (Shvarts, 1959a). On this basis, the morphophysiological response to environmental conditions is one of the most important characteristics of the species and may be used as a criterion of the species status of individual forms (Shvarts, 1954). These views are based on the concept that adaptations of intraspecific forms are reflected in specific morphofunctional features of individuals, and specialized animal species solve this problem at the biochemical level (the tissue type of adaptations, which is more efficient in terms of energy).

Shvarts, being disposed toward a theoretical way of thinking, always attached great importance to planning and carrying out the work on obtaining concrete factual material under natural and laboratory conditions. He organized and participated in numerous expeditions to the Transural region and the Far North. The vivarium of the institute was organized on his initiative.

Shvarts had been particularly fascinated with Subarctic. The unique natural conditions and relative simplicity of northern biogeocenoses helped to realize many of his ideas. The vast data on ecological and morphophysiological features of animals inhabiting this zone, accumulated in the course of northern expeditions, provided the basis for a series of studies on the modes of adaptation to subarctic conditions in terrestrial vertebrates (Shvarts, 1963; Shvarts and Ishchenko, 1971).

The general biological significance of this series of studies is accounted for by the fact that Shvarts revealed the presence of similar adaptations in representatives of different classes (mammals, amphibians, and birds). This concerns the increased ability to accumulate energy reserves in the organism, higher developmental rate, broader food spectrum, and higher activities of digestive enzymes. These facts provided evidence that adaptation to extreme conditions in animals of different systematic groups is ruled by the same general laws.

Being a universal zoologist, Shvarts also devoted much attention to theoretical problems of biogeocenology. The revelation of general principles determining the role of animals in biogeocenoses convinced him of the necessity of developing ecological foundations for the management of biogeocenoses and their productivity. Since the efficiency of each link of the trophic chain is determined by properties of the dominant species and their populations, and the efficiency of the latter depends on their structure, the ecological approach to improving productivity of biogeocenoses (through directed modification of population structure) appears to be feasible even now. In the future, studies in this direction may be prerequisite to the creation of artificial biogeocenoses functioning more efficiently than natural biogeocenoses (Shvarts, 1967c, 1971).

The development of a new branch of ecology is associated with Shvarts' work. Corresponding research deals with the fact that growing and developing organisms release chemical substances (exometabolites) into the environment, which function as regulators of processes at the population level. Shvarts considered these studies very important (Shvarts and Pyastolova, 1970a, 1970b, 1970c). A series of studies performed under his leadership on larvae of amphibians, mosquitoes, and fishes resulted in several theoretical conclusions comprehensively substantiated in the book *The Group Effect in Aquatic Animal Populations, and Chemical Ecology* (Shvarts *et al.*, 1976).

Although Shvarts' studies are mainly theoretical, he always tried to find a practical field of application for his theoretical concepts. This was the main strategy of his scientific activity. In this connection, an illustrative example is the cycle of studies directly related to game husbandry (Shvarts, 1959b, 1969b, 1970b).

Shvarts always considered training of highly qualified scientific personnel to be a guarantee of successes in ecological research. His former students work fruitfully in Yakutia and Karelia, in the Urals and Ukraine, and in Central Asia and the Caucasus.

This is a brief description of the most important landmarks in Shvarts' scientific activity. In fact, the scope of his interests in ecology was significantly wider. All those who had an opportunity to know Stanislav Semenovich and work together with him were impressed by his gift of making wide generalizations, great erudition, and diligence.

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