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Academician Stanislav Semenovich Shvarts: The Proclaimer of Population-Ecological Thinking

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Abstract—This paper is dedicated to the 100th anniversary of the birth of Stanislav Semenovich Shvarts, an outstanding Soviet ecologist. Consideration is given to his role in the establishment of ecology in the Soviet Union, its development at national and international levels, and the evolvement of special fields of ecological science currently pursued in Russia, namely, population, evolutionary, and human ecology. Special attention is devoted to the influence of Shvarts' theoretical concepts on the development of ecological forecasting and ecological foundations of nature conservation and effective natural resource management. It is concluded that Shvarts was the one who gave rise to population-oriented thinking in ecology.

Keywords: ecology, population, biosphere, patterns of evolution
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This year ecologists will commemorate the 100th anniversary of the birth of Stanislav Semenovich Shvarts, Academician of the USSR Academy of sciences, an outstanding scientist whose name is associated with major achievements in different fields of theoretical and applied ecology. His life was short but eventful. Born April 1, 1919 in Dnepropetrovsk, he spent his childhood and youth in Leningrad. In 1937 the was admitted to the Faculty of Biology at the Leningrad State University, where classes were held at that time by many prominent scientists who exerted a strong influence on the formation of Shvarts' scientific views. His direct teachers were Daniil Kashkarov, who shared with him his interest in general theoretical problems of ecology, and Pavel Terentiev, from whom he adopted a rigorous mathematical approach to the phenomena at issue.

When the war began in 1941, Shvarts volunteered to the Leningrad People's Militia Army, was wounded, suffered concussion, and was mustered out of service. Having survived the Siege of Leningrad, he moved to Saratov, where the university was evacuated. Shvarts passed examinations without attending lectures and ed for some time as zoologist at a plague control station. Then returned to the university to embark on postgraduate studies and in 1946 presented his candidate's dissertation entitled "The Effectiveness of Cryptic Coloration." In the same year he moved to Sverdlovsk (now Yekaterinburg), and then all his scientific life was linked with the Institute of Biology (since 1964, Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of sciences). In 1954 Shvarts defended his doctoral dissertation "Experience in Ecological Analysis of Some Morphophysiological Traits in Terrestrial Vertebrates" (1954), which was based on extensive data obtained in the course of his studies in the Urals and Western Siberia. The milestones of his scientific career are as follows: 1957, professor; 1996, corresponding member of the USSR Academy of Sciences; 1970, full member of the USSR Academy of Sciences; 1955–1976, director of the Institute of Plant and Animal Ecology; 1970, founder and editor-in-chief of *Ekologiya* (*Russian Journal of Ecology*). Shvarts held this chair until his death on May 12, 1976.

To appreciate the significance of Shvarts' ideas for the development of ecology, it should be taken into account that the content of the term "ecology"—as understood by not only scientific community but also by governing organs and society as a whole—has markedly changed since the mid-20th century. This term currently refers to a broad range of issues, as clearly follows from the program of "The Year of Ecology" in Russia (2017): it included events dealing with a variety of matters, from control of illicit garbage dumping to "ecology of dance," but unfortunately there were practically no major scientific meetings or publications contributing to the development of fundamental ecological science.

Gennady Rozenberg, in his paper "Once Again on the Question of What Ecology Is," justly notes that "the notion of ecology itself has lost any clearness: it is not always possible to understand whether the matter at issue is about ecology proper (i.e., biological science) or about pollution of the environment, nature conservation, sociopolitical movement, establishing

of a universal religion and 'cosmomorphology'" [1, p. 331]. Having analyzed 80 definitions of this term, he concludes that they separate into three groups: "biological," "social," and "mixed." My card file already includes more than 200 such definitions that generally belong to the same three groups, but the proportions of definitions falling into the second and third groups have increased during the past few years, whereas that of classical, biological definitions has remained almost unchanged. In this relation, it should be reminded that the Greek οίκος (oikos) means "household," and λόγος (logos) means knowledge; i.e., ecology is the science of household (of nature) and of relationships of organisms with the environment.

For decades, Russian and international authors have defined ecology, and Shvarts was one of them. In one of his best-known books, *The Evolutionary Ecology of Animals,* he wrote: "...irrespective of the well-known transformation of biologists' views on the purpose and methods of ecology, its basic task has remained unchanged now for the course of a hundred years. This task is to investigate the lives of animals and plants in their natural habitats, in nature" [2, p. 7]. He then defines ecology as "the science that that studies the interrelationships of animals with the environment at the population level" [2, p. 13] and emphasizes that "ecology as the science of populations fills an existing gap in the full understanding of life on earth" [2, p. 14]. Subsequently he noted that "Ecology as the science of the life of nature has its "Indian summer" now. It emerged more than 100 years ago as a theory of the organism–environment interrelation but has transformed into the science of the structure of nature, the science of how the living cover of the Earth in its entirety is functioning" [3, p. 102].

Shvarts' scientific interests were remarkably broad. His studies address to some extent almost all problems of modern ecology. However, as noted in the preface to one of his books, from his first steps in science to the last days of his life Shvarts was especially interested in the problems of evolutionary ecology, i.e., in ecological mechanisms of population transformation and speciation [4].

According to the Russian Science Citation Index, Shvarts' publications have been cited more than 4000 times over the period of 1998 to 2017 (20 years after his death). The largest number of references are to two monographs on evolutionary ecology and related articles; then follow the book and articles on the method of morphophysiological indicators. This is evidence for the continued relevance of the problems he studied and high demand for his scientific legacy.

Academician Pavel Gorchakovskii—Shvarts' long-term colleague at the institute and editorial board of the journal—named him "proclaimer of ecological thought" [5]. In my opinion, this definition perfectly fits the scientist who largely contributed to the development of ecology into a major field in science, but with a slight correction that appears important to me. Taking into account the important role he attached to the study of populations, I would rather call him the proclaimed of population-ecological thinking.

The contribution of Academician Shvarts to ecology as a biological science has been evaluated in sufficient detail in my papers and book coauthored with Lev Dobrinskii [6–9] and Alexei Vasil'ev [10]. The complete list of his publications (256 entries, including scientific and popular-science articles, abstracts, and presentations at conferences) is given in the book devoted to his biography [11]. Therefore, I consider it appropriate to remind the readers only the essence of those basic ecological ideas that have placed Shvarts among the most prominent ecologists of the 20th century and determined the development of ecological thought in science and society for many years ahead.

Publication of the monograph *The Evolutionary Ecology of Animals* in 1969 [2], where Shvarts summed up and generalized ample data and ideas accumulated in the course of 5-year-long studies, was a major step in the investigation of problems in this field of science. This book gained wide recognition and soon became a rarity. It was translated into English and published in the United States in 1977 [2]. Shortly after its publication Shvarts began to contemplate the second, enlarged edition in which he planned to elaborate in more detail on the problems that had not received sufficient attention previously. He started working on this book, which he named *Ecological Regularities of Evolution,* but failed to complete this work because of his illness. Nevertheless, the book was published in 1980 [4]. The manuscript was prepared for publication by Nikolai Danilov, a friend of Shvarts who shared his ideas/.

Today, 50 years after publication of the first monograph, it is clear that the ideas expressed in it have provided a basis for modern population and evolutionary ecology. Shvarts emphasized that ecology is the science of populations. He formulated and proved the thesis that the population is a basic or, for higher animals, the only form of existence of the species that "possesses all the necessary conditions for independent existence and development during the course of an unlimited period of time" and is "capable of reacting adaptively to changes in the external environment" [2, p. 169]. The literature on the theory of populations and particular data on the population structure of species is overabundant. The above idea by Shvarts is relevant today, even though the term "population" (as well as "ecology") has gained wide use not only in biology but also in other fields of science and social life, primarily those concerning demographic features of individual countries or regions, social problems, etc.

It is appropriate to remind that, discussing human ecology, Shvarts wrote that no one knows better than an ecologist how many population phenomena there are in human behavior [3]. He incited demographers and sociologists to devote attention to the interrelation

between the dynamics of territorial structure of human populations and the dynamics of their genetic composition as well as to that between the dynamics and age structure of human population, which he considered no less interesting. He maintained that these issues heed most thorough study and confirmed this with a number of actual examples. Shvarts at that time saw no grounds to discuss human population ecology, since the main task in population ecology is to analyze the law governing the establishment, dynamics, and self-regulation of populations as elementary forms of the existence of species [13], whereas the life of human populations is governed primarily by social rather than ecological laws. Hence, he considered that human population ecology does not deserve to be classified as an individual field of science, although the conclusions of population ecology should be taken into account in sociology, sociopsychology, demography, and other human sciences. He also emphasized that the structure and functions of animal populations principally differ from those of human populations and that these differences are far greater than those between human and animal physiology [3].

The concept of independence of the population level of biological organization (along with the molecular, organismal, and biocenotic levels) made it necessary to develop methods for studying particular populations. Compared to higher-rank groups, populations differ from each other less distinctly, and methods for their morphophysiological and ecological analysis should be sufficiently accurate and refined. For ecological analysis, it is feasible to use methods allowing the physiological status of particular populations to be assessed with regard to their sex- and age-specific and seasonal features, but this assessment is not an objective in itself but only a means to analyze the responses of populations to changes in ambient conditions.

Such a method was developed by Shvarts beginning from is doctoral dissertation and was completed with publication of the book *The Method of Morphophysiological Indicators in the Ecology of Terrestrial Vertebrates* written in coauthorship with Smirnov and Dobrinskii [14]. The essence of this method is that the conclusion about the originality of a given population is made on the basis of analysis of a complex of morphological and physiological traits. It gained widespread use in zoological practice and markedly contributed to the development of ecology in the Soviet Union. The results obtained using this method allowed Shvarts and his disciples to make several principal generalizations concerning the problem of the species in terrestrial vertebrates, evolutionary ecology, and pathways of animal adaptation to different conditions of existence.

Owing to Shvarts' studies, the theory of populations and population ecology is tightly linked with the problems of the species and evolution, which are of primary importance in biology. It is not accidental that these problems are considered in conjunction with each other in the aforementioned books *The Evolutionary Ecology of Animals* [2] and *Ecological Regularities of Evolution* [4]. The ideas were formulated for the first time that have withstood the test of time and have been confirmed by tens of researchers. Thus, Shvarts' ideas that "the problem of the species ca only be solved on an ecological basis and "ecological characteristic is the main characteristic of the species" have become a rule, as well as the thesis that microevolution begins with emergence of irreversible changes in the genetic structure of population and culminates in speciation.

The main drivers of evolution, along with natural selection, are ecological mechanisms of transformation in the genetic structure of populations: changes in the ecological structure of a population inevitably lead to changes in its genetic composition. Ecological mechanisms of the evolutionary process manifest themselves in three basic aspects, causing changes in the age structure of a population (age-dependent selection), dynamics of its abundance (nonselective elimination), and its spatial structure. Age-dependent selection leads to sharp changes in the genetic structure of the population; nonselective elimination usually has a strictly selective effect on its ecological and, hence, also on genetic structure; and a complex spatial structure protects the population from accidental impoverishment of its gene pool (restricts genetic-automatic processes) and at the same time created conditions for rapid adaptive transformation of its genetic structure. Speciation proceeds within the "old" species based on the formation of a subspecies that differs from other conspecific forms in certain tissue features (the establishment of a principally new type of adaptations is closely connected with the phenomenon called preadaptation [2, 4]. Deciphering of ecological mechanisms of population transformation provides a basis for developing the theory of control over the evolutionary process under natural conditions by means of directed alterations in the ecological structure of populations (a new population with a specified genetic composition may be created within a relatively short time).

Thus, based on reasoning in terms of evolutionary ecology, Shvarts arrived at the following scheme of speciation: development of a population in a specific environment—emergence of morphophysiological features that alter population relationship with the environment—progressive adaptation, development of tissue adaptations—reproductive isolation based on tissue incompatibility—speciation [2, 4].

Prominent Polish ecologist Kazimir Petrusevich noted that the vast amount of material on numerous morphophysiological indicators in tens of species, which Shvarts and his disciples collected and processed, confirmed the thesis that "speciation is a distinct stage of adaptation, namely the formation of new and energetically more feasible adaptations; therefore,

specialized species are always better adapted than specialized intraspecific forms." In view of basic general biological significance of this phenomenon, Petrusevich proposed it to be elevated to the rank of "**Shvarts's ecological rule**" [15, p. 97].

The majority of Shvarts' studies are theoretically oriented, but he always sought to find practical application for his theoretical concept, and this was the main strategy of his scientific activities. The concept of the population served as a theoretical basis for elaborating on the most important ecological problems and thereby provided prerequisites for scientifically sound rational management of animal resources, e.g., for determining the optimal population density at which the maximum commercial harvest is compensated by reproduction. Hardly anyone doubts today that, in terms of game management, the population is an elementary object of commercial hunting. Notions such as "ecological reserve" and "ecological vacuum" have become generally accepted. Many practical problems of animal introduction and acclimation are approached from new theoretical positions.

Shvarts devoted his attention not only to present-day population ecology. He also contemplated prospects for its future development and assigned special significance to long-term research planning. Analysis of the current state of ecology at that time allowed Shvarts to consider that the next 20 years would be the period of evolvement of the explicit ecological theory based on a synthesis of ideas of population ecology and biocenology. problems that he regarded as particularly important and urgent are as follows: to create ecological classification of economically most important animals based on the idea of population structure of the species; develop research on the patterns of population regulation of biogeocenotic processes; analyze the dynamics of ecological structure of populations in different species under different environmental conditions; evaluate ecological mechanisms of the evolutionary process; assess geographic variation of specific ecological features in the most important animal species from different taxonomic groups; analyze metabolic regulation of population phenomena and processes; develop principally new methods for regulating the abundance of animals in nature; and construct mathematical models of population processes.

In the last years of his life (1975–1976) Shvarts repeatedly addressed problems of the biosphere, devoting special attention to its changes under the impact of economic activities of industrial society, nature conservation issues, and ecological forecasting. The thesis is maintained in all his studies that it is ecology that provides a scientific basis for solving nature conservation problems. In speaking at the session of the USSR Academy of Sciences dedicated to its 250th anniversary, Shvarts actually presented a unifying theory for a long term. In his opinion, the developing society will have a progressive impact on nature even if all industries take requisite measures to protect the environment. Therefore, the struggle for the healthy biosphere should be waged in two ways: by reducing to a minimum the direct adverse consequences of industrial impact on nature and by developing measures to ensure the possibility of normal functioning of the biosphere and its constituent biogeocenoses under new conditions [13].

According to Shvarts, relationships of humans with their mother nature and of the biosphere with the sphere of human consciousness and mental activity—the noosphere—are becoming one of the most important and difficult problems for all mankind. Conflicts arising because of this are countless, diverse, and in the aggregate are often taken as a global ecological crisis. However, "on closer examination is proves that most of them have a common basis whose essence is in the contradictory interaction of two systems capable of self-regulation, the biosphere and human society" [13, p. 61]. The essence of ecological crisis is not that the biological resources of nature will perish because of ill-considered human actions; it is that in such a case the self-regulatory capacity of natural complexes will be ruined or the system of self-regulation will begin to operate against mankind. Having analyzed main trends in the development of the biosphere, Shvarts gives a general ecological forecast for the next few decades [13, p. 71–72]: "Significant change in the structure of biogeocenoses; increase in the role of population processes in the maintenance of biocenotic balance; development of specific anthropogenic landscapes capable of self-restoration and self-regulation and characterized by increased stability and biological purification capacity, as well as of biogeocenoses with high biological productivity in territories where only limited anthropogenic development is possible; the maintenance of general balance at the level providing for the optimal development of human society." The final words sound as if they were his will: "For these goals to be achieved, ecological expertise must be incorporated into industrial and agricultural production and industrial culture must be inoculated in the practices of the exploitation of nature. Instead of passive "nature conservation," there will be active attempts to create an optimal natural environment, to create biogeocenoses capable of self-regulation in an environment altered by man" [13, p. 72].

The best-known book by Shvarts *The Evolutionary Ecology of Animals* [2] ends with an optimistic forecast that a real possibility exists to develop methods for directed modification of population structure in different species under different conditions and, in the longer term, to gain control over evolution. Unfortunately, ecologist's dream of controlling evolution has not yet come true, and it remains for next generations of researchers to implement this dream.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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