Evolutionary Ecology in the 21st Century: New Concepts and Development Prospects

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Abstract—The ideas of the evolutionary ecology of the 20th century and its modern conceptual space are considered with regard to new knowledge of the contents of population and evolutionary synecology. The article proposes (1) a population cenotic approach to analyzing the covariation of cenopopulations of sympatric species and taxocenes in space and historical time; (2) an approach to assessing the intragroup morphological disparity in cenopopulations of sympatric species and taxocenes as a measure of morphogenetic stability. Consideration is given to experimental evolutionary ecology as a particular methodological area. Prospects for the formation of evolutionary ecology as an interdisciplinary applied science are discussed in view of the necessity of predicting regional biocenotic crises and rapid coevolutionary changes in biotic communities in a technogenic environment against the background of predicted unfavorable trends of climate changes.

Keywords: evolutionary ecology, synecology, cenopopulation, taxocene, community, variability, morphological disparity, microevolution, coevolution

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On April 1, 2019, it will be 100 years since the birth of Academician Stanislav Semenovich Shvarts, and his key monograph *Evolutionary Ecology of Animals* [1] was pubished exactly 50 year ago. The ideas of evolutionary ecology (EE) as a particular area of ecological and evolutionary-biological studies have significantly changed during this period. The composition of the biota was rapidly changing in all regions of the earth in the late 20th and early 21st centuries due to increasing technogenic pollution and urbanization of lands, as well as to the extermination of dominant resource species of animals and plants, destruction of renewable natural resources, and extinction of vulnerable species [2]. The combined influence of anthropogenic and climatic factors has led to an increase in the number of biological invasions of alien species, as well as to the formation of "hybrid" recombinant biotic communities with new biological properties [3]. A particular epoch that recently began in the Earth's history—the Anthropocene—has been distinguished [4–6], where the impact of the technically and technologically equipped and quantitatively growing humankind on the biosphere has become an important factor that significantly influences its functioning. As a consequence, regional ecological crises and global ecological crisis are expected to take place according to recent predictions [7–9]. It is considered that the necessity of predicting critical ecological changes will soon make evolutionary ecology an applied science that will take the same leading position in biology as that currently belonging to molecular biology [10–13].

Many theoretical concepts of biology that were dominant throughout the 20th century have been reviewed in recent decades. The contents and areas of research have changed in genetics, development biology, ecology, and evolutionary biology, which is due primarily to the emergence of new technological opportunities in molecular genetics. Of special significance is also abundant direct evidence for the role of epigenomic changes (DNA methylation, changes in the localization of mobile genitic elements, etc.) in the manifestation of long-term phenotype modifications and for the reality of transgenerational inheritance of epigenetic changes in the genome structure and functioning due to stress environmental effects [14–16]. As a result of these discoveries, the ideas that seemed "hardly probable" or "completely erroneous" in the 20th century (in particular, the problem of "inheritance of acquired characters" [17]) have become "fully proven" and widely discussed [14–16, 18–20]. This has made it necessary to revise evolutionary concepts, including the theory of modern synthesis (MS).

Since the late 20th century, the epigenetic theory of evolution (ETE) proposed by Shishkin [21, 22] and based on the ideas of Schmalhausen [23, 24] and Waddington [17, 25] has been considered as an alternative to MS. The rapid development of epigenetics in the 21st century and growing awareness of its leading role

in many fields of biology [16, 26], medicine [27], and agriculture [28] have recently provided a strong basis for the ETE, which rests on fundamental knowledge and technologies in the field of epigenetics and epigenomics.

The intention to preserve the leading role of MS and, at the same time, eliminate the inconsistency of genocentric ideas of the mechanisms of the evolutionary process has led to the development of the concept of extended evolutionary synthesis (EES) [27, 29, 30]. According to the EES, it is necessary to supplement MS with epigenetic ideas of the phenomenon of soft heredity, which is based on epigenetic heredity and the transgenerational inheritance of transformed epigenetic DNA profiles. It is proposed to combine these ideas with the niche construction theory (NCT) [30, 31], i.e., to combine the ecological and evolutionary views on the actively formed niche with genetics and epigenetics. Since the new epigenetic interpretation of the mechanisms of evolution in terms of the extended theory of evolution and ETE assumes rapid evolutionary-ecological changes during relatively short historical periods, there is a real opportunity at least to try to reveal and predict the microevolutionary process, if not control it.

The revision of theoretical ideas based on the extended and/or epigenetic theories of evolution should also concern evolutionary ecology (EE) which was introduced and considerably developed by Shvarts [1, 32]. Since, in his opinion, it was the MS concept that generally served as a basis for EE, it is necessary to assess the current contents of EE compared to the initial ideas. Therefore, the objective of this article is to compare the initial and modern concepts of evolutionary ecology and estimate directions of its further development.

THE FORMATION OF EVOLUTIONARY ECOLOGY

Evolutionary ecology is an interdisciplinary science: it partially combines evolutionism (evolutionary theory), population and community ecology, biocenology, historical ecology, biogeography, phylogeography, and phylocenogenetics. Presumably, EE had already existed before being given this name. The features of EE began to be observed in the evolutionary theory of J.-B. Lamarck. The ecological and evolutionary concepts that were developed in Russia by K.F. Rouillier can also be assigned to EE. Charles Darwin should be considered the first "evolutionary ecologist" who advanced the idea of competition and the resulting evolutionary-ecological mechanism of natural selection. K. Petrusevich titled one of his articles as "Darwin Theory of Evolution Is an Ecological Theory" [33]. D.N. Kashkarov emphasized that "...an ecologist can and must be interested in issues of evolution." [34, p. 196] A significant contribution to ideas leading to modern EE was made by Ch. Elton [35], Kashkarov [34], and S.A. Severtsov [36, 37] and later by G. Hutchinson [38, 39] and R. MacArthur [40].

The works of S.A. Severtsov in the 1930s–1940s can be considered as a pioneer version of evolutionary ecology [36, 41]. S.A. Severtsov was probably the first to use the phrase *evolutionary ecology* in his works. He initially determined the cycle of his research as a study of the evolution of "relationships with an environment in conjunction with morphogenesis," since he aimed to substantiate the viewpoints of A.N. Severtsov on the biological progress and morphological patterns of evolution, including the ecological interpretation of aromorphosis and idioadaptation phenomena. He then arrived at a broader understanding of the problem and defined it as a study of "the evolution of ecological relationships and ... changes in the forms and intensity of competition due to adaptiogenesis" [37].

Of interest is a relatively early reference to the term *evolutionary ecology* by V.N. Beklemishev [42]. While considering the problems of ecological parasitology, he developed the ideas of the necessity of creating comparative ecology using the life schemes of a species ("all relationships of the species with all elements of its habitat, first and foremost, the set of adaptations of the species to the set of its existence conditions") as comparison units [42, p. 8]. There is an equivalent to this term in the English-language literature, namely, "life history". According to the opinion of Beklemishev, the comparative ecology of species life histories can become a basis for creating evolutionary ecology. However, he believed that the emergence of evolutionary ecology was so far a remote task, since its basis, i.e., a system of comparative ecology, had not yet been established. This version of "evolutionary ecology" contextually focused on the development of evolutionary parasitology and comparative parasite ecology and was then not developed by the author [43].

According to the opinion of Shvarts, who established the fundamentals of the Russian version of evolutionary ecology which is the most popular in the world [1, 32, 44], one of its precursors was Gordon Orians [45]; he believed that the theory of natural selection is the general theory of ecology. He was probably the first to use the term evolutionary ecology in the English-language literature; however, it is most likely that he used this phrase metaphorically. As a basis, Orians took the Ernst Mayr idea of the division of entire biology into functional and evolutionary biology and did the same with ecology (functional ecology and evolutionary ecology). Orians considered an outstanding ecologist and evolutionist David Lack as an example of a typical supporter of evolutionary-ecological ideas. Lack himself [46], whom Shvarts considered one of the precursors of EE, made a reference to Orians's article and termed this area in the title of his paper as *Evolutionary Ecology*. According to his concept, the main goal of this area was to study the evolu-

tionary causality of the ecological specificity of species and intraspecific forms, as well as the formation and development of ecological adaptations. According to Lack, it is necessary to differentiate the direct ecological features of organisms under certain conditions and those which are established as ecological adaptations proper in the process of evolution.

Shvarts aimed to show that evolutionary ecology focuses on "studying changes in organism relationships in the process of the phylogenetic development of individual groups" [1, p. 9], as well as on studying the ecological mechanisms of evolution based on the experimental study of "the correlation between the ecological and genetic structure of natural populations, on the one hand, and their productivity and adaptability, on the other" [1, p. 174]. Therefore, we should agree with Yu.I. Chernov [41] that the formation of evolutionary ecology throughout the world should be primarily related to the names of S.A. Severtsov, D. Lack, and S.S. Shvarts.

Shvarts took the main MS ideas as a genetic basis of evolutionary-ecological concepts. He understood that neo-Darwinism cannot explain many key aspects of evolution, including the species formation (since it cannot be reduced only to the intraspecific differentiation), and macroevolution. Shvarts also believed that "the indirect role of phenotypic mechanisms in evolution is presumably more serious than this is believed in neo-Darwinism." [1, p. 12]. In addition, he emphasized that "... The disregard of issues of development physiology, phenotypic genotype implementation, and epigenetics by the synthetic theory of evolution should probably also be considered as one of its disadvantages; however, this disadvantage cannot be overcome on the basis of Lamarck concepts. In contrast, the application of some principles of ecology for the decision of this problem may prove to be very useful." [1, p. 12] The incomplete correspondence of EE (as understood by Shvarts) to the postulates of neo-Darwinism follows from his statement: "The "species or not a species" issue is solved at the ecological rather than physiological or genetic level." [47, p. 15]. This is reflected even more strictly in his other statement: "...species are not themselves that they couldn't cross, but they can't cross because they are species [1, p. 149]. These statements clearly show the primacy of ecology rather than genetics in the species formation. In his view, it is ecological mechanisms and factors that primarily determine this process. The latter clearly differed from the concepts of neo-Darwinism in the mid-20th century.

However, Shvarts preferred to use MS in his theoretical constructions as the most comprehensively developed evolutionary theory in those years. Thus, when speaking about the prehistory of the formation of EE, he noted a great role of concepts of ecological genetics for EE which were developed by I.M. Lerner [48] and E.B. Ford [49]. He believed that this area is the closest to the essence of EE as understood by him; however, it corresponds to the principles of genetics rather than ecology. Since the most important key blocks of Shvarts's evolutionary-ecological theory of species formation [1, 32, 47] represented the initial processes of population microevolutionary phenomena, he accepted neo-Darwinism as a theoretical basis of EE. According to Shvarts, "The population is a biological unity, the genetic and ecological manifestation of which is interdependent. The interconnection > of the ecological and genetic in the population is the background against which the elementary evolutionary phenomena are displayed." [1, p. 18] Therefore, he believed that the main task of EE was to comprehensively study the driving forces of evolution based on its ecological mechanisms [1].

The further development of evolutionary-ecological concepts is associated with synecological ideas proposed by E. Pianka [50], P. Giller [51], and M.L. Rosenzweig [52].

It is interesting to compare the general evolutionary ecological concepts of Shvarts [1, 32] with the EE version presented by Pianka [50]. The main feature of EE as understood by Shvarts is that it was aimed at using methods of population biology for studying the evolution process and creating a new evolutionary, ecologically-oriented theory. This trend is also relevant nowadays. The evolutionary ecology of Pianka was focused on using evolutionary notions to explain population phenomena, as well as on studying the functioning and origin of communities. Chernov came to the conclusion that EE as understood by Pianka is actually general ecology, based on the assumption that "...ecology is, in a sense, entirely evolutionary" [53, p. 85].

Since it is important to take into account not only population-ecological but also synecological aspects, Chernov [41] proposed to include three main areas in the content of EE: (1) ecological factors of the microevolutionary process and species formation; (2) adaptiogenesis (including adaptive radiation and the invasion of new adaptive zones); (3) cenotic evolution (=evolution at the supraorganism level). In the latter case, he meant ecological forms of organization, such as "biocenoses, communities, population and socioecological structures, coadaptive complexes, morphoadaptive types, and life forms."

According to the opinion of Chernov, "Based on the ideas of Shvarts, evolutionary ecology is mainly evolutionary population ecology, i.e., a study of ecological mechanisms and factors of the microevolutionary process that takes place in populations" [53, p. 88]; i.e., it is related to the first area. However, we can only partially agree with this, since Shvarts and his school also paid much attention to studies related to the second area, i.e., adaptiogenesis. In addition, their research was based on studying the variability in the morphological and morphophysiological features of a large number of species under natural conditions and spe-

cies from experiments on the simultaneous breeding and crossing of intraspecific forms and taxonomically controversial species from different geographical sites and natural zones [47, 54–57]. The issues of evolution at the biocenotic level (the third area of EE according to Chernov) were also of interest for Shvarts; however, he did not see any ways for the real decision of this problem and came to the conclusion that "the evolution of organisms is accompanied by changes in the structure and organization of their communities and, ultimately, of biosphere. What is the relationship between these processes? The author does not consider it possible even to address the solution of this problem in its entire complexity. One can believe that this time has not yet come. However, it will come tomorrow." [58, p. 213]. Nevertheless, Shvarts came to the conclusion that "...the notion of evolution cannot be limited by the phylogenesis of individual species or groups of organisms; it also includes the evolution of natural communities, as well as general changes in fauna and flora and the evolution of biosphere. The evolutionary process in its ordinary sense is significantly determined by the evolution of biogeocenoses." [58, p. 222] Therefore, it can be concluded that all the three EE areas indicated by Chernov were outlined in the works of Shvarts and his scientific school.

A book of M.J. West-Eberhard [59] with revolutionary ideas for that time, namely, the ideas of the role of phenotypic plasticity, modifications, and rapid developmental changes in evolution, which was published in the 21st century, became a landmark for the development of EE. Generalizations of E. Yablonka and M. Lamb [14, 18, 60] on the transgenerational inheritance of stress-induced epigenetic genome changes are also important. New ideas of the role of epigenetic heredity as a means of rapid changes in morphogenesis require the review of main concepts not only in the field of the theory of evolution but also in the field of EE. Shvarts also focused on a particular value of the analysis of the phenotypic variability (modifications) and processes of morphogenesis in evolutionary-ecological studies [47]. Based on Shmal'gauzen's idea of stabilizing selection [61], he formulated a unique concept of optimal phenotype in EE [54].

At the turn of the 20th and 21st centuries, the key role for the development of the second and third EE areas (according to Chernov) was played by new concepts in the theory of coevolution which were formulated by J.N. Tompson [62, 63]. Rosenzweig's substantiation [52] of the concepts of "win-win ecology", or "reconciliation ecology") can be considered the next stage of the EE development, which focuses on assessing species-area relationships (SPARs) and the area of their natural communities that remained relatively unchanged against the background of the historical human activity. The Rosenzweig concept should be taken into account in assessing the sustainability of biodiversity and predicting ecological crisis phenomena during changes in regional communities and ecosystems.

In the last years, the key role for EE is played by the development of the concept of extended evolutionary synthesis (EES) [11, 64]. This concept influences the understanding of mechanisms of rapid microevolution and species formation by supplementing them with ideas of epigenetic inheritance (soft heredity) and mechanisms of active niche formation by living organisms (in accordance with the NCT). However, I believe that the real extended synthesis is still hardly developed to date, since the authors of EES currently almost completely do not take into account or only mention the influence of biotic communities on the evolution of their components, which was previously widely discussed by some researchers, e.g., V.V. Zherikhin [7], in the analysis of mechanisms of phylocenogenesis.

In conclusion to the brief sketch on the formation of EE, one should mention the book of A.S. Severtsov [65] *Evolutionary Ecology of Vertebrates*, which contains new materials and concepts. The book fully presents the views of the author on the sources and essence of this area and proves the necessity of maintaining the intraspecific and species diversity to provide the "evolutionary stasis" and relationship of evolutionary processes with phylocenogenesis. A.S. Severtsov proved an important idea that phylocenogenesis occurs not so much on the basis of species genesis and ecogenesis as on the basis of the succession of life forms and biomorphogenesis, which are required for the adaptation to new adaptive zones.

CONCEPTUAL SPACE OF EVOLUTIONARY ECOLOGY

Evolutionary ecology is part of ecology; however, its conceptual space is determined insufficiently strictly. Inconsistencies are also observed in the understanding of the conceptual space of ecology itself. D.N. Kashkarov [35] distinguished two aspects in ecology: autecology and synecology. N.P. Naumov [66] believed that the subdivision into autecology and synecology was not strict and distinguished the ecology of individuals, populations, and communities (=biocenology). S.S. Shvarts [1, 32, 58] distinguished autecology, population ecology, synecology, and biogeocenology. A.S. Severtsov believed that "The interactions of organisms with an environment can be studied at the level of an individual (autecology or ecophysiology), at the level of populations and species (population ecology or synecology), at the level of ecosystems (biocenology), or at the level of entire biosphere" [65, p. 4]. I.A. Shilov attempted to construct a three-dimensional pattern of ecology, where the population was taken as the origin of coordinates [67, p. 241]. He showed the direction from an organism to the population along one axis, the direction from the population to biocenosis and biogeocenosis along the second
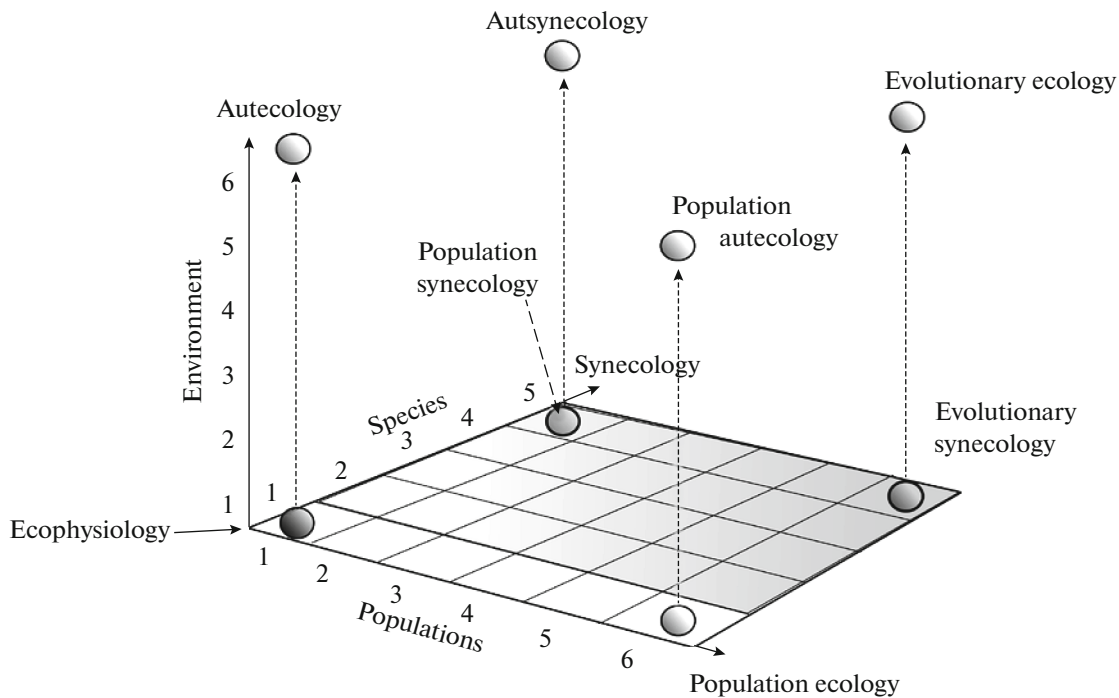
Fig. 1. Conceptual space of evolutionary ecology and its main research areas in the form of a three-dimensional model (see the explanations in the text).

axis (=ecosystem), and the direction from the population to the species and then to the kingdom along the third axis. A particular place in this space is occupied by Biosphere, which is the center of relationships with biogeocenoses, on the one hand, and with kingdoms, on the other. Shilov believed that the population in this relationship can be considered (1) as a biochorological unit (according to Naumov) and (2) as an evolutionary unit (according to Shvarts).

Evolutionary ecology uses populations and species as study objects and considers them in different environmental conditions. Let us try to construct a three-dimensional conceptual space of EE using three main variables: (1) population variable (the number of populations under study), (2) species (the number of species under study), and (3) environmental gradient (Fig. 1). For different numbers of populations, the first axis of the figure actually describes the direction that characterizes population ecology in its broad interpretation. The second axis describes the direction for a set of species that characterizes synecology. The third axis includes environmental states, the response to which indicates the research area that corresponds to autecology.

We placed an organism at the origin of coordinates, i.e., in the zero position (see Fig. 1); therefore, if we take individuals from a certain population of a species and assess their physiological response to environmental changes (along the third axis), this study will meet the goals of ecological physiology (ecophysiology)

and/or *organismic autecology*. Since the time of the emergence of the term of autecology (from Greek autos—self), it is related both to the study of the limits of conditions that organisms choose for their existence and to the characteristic of relationships of individuals with an environment. This allows us, without any contradiction, to study the aspects of autecology of not only separate individuals but also groups of individuals (populations or communities), i.e. supraorganism systems themselves. This makes it possible to deliberately use the term of autsynecology for characterizing the relationships with the environment of local populations of sympatric species included in a community (a taxocene).

Let us consider (see Fig. 1) the situation when only one species, one environmental state, and one population of this species are taken. This model allows one to study the diversity of responses of individuals from a specific population in the same place and for a short period under similar environmental conditions. This type of research corresponds to population ecology. However, the study of the diversity of responses of individuals within the population will be characterized more exactly as *intrapopulation ecology* and actually corresponds to the term of demecology, which is sometimes used instead of the notion of population ecology. This example clearly shows that this variant is undesirable, since populations consist of elementary colonies or demes (=micropopulations). Along the third axis, we can consider, for example, seasonal or

interannual changes in a certain population, i.e. when the environmental conditions change. In this case, we deal with an autecological population study or, more precisely, *population autecology*. If we compare several populations of the same species along the first axis, which, however, will be subject to the same biotopic conditions for a short period (e.g., the comparison of bank vole populations along the floodplain forests of the Ural River in July), the study will be carried out within the framework of *interpopulation ecology*. The complication of the model by the shift along the third axis will allow us to study several spatially and temporally (e.g., by seasons) remote populations of the same species. Below, we will carry out a research within the framework of *interpopulation autecology* by analyzing the response of different populations of the same species to seasonal environmental changes.

Let us now consider another situation, when one cenopopulation in each of several species inhabiting the same biotope in the same locality during the same season is studied syntopically and synchronously. In this case, the synecological task, i.e., the issue of how cenopopulations of different sympatric species respond to the same conditions (e.g., drought) is solved. This type of research corresponds to an area that we propose to term *population synecology*. The general concept of such studies may differ. For instance, we can study the cenopopulation of the same species in different years at different levels of its abundance and different levels of completeness of the species composition of the taxocene. The study of the response of the dominant species *Clethrionomys glareolus* to a high and low abundance of the population and to different species compositions (oligo- and polyspecific compositions) of the taxocene in different years revealed a sharp switch of morphogenesis and a sharp change in the shape of the mandible at different abundance constellations and completeness levels of the taxocene species composition [68]. When the shift along the third axis is also taken into account, i.e., when the response of cenopopulations of different species to different environmental conditions (seasons, years, and anthropogenic impacts) is studied, this type of research ("species × environment" interactions) will correspond to population autsynecology.

Below, let us present the situation when cenopopulations of several species (e.g., shrews or rodents) from geographically remote localities are analyzed relatively synchronously and syntopically. These data characterize a task that makes it possible to reveal the interconnected responses of taxocene species to changes in ecological conditions in remote biocenoses and assess their coadaptive properties [69]. This situation corresponds to an area that I propose to term *evolutionary synecology*. If we add the analysis of environmental changes along the third variable to this task (which is relevant when studying geographically remote communities (taxocenes)), this type of research will for-

mally correspond to *evolutionary autsynecology*. The aspects of population and evolutionary synecology, taking into account autsynecology, reflect the main problems of evolutionary ecology in its broad understanding [41, 53].

The general 3D model does not include the fourth measurement, i.e., time; however, environmental time changes partly compensate for this lack. It is easy to imagine that the 3D pattern is animated when the fourth variable (time) is mentally added to this model: "populations" will emerge like small balls, fluctuate in size (abundance), drift along the third axis (under different conditions), etc.

Therefore, this 3D model adequately describes the conceptual space of evolutionary ecology and main components of its disciplines: population ecology, population autecology, population and evolutionary synecology, and population and evolutionary autsynecology. Additions in the form of the terminological prefix aut- are presumably not required in the latter two cases, since it is difficult to present fully identical ecological conditions in studies within the framework of population and evolutionary synecology. It can be concluded that the conceptual space of evolutionary ecology really includes autecological, population-ecological, and synecological study components and all their possible compositions.

The inclusion of aspects of population and evolutionary synecology in the scope of EE interests makes it possible to initiate new study areas and opportunities. Some of these EE aspects are already known: the study of different aspects of coevolution and, in particular, mutual diffuse coevolution of species in a community [62, 63]; analysis of evolutionary-ecological mechanisms of sympatric speciation [70], including the rapid emergence and differentiation of fish flocks [71, 72]; the determination of feedbacks between ecological and evolutionary events in historical characteristic times [13, 73]; the study of rapid microevolutionary events as a result of biological invasions [74, 75] or chronic anthropogenic impacts [76]; the comparison of the effect of the principle of Chernov compensation at different levels of biological organization [68, 77]; the comparative phylogenetic analysis of communities and ways of their formation [78]; the solution of problems of urbanistic evolutionary ecology [13, 79], etc.

On the whole, the problem of rapid morphogenetic changes in populations and communities due to stressing effects, as well as analysis of rapid changes in morphogenesis on the basis of the transgenerational inheritance of stress-induced epigenetic changes, are important for EE [14, 20]. The scope of this article does not make it possible to consider the entire set of rapidly developing evolutionary-ecological studies. Therefore, I will focus only on some of them.

POPULATION AND EVOLUTIONARY SYNECOLOGY

The problems of synecology had long been outside the interests of population and evolutionary biologists, although evolutionary processes occur in communities and are mainly, if not always, controlled and directed [7, 32, 53]. The introduction [76, 80] of the following concepts into synecology should be considered an essential task for the near future: (1) population concepts and methods for the transition to population and evolutionary synecology and (2) methods of two-level assessment of the ecological state of cenopopulations of sympatric species and their communities, which are aimed at developing population-cenotic concepts. It is also necessary to predict the beginning of crisis cenotic phenomena.

In my view, local communities of taxonomically close sympatric species within a facies or a tract represent taxocenes (the term of Hutchinson [38]), i.e., taxonomically close components of cenoses that perform similar (mainly trophic) and environment-transforming functions. Taxocenes are phylogenetically closely related ecological guilds, the fragments of communities that can be considered as their models. Syntopic settlements of each species in a taxocene inhabiting a local biotope for relatively sedentary species (e.g., mollusks, many insect groups, shrews, and rodents) are termed *cenopopulations* that ecologically interact with each other due to the common habitat and use of similar resources.

The term *cenopopulation* is widely used by botanists and means a territorial grouping of a particular species that is confined to a specific biocenosis and, consequently, to a specific biotope. Zoologists prefer other terms: deme, parcel, locality, or settlement. These small territorial groupings, which are potentially or actually connected to each other by migrants and, therefore, form a single population (=metapopulation), are also commonly termed *micropopulations* [1, 32]. They characterize only a part (a territorial fragment) of the population of a certain species and are not formally related to a biocenosis. Therefore, while comparing individuals from the syntopic settlements of sympatric and taxonomically close species that were simultaneously collected in the same biotopes, we deliberately use the term *cenopopulation* for these local groups. Within a taxocene, cenopopulations of each species inhabit a common biotope and can be simultaneously considered as micropopulations. However, when we use samples from syntopic groups of several sympatric, biotopically and territorially coinciding species, only the term *cenopopulation* appears to be justified, while the use of the territorial term *micropopulation* loses its sense for these groups in this case. If we deal only with one species, it is more logical to term its local biotopic settlements as *micropopulations* or *demes*.

The simultaneous intra- and intergroup analysis of syntopic cenopopulations of sympatric species included in a taxocene makes it possible to compare their responses in the form of an increase in the variability in their features to changes in conditions within the framework of population synecology. It allows one to assess the parallelism or independence of the manifestation of intra- and intergroup covariation in morphogenetic, physiological, and behavioral responses, i.e. the coevolutionary potential of sympatric species [69]. The opposite responses may indicate the antagonism of ecological species demands, while the parallelism of responses may indicate a high coadaptive potential, i.e., the total adaptive morphogenetic and morphophysiological responses. Analysis of the intragroup diversity makes it possible to assess the resistance of the cenopopulation to the constellations of environmental conditions in different seasons and years. The same method can be used to assess time changes in the total taxocenotic diversity for several syntopic and simultaneously analyzed cenopopulations of sympatric species of a local taxocene. A similar comparison is carried out during the parallel study of several taxocenes including cenopopulations of the same species in geographically remote localities, i.e., under different conditions; however, allotopic, rather than allochronic samples from cenopopulations of several species are compared in this case. For instance, methods of geometrical morphometry [69] make it possible to arrange the ordinates of individuals of different species in the general morphospace and analyze only the variation in the shape of objects.

In turn, the combination of all tasks, i.e., the parallel time and space comparison of geographically remote but syntopic cenopopulations of several sympatric species represents the subject matter of evolutionary synecology and/or evolutionary ecology as broadly understood [41]. This integrated combined analysis of the variation of the properties of the phenome in its broadest interpretation (from the morphological features to behavioral features of an individual at different stages of ontogenesis) enables one to determine the sympatric species that is best adapted to the conditions of the local biotope by the manifestation of the variability and diversity of the studied features. The variability of the individual features of a species or its intragroup diversity, assessed by the total of its features will increase under unfavorable conditions and, on the contrary, decrease under favorable conditions for the species [80, 81].

The phenomenon of increase in the range of variability of features in an unfavorable environment was experimentally established and described by N.V. Glotov as an effect of a provocative environmental background [82]. We propose to term it *the principle of Glotov*. It allows us to identify species cenopopulations with different levels of morphological disparity. The conclusion can be made after assessing the level of ordinate dispersion in the multidimensional morphospace using methods of geometrical morphometry [83] with

random number alignment of samples (rarefaction procedure). For instance, it was established that the morphological disparity of dominant species was significantly lower than that of subdominant species [80, 85]. The natural reconstitution of the rodent community after nonselective elimination in the vacated area led to a significant decrease in the level of intragroup morphological disparity in the impact zone for the species that was previously a subdominant with a low abundance in the control; this reflects a decrease in the stress level of morphogenesis. According to another research [69], the comparison of the geographical covariation of three sympatric shrew species of the genus *Sorex* showed the manifestation of the geographical parallelism of transformations of their morphogenesis; this made it possible to discriminate individuals of different taxocenes with the probability of over 95%, irrespective of the species which they belong to. A decrease in the morphological disparity of the population of the dominant species when the completeness of the species composition of the taxocene was as high as possible was also revealed; however, this parameter significantly increased when it was incomplete [68]. These facts indicate the actual influence of interactions of sympatric species of a local community on morphogenesis processes and the dynamics of both cenopopulations and the taxocene.

Therefore, the application of methods from the methodological repertoire of population biology for solving the tasks of population and evolutionary synecology makes it possible to assess the ecological state of both individual cenopopulations of sympatric species and local taxocenes. The development of this methodology contributes to revealing and predicting regional biocenotic crises.

EXPERIMENTAL EVOLUTIONARY ECOLOGY

The unification of the two areas—experimental methods of systematics, discussed by S.S. Shvarts [47, 86] in terms of evolutionary ecology, and experimental ecology discussed by A.V. Pokrovskii and V.N. Bol'shakov [87]—generates a new area that I propose to term *experimental evolutionary ecology* (EEE). However, neither Shvarts nor Pokrovskii nor Bol'shakov wrote about this area and none of them used this terminology, although it was significantly implied and directly results from many of their works.

The idea was simple and, at the same time, practically effective. If representatives of different taxa taken from different conditions or geographical points (e.g., from forest steppe and forest tundra) are cultivated under the same laboratory vivarium conditions, the morphophysiological or other peculiarity of their progeny will reflect the degree of evolutionary divergence of taxa. If the intergroup variability is not manifested, this will indicate the evolutionary-ecological and phenogenetic similarity between the forms being compared, as well as their historical and phyletic homogeneity.

In my view, there are three main areas in experimental evolutionary ecology: (1) experimental assessment of the degree of evolutionary divergence of forms under laboratory conditions (here, problems of experimental systematics and evolutionary-ecological problems can be solved); (2) population-ecological experiments under laboratory conditions and/or in nature (problems of the population ecology of certain species and evolutionary-ecological problems); (3) population-cenotic "experiments" and monitoring of species and taxocene responses. If the variability and/or morphological disparity are studied at the level of taxocenes, a generalized analysis of objects without taking into account their species identity (i.e., a total analysis of simultaneously obtained natural samples of sympatric syntopic species that were randomly aligned with respect to the number of observations is carried out).

Let us consider a specific example concerning EEE. Laboratory colonies of two vole species—narrow-skulled vole and root vole—were simultaneously created at the vivarium of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, under the supervision of Pokrovskii [87]; each of these species included two subspecies: the northern and southern ones. The species exhibit sympatry on a significant part of their ranges; in addition, sympatric forms were observed in the northern and southern subspecies of both species. Since the animals were bred under balanced conditions, their morphogenetic peculiarity could be assessed by the complex of 46 phenes of nonmetric traits [88]. The discriminant canonical analysis of the value of the principal components of individual phenetic compositions of the northern (*Lasiopodomys gregalis major*) and southern (*L. g. gregalis*) subspecies of narrow-skulled vole with the northern (*Alexandromys oeconomus hahlovi*) and southern (*A. o. oeconomus*) root vole subspecies revealed significant differences along all the three axes. Interspecific differences were clearly observed along the first discriminant canonical function and an unidirectional parallel shift of ellipsoids, which characterizes the variability in manifestations of phenetic compositions of both southern subspecies in relation to the ellipsoids of both northern forms, was observed along the second function [88, see Fig. 1]. In other words, there are mainly simultaneous structural changes in the manifestation of a wide range of homologous phenes of nonmetric traits along the second axis for both species in their direction to the south and north.

The manifestation of phenes is resistant to the direct effect of different ecological factors. This made it possible to use the intraindividual (phenogenetic) variability in discrete morphostructures for the indirect assessment of the level of epigenetic differences between the animal groups being compared (the measure of their epigenetic divergence [89]. The level of

epigenetic divergence was estimated as the squared generalized Mahalanobis distance. The measure of the epigenetic divergence is additive and includes at least two components: the phylogenetic and evolutionary-ecological ones. The phylogenetic component was about 76% of the total intergroup variance. The evolutionary-ecological component combined about 24% of intergroup variance and was divided into the species-specific (the "taxon" x "habitat" interaction) and ecological-historical subcomponents (about 9 and 15%, respectively) (the parallelism of the manifestation of phenes as the result of the historical adaptation of similar ecological conditions by taxa). The phylogenetic component of the variability was many times higher than the evolutionary-ecological component. However, a significant manifestation of the ecological-historical component indicates that both species were characterized by the formation of similar irreversible morphogenetic differences between northern and southern subspecies. The latter can be explained as a manifestation of parallel, generally directional adaptive microevolutionary changes in the morphological structures of the axial skull and mandible in sympatric species.

As a second research area within the framework of EEE, population-ecological experiments under laboratory conditions and/or in nature imply the following aspects. Long-term monitoring of populations in natural conditions on the basis of the periodic sampling of individuals differs little from the same monitoring under laboratory conditions. The combination of both population monitoring techniques, i.e., the parallel analysis of even-aged individuals from natural populations and laboratory groups generated from them provides the most interesting and informative results both for evolutionary and population ecology, since laboratory conditions eliminate all interspecific (cenotic) interactions, simplify intrapopulation interactions, and provide an excess of resources, which models an ecological environment other than that in nature.

The advantages of the monitoring of natural populations, e.g., animal populations, are that individuals are in a natural environment, there are interpopulation and cenotic interactions, and feeding is usually various and adequate and, at the same time, is not regularly excessive. Since natural conditions are uncontrolled, the material should be collected for a long time to reveal possible similar natural situations. The morphogenetic response of different structurally functional groups in a population (biotypes or morphs) [90] to certain environmental conditions can be revealed for calculating their widest range using only synchronous and syntopic samples [91].

Population-cenotic "experiments" and taxocene monitoring represent another area within the framework of EEE. In this regard, analysis of different forms of covariation of sympatric species under natural rather than laboratory conditions is of particular interest. This can be expressed in manifestations of geographic, chronographic, or biotopic covariation for different species of the same taxocene. The parallel analysis of the morphological variation of synchronous samples of sympatric species inhabiting a local biotope corresponds to the above-presented example of the parallel study of morphogenetic responses of different forms under the same laboratory conditions. Therefore, the study of syntopic allochronic samples of representatives of sympatric species is directly analogical to the laboratory comparison transferred to natural conditions. The regular (annual) collection of data on allochronic syntopic samples of sympatric species in a natural environment in the same season and during the same time period can serve as the simplest analog of laboratory studies to monitoring observations under natural conditions [80]. Therefore, the simple parallel monitoring of sympatric taxocene species makes it possible to assess the evolutionary-ecological mechanisms of interspecific interactions, as well as the synecological nature of coevolutionary changes in morphogenesis in communities.

CONCLUSIONS

When developing the concepts of evolutionary ecology 50 years ago, Academician Shvarts set a wide range of tasks and a general study trend that is also largely relevant nowadays, in his 100-year Anniversary [10, 12]. Although the theoretical ideas of the mechanism of species formation that were advanced by Shvarts [1, 32] should be currently refined, taking into account new discoveries, his evolutionary-ecological basis has changed insignificantly. In my opinion, the species formation stages that are based (according to Shvarts) on the emergence of irreversible morphophysiological features which change the relationship between populations and the environment and include tissue adaptations are directly related to ecological epigenetic mechanisms widely discussed in terms of EES [16, 19, 20, 91]. Shvarts's idea of regular homeostatic fluctuations in the genetic structure, which explains regular seasonal phenotypic changes, should be replaced by the concept of currently known homeostatic changes in the epigenetic system, as well as the concepts of phenotypic plasticity and threshold switches in morphogenetic programs [18, 59, 60, 68]. The role of ecological mechanisms in evolutionary changes due to changes in the ecological structure of populations has begun to be realized very recently [11, 19, 64].

I believe that the ecological mechanisms of evolution that were outlined by Shvarts should be supplemented based on the concept of extended evolutionary synthesis. It is necessary to study both the epigenetic consequences of changes in the ratio of all structural and functional groups in a population and changes in the species ratio in a community (a taxocene), as well as feedbacks between ecological and evolutionary pro-

cesses in populations and communities [13, 73, 92]. The relationship between micro- and macroevolutionary processes that was presented by Shvarts [1, 32] is still widely discussed but has not yet been solved [93]. Nevertheless, its solution seems to be quite realistic in terms of EES and ETE [92].

It can be assumed that the role of evolutionary synecology (ES), which is currently only at an early stage of its development, will increase among other EE areas in the near future. It is ES that will focus on studying and modeling the coevolution of communities, determining the mechanisms of sympatric speciation, and predicting rapid changes in populations and communities. The main advantage of ES is the two-level population-cenotic approach [53, 81] to manifestations of the covariation and morphological disparity of cenopopulations in local taxocenes [80]. The concepts of experimental evolutionary ecology are well consistent with ES approaches and the epigenetic concept of rapid morphogenetic changes in terms of EES [94, 95], as well as with the ideas of mechanisms of diffuse coevolution [62, 63], and can be considered as a particular methodological area of EE.

The proposed approaches to the two-level population-cenotic analysis of sympatric species, including that based on population and evolutionary synecology and molecular genetics and geometrical morphometry, are prospective for assessing the ecological state of individual cenopopulations and local taxocenes and their morphogenetic changes. The further development of evolutionary-ecological concepts of new ways and methods of predicting regional crisis biocenotic phenomena and ecological epigenetic mechanisms of population-cenotic changes will contribute to the practical solution of problems of management of initial evolution processes, as well as tasks of directional changes in the structure and functional properties of cenoses [52]. This is generally in line with the expectations advanced by Shvarts [1, 32] and even partially surpasses them in terms of the possible construction of hybrid (recombinant) cenoses [3] including alien invasive species [74].

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COMPLIANCE WITH ETHICAL STANDARDS

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