The Evolutionary-Ecological Principle of Turesson-Schwartz and Experimental Aspects of Evolutionary Ecology

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Abstract—The experimental assessment of the morphogenetic reactions of intraspecific and close forms to the same developmental conditions, independently proposed for plants by G. Turesson and for animals by S.S. Schwartz, has a common methodological basis. We have defined it as the evolutionary-ecological Turesson—Schwartz principle (TSP), according to which evolutionary divergence is reflected in the different orientation and intensity of the morphogenetic reaction of intraspecific forms and species to similar developmental conditions. TSP allows one to compare the fan of modifications in remote forms, to assess the degree of their evolutionary and ecological divergence, and the similarity of ecological niches in morphofunctional features. The principle supports the possibility of assessing the morphogenetic responses of coenopopulations of closely related sympatric species to natural, anthropogenic or simulated changes in development conditions. Research of this kind is possible in three directions: experimental assessment of the evolutionary divergence of forms during development under similar controlled conditions; population-ecological experiments in the laboratory and/or in nature; and population-cenotic "experiments" in synecological studies and monitoring of communities. The Turesson—Schwartz principle potentially allows one to approach the identification and prediction of regional biotic crises in laboratory and natural conditions, assessing the sustainability of the development of cenopopulations of sympatric species under similar conditions.

INTRODUCTION

The problem of identifying rapid evolutionary changes on historical rather than geological scales of characteristic times arose after the discovery of numerous documented examples of such phenomena [1—4]. Interest in the problem has increased in recent decades due to the relatively recent discoveries of transgenerational inheritance of stress-induced epigenetic changes associated with morphogenetic changes [5—7]. In this regard, epigenomics and recently developing ecological epigenetics now play a special role in the formation of a new ecological picture of the world [8—10]. The study of the phenomenon of epigenetic inheritance and its role in evolutionary biology becomes fundamentally important [10, 11]. These areas are essential for understanding the mechanisms of rapid evolutionary-ecological changes in the biota [12—14]. It is precisely due to these areas of science that the foundations of traditional concepts in the field of evolutionary theory are largely being revised, and new concepts are being formed about the role of transgenerational plasticity in rapid evolutionarily significant changes in morphogenesis [15—17]. Of particular interest in this regard are examples of rapid sympatric differentiation and evolutionary divergence of cichlid and carp fishes of the Great African Lakes, where so-called flocks of species are formed [18, 19], being probably associated with transgenerational epigenetic rearrangements of morphogenesis [20].

Many researchers believe that, along with new molecular genetic directions, the leading position in biology will belong by the middle of the 21st century to evolutionary ecology; a special interdisciplinary scientific direction at the intersection of the interests of ecologists and evolutionists [12, 21—23]. The most important for us are research using approaches of functional and trait-based ecology, relying upon the study of variability [24—26]. Let us recall in this regard that the chapter written by S. Mather and J. Damuth in the collective monograph devoted to the problems of evolutionary ecology [27] emphasized: "The field of evolutionary ecology is essentially the study of variations within individuals, among individuals, among populations, and among species. For several reasons, evolutionary ecologists need to know the causes and consequences of variations in traits that affect the performance, behavior, lifespan, and fertility of individu-

als in their natural habitat. ... By understanding the causes and consequences of phenotypic variability within and between populations, we can discover evolutionary processes operating at different ecological levels." [27, p. 3]. Not only do I fully agree with the position of the authors, but I also believe that parallel analysis of the variability of homologous traits of closely related species under similar developmental conditions does indeed allow us to obtain important evolutionary-ecological conclusions.

Earlier, in a review article [28], I briefly considered the history of the formation and promising directions of evolutionary ecology. Many researchers mentioned in the article contributed to the ideas leading to evolutionary ecology: C. Elton, D.N. Kashkarov, S.A. Severtsov, J. Hutchinson, R. MacArthur, D. Lack, S.S. Schwartz, E. Pianka, and others. Nevertheless, one should agree with Yu.I. Chernov [29] that the emergence of "evolutionary ecology" in the world must be primarily associated with the names of S.A. Severtsov [30, 31], D. Lack [32], and S.S. Schwartz [33, 34].

Evolutionary ecology, as a number of authors believe [21, 22, 35], will occupy one of the central places in biology by the middle of the 21st century due to the need to predict rapid biotic restructuring caused by significant anthropogenic, climatogenic, and biotic (synecological) changes in the environment. There is a high probability of the emergence of global and regional biocenotic crises as a result of a general decline in biodiversity and increased anthropogenic impact on the biota [23, 35, 36]. An increase in the number and proportion of invasive species, a change in the composition of communities, the elimination of vulnerable autochthonous species, the replacement of native community species by species that were previously coenophobes, as well as the mass extinction of rare and specialized groups of species are predicted [2, 13, 36]. Acceleration of microevolutionary processes is expected, moreover, not only at the microbiome level, and, as a result, a rapid avalanche-like transformation of biological communities may occur [14, 17, 36]. Therefore, it can be assumed that evolutionary ecology must inevitably move from the field of theoretical research to the sphere of applied, experimental, and socially oriented science, which human ecology already is today.

In recent decades, there has been a wide discussion of the need to revise evolutionary-ecological concepts within the framework of the Extended Evolutionary Synthesis (EES) concept, which emerged at the beginning of the 21st century [see 7, 35, 37, 38]. The EES concept is based on a new understanding of the role of epigenetic inheritance , the ability of transgenerational inheritance of epigenetic changes associated with the developmental process, in historically rapid restructuring of morphogenesis [5, 10, 17, 39]. It includes the Niche Construction Theory (NCT) [40, 41]. According to NCT, all organisms are capable of actively changing the conditions of their individual and group environments, including by building nests, burrows, trapping nets, cocoons, and other shelters, as well as changing the course of morphogenesis and their behavior, influencing the processes of environment formation and environment transformation. All this inevitably affects the living conditions of individuals of subsequent generations of a particular species as well as other species, changing the vectors and degrees of selection pressure, which inevitably turns the phenomenon of "niche construction" into a specific evolutionary-ecological factor [41]. The emerging new challenges foreshadowing the onset of crisis biocenotic phenomena in many regions of the Earth that lead to regional biotic crises require the development of evolutionary-ecological approaches for their early forecasting.

Therefore, the goal of this review is to analyze the background of the emergence and substantiation of the role of the Turesson−Schwartz methodological principle in the development of an experimental direction in the mainstream of evolutionary ecology research as a possible tool for forecasting and detecting regional population and cenotic crisis phenomena of the biota in rapidly changing environmental conditions of the progressive Anthropocene [42]. Particular attention is paid to assessing the potential of using disturbances in group morphogenesis to indicate the onset of crisis maladaptation of biota components.

THE THURESSON−SCHWARZ METHODOLOGICAL PRINCIPLE

The combination of two research areas, experimental methods of taxonomy discussed by Academician S.S. Schwartz [33, 43] from the standpoint of evolutionary ecology and experimental ecology, which was written about by A.V. Pokrovskii and V.N. Bolshakov in the monograph *"Experimental Ecology of Voles"* [44], leads to the need to form a special experimental aspect of research in the mainstream of evolutionary ecology. Let me remind that S.S. Schwartz [43] proposed to synchronously grow representatives of different intraspecific forms and closely related species in the same vivarium conditions and judge the degree of their evolutionary divergence and taxonomic status based on their phenotypic response to habitat conditions. It is quite possible that S.S. Schwartz, when organizing a series of experimental studies in vivarium conditions, relied on similar studies by other zoologists, V.S. Kirpichnikov [45] and N.I. Kalabukhov [46], whose works he cited in articles and books.

The idea was very simple, but it worked extremely effectively in practice. If representatives of different intraspecific taxa taken from remote and geographical points with different landscape and climatic conditions (for example, from forest-steppe and forest-tundra) are grown in ecologically similar laboratory vivar-

ium conditions, then the manifestation of the uniqueness of their descendants in morphophysiological and other characteristics will reflect the degree of evolutionary divergence of the taxa. If intergroup variability in characteristics does not appear, then this will indicate the evolutionary-ecological and phenogenetic closeness of the compared forms, their historical and phyletic community.

Actually, this experimental approach largely coincided with the method of identifying ecotypes, which was previously developed in botany by G. Turesson [47]. Turesson proposed to transfer representatives of plant species growing in contrasting biotopes from different parts of their range to homogeneous similar conditions of a botanical garden or greenhouse and then to trace their development and compare the implemented phenotypes. If the transferred objects still differed from each other under the same cultivation conditions, they were attributed to different ecotypes. However, if they did not differ, this was the basis for recognizing them as genetically similar. In fact, Turesson's studies were a prototype of further work in the field of experimental direction of ecological genetics of plants.

A similar method of assessing morphological similarity in the development of different intraspecific forms and species in the same conditions for both plants and animals has a long history. One of the first experimenters was probably the outstanding botanist Alphonse de Candolle [48], who tried to evaluate the nature of the manifestation of species modifications and conducted experiments on parallel cultivation of plant forms of the same species originating from different places with different climates in similar conditions. As a result, he came to the conclusion about the presence of a number of hidden physiological races within a morphologically homogeneous species. This formulation of the question was very close to that which was later supported in the early 20th century by the already mentioned Swedish botanist G. Turesson. Turesson's research were followed by the well-known similar experimental and theoretical studies by Russian geneticists and botanists M.N. Rozanova [49, 50] and E.N. Sinskaya [51, 52], who experimentally grew and compared ecotypes of both representatives of intraspecific forms and different species and genera. M.N. Rozanova revealed the parallelism of ecotypes, modifications, and hereditary variations in closely related species using buttercups (Ranunculus) as an example under similar cultivation conditions and considered the possibility of using experimental genetic methods of analysis in taxonomy. According to E.N. Sinskaya, a species is a complex system of related ecotypes. She came to the conclusion that: "The more variable and diverse the conditions of the habitats where these plant forms have historically developed, the more pronounced their reactive capacity, the wider the scope of their modification variability" [52, p. 240]. Interest in the problems and methods of "genecology" proposed by Turesson was also shown by outstanding scientists such as academicians N.I. Vavilov [53] and V.L. Komarov [54].

Similar experimental studies in terms of method were also carried out by the geneticist and ichthyologist V.S. Kirpichnikov on representatives of three different races of carp: Amur, Volga, and Taparavan (from Georgia) [45, 55] raised in fish farms in the Leningrad, Moscow, and Kursk oblasts. After comparing the imported individuals of these races and their descendants after several years of "acclimatization" for a set of characteristics, including the rate of maturation and growth, he came to two main conclusions. First, he established high phenotypic plasticity and the manifestation of initially hidden modifications in experimental groups of fish of each race and, second, he discovered the stability of several characteristics that are typical of the races when they are raised in new conditions, i.e., the hereditary determinacy of typical interracial differences. However, V.S. Kirpichnikov who pointed out the prospects and importance of experimental fish taxonomy in his early publications stating that "... without an experimental method, intraspecific taxonomy of fish will not be able to advance further" [45, p. 216], unfortunately, never returned to this topic again, focusing exclusively on solving genetic problems using fish as an example.

Another well-known physiologist and zoologist, N.I. Kalabukhov [46], conducted ecological-physiological experiments on several closely related mammal species from different taxonomic groups, attempting to evaluate their response to similar conditions based on several physiological characteristics, interpreting the ecological-physiological differences between them as a manifestation of divergence. We emphasize that he compared only the physiological "responses" of animals taken from the natural environment to the developmental conditions. His approach is in many ways similar in concept to that proposed earlier by G. Turesson, but the morphogenetic responses of different species taken from different parts of their range were of little interest to him. He preferred to evaluate only physiological differences between morphologically different forms, thereby trying to identify their adaptive nature. N.I. Kalabukhov was interested in the responses of the "organism" as a representative of the species rather than the "population" as S.S. Schwartz did when he relied on morphophysiological indicators. This was one of the main distinctions in the experimental evolutionary-ecological studies of the scientific school of Academician S.S. Schwartz [33, 44].

All the above-mentioned researchers, both "predecessors" and followers of the ecological-genetic studies of G. Turesson and the evolutionary-ecological studies of S.S. Schwartz, convincingly demonstrated the possibility of obtaining an assessment of the degree of divergence of phenotypic traits in the process of

parallel cultivation of intraspecific forms and closely related species in both similar and contrasting conditions, most often using morphometric and habitual traits. However, when assessing the degree of their phenotypic divergence, one can also use physiological, biochemical, immunological, epigenetic, signaling (acoustic), ethological, trophic, and other characteristics that can complement the overall evolutionary-ecological picture of intra- and interspecific divergence.

From the above, it can be concluded that there is a common methodological basis for the approaches proposed by the founder of ecological genetics botanist G. Turesson for plants and one of the founders of evolutionary ecology zoologist S.S. Schwartz for animals, as well as other scientists mentioned: botanists and zoologists. It is the possibility of evolutionary-ecological interpretation of the experimental assessment of the directions and expression of morphogenetic responses of individuals of different intraspecific forms and related species to similar conditions of their development. It is known that along with general philosophical or biological principles, more specific principles, including methodological ones, appear in science. Therefore, we consider it possible to call this new methodological principle the evolutionary-ecological principle of Turesson-Schwartz and give it the following definition: the multidirectional nature and different expression of the morphogenetic response of intraspecific forms and related species to similar conditions of development are an indirect indicator of the degree of their evolutionary divergence. In other words, relying on the Turesson—Schwartz principle (TSP), it is possible to experimentally reveal the dissimilarity of the fan (spectrum) of modifications in compared geographically and evolutionarily distant forms, to assess the degree of their evolutionary-ecological divergence and similarity of ecological niches by a set of features.

The use of the names of Turesson and Schwartz as eponyms of the TSP is due to the fact that it is they who made the main contribution to the emergence and development of experimental areas in ecological genetics and evolutionary ecology, which are based on the comparison of morphogenetic and morphofunctional responses of intraspecific forms and related species. Meanwhile, the names of A. De Candolle, V.S. Kirpichnikov and N.I. Kalabukhov, even despite their formal priority in botany and zoology in this regard, cannot be considered as symbols of this area of research, since the main scientific activity of these outstanding scientists was associated with other scientific aspects. A. De Candolle is widely known and associated with the study of the centers of origin of cultivated plants, V.S. Kirpichnikov is known for genetic studies, hybridization, and selection of fish, and N.I. Kalabukhov is one of the pioneers in ecological physiology.

It seems to me that this evolutionary-ecological approach can be extended to natural situations with a combined comparison of morphogenetic responses in a population of the same species or populations of different species over time. A parallel comparison of the associated variability of representatives of coenopopulations of sympatric species in different years both over short (adjacent years or 2—3 years) and long periods of time (more than 20 years) makes it possible to evaluate morphological changes (morphogenetic responses) of different species to the same changes in environmental factors [56, 57]. Such a prospect arises when using long-term museum collections. Since mass collection of material on different species in different years is a common procedure, it becomes possible to compare collection materials gathered in the past with modern collections. This allows one to evaluate both short-term and long-term chronographic variability in syntopic sympatric species in the corresponding similar conditions of their development.

Combining these two aspects, a combination of growing forms from natural sympatric and allopatric populations of closely related species under similar laboratory conditions and parallel comparison of their natural "peers" in natural conditions, theoretically allows us to "experimentally" evaluate their coevolutionary and coadaptive potentials [58, 59].

Let us emphasize that, speaking about the application of experimental research in the mainstream of evolutionary ecology, we do not mean evolutionary experiments in real time. This, unfortunately, is almost impossible, since evolutionary changes themselves usually occur over very long time periods, although they can also occur over relatively short historical rather than geological times. Experiments are in this case understood as the possibility of identifying the responses of morphogenesis of different species and communities to similar changes in the environment in order to assess their adaptive potentials, the ability to adaptively modify development in changed conditions. In principle, such studies are possible at any speed and duration of the evolutionary process and make it possible to compare the adaptive potential of the development of syntopic and synchronous populations/coenopopulations of closely related species in a community.

The need to apply experimental approaches in evolutionary ecology is not new. According to one of the founders of evolutionary ecology David Lack: "Evolutionary ecology will undoubtedly benefit from field experiments" [32, p. 230]. In a recent article devoted to the ecological and evolutionary revision of the concept of key innovations, i.e., the features of organisms that allow species to use previously inaccessible ecological resources, A. Miller et al. [60], proposed "an integrative approach to the study of key innovations that requires experimental approaches to form and functions" [60, p. 122].

Using the Turesson–Schwartz principle in experimental studies in the mainstream of evolutionary ecology, we can distinguish, as I believe, three main directions (there may be more directions, if we take into account the molecular-epigenetic, ethological, and other aspects): (1) — experimental assessment of the degree of evolutionary divergence of forms during development under laboratory conditions (vivarium/phytotron, greenhouse), which is largely associated with solving problems of experimental taxonomy, but also allows testing evolutionary-ecological problems; (2) — population-ecological experiments in the laboratory and/or in nature aimed at studying both the population ecology of specific species and solving evolutionary-ecological problems; (3) — population-cenotic "experiments" and community monitoring based on experimental synecological studies to assess the response of representatives of sympatric species to natural, anthropogenic, or simulated changes in environmental conditions. In the latter case, it is also possible to assess the response of the communities themselves as such. In doing this, in the sets of syntopic and synchronously obtained natural samples from cenopopulations of sympatric species, which are randomly equalized in volume, a generalized analysis of the variability and morphological diversity of all individuals or centroids of cenopopulations is carried out without taking into account their species membership in the "taxon-free" mode [24, 61].

EXPERIMENTAL APPROACHES IN THE MAINSTREAM OF EVOLUTIONARY ECOLOGY

Let us consider a specific example of experimental studies in the mainstream of evolutionary ecology. At the vivarium of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, laboratory colonies were created in parallel for two species of voles, the narrow-skulled vole and the root vole, each of which was represented by two subspecies: northern and southern [44]. The species sympatrify over a significant part of their ranges, and the sympatric forms are both the northern and southern subspecies of both species, respectively. Since both species and representatives of their subspecies were bred in relatively similar vivarium conditions, the available collection materials made it possible to evaluate the morphogenetic response of these forms to similar conditions of maintenance based on a complex of nonmetric traits of the axial skull and lower jaw. The results illustrate the potential of the experimental approach in evolutionary ecology and the scientific prospects for studying the morphogenesis of sympatric species in a vivarium [62]. Based on the analysis of the individual occurrence of 46 discrete homologous phenes of non-metric traits of the axial skull and lower jaw in individuals from the four laboratory colonies of voles mentioned above, a multivariate ordination of the phenetic compositions of individuals was performed using the principal component method. As a result of further discriminant canonical analysis of the values of the components characterizing the conjugate variability of individual compositions of the phenes in the northern (*Stenocranius gregalis major*) and southern (*S. g. gregalis*) subspecies of the narrow-skulled vole with the northern (*Alexandromys oeconomus hahlovi*) and southern (*A. o. oeconomus*) subspecies of the root vole, significant differences were revealed along all three axes [see 62]. Interspecific and intergeneric differences were manifested along the first discriminant canonical function, and a unidirectional parallel shift of the ordinate dispersion ellipsoids characterizing the variability of both southern subspecies in relation to their northern forms was observed along the second. In other words, both species, as they move south and north, show largely parallel structural changes in the manifestation of a large number of homologous phenes of nonmetric traits.

The manifestation of phenes is resistant to the direct action of various ecological factors [63], which made it possible to use the intra-individual variability of discrete morphostructures for indirectly assessing the measure of epigenetic divergence between the compared groups of animals [64]. The measure of epigenetic divergence estimated as the square of the generalized Mahalanobis distance (D^2) is additive and includes at least two components: phylogenetic and evolutionary-ecological ones. The phylogenetic component accounted for approximately 76% of the share of total intergroup variance. The evolutionary-ecological component combined approximately 24% of the intergroup variance and was subdivided into species-specific (the "taxon" × "habitat" interaction) with 9% and ecological-historical, with about 15% (the latter reflects the parallelism of the manifestation of phenes as a result of the historical adaptation to similar ecological conditions by taxa). A significant ecological-historical component indicates that both sympatric species have historically developed similar irreversible morphogenetic differences between the northern and southern subspecies. The latter also indicates the manifestation of parallel reorganizations of the morphological structures of the axial skull and lower jaw in sympatric species, which are mainly of a directed adaptive nature [see 65].

Properly speaking, "evolutionary experiments" are also within the scope of interests of evolutionary ecology. However, the example given above does not apply to them and is connected with the aspect of experimental evaluation of morphogenetic responses of species to the same laboratory and natural conditions, i.e., a variant of a "passive" experiment. Therefore, it is possible to consider active and passive experiments in the mainstream of evolutionary ecology. Speaking about active experiments, i.e., "experimental evolution," we recall that back in the late 19th century William Dallinger [66, 67] cultivated colonies of unicellu-

lar organisms in a special incubator, first at a normal temperature of 60° F, and then gradually increased it over the course of 7 years, raising it to 158° F. The control initial cultures experienced severe stress already at a temperature of 73° F and did not survive at the maximum achieved. On the contrary, cultures capable of living normally at the maximum temperature barely grew and quickly died at the initial temperature of the environment of 60° F. Dallinger came to the conclusion that he had succeeded in experimentally confirming the phenomenon of Darwinian adaptation to changed incubator conditions.

There are also many other examples of "experimental evolution" in microorganisms [4, 68], other invertebrates [69], and vertebrates [70−72], which are associated with selective experimental reorganization of morphogenesis under changed development conditions. However, we emphasize once again that the above-considered assessment of the morphogenetic response of northern and southern subspecies of two vole species to the same development conditions in the laboratory does not pertain to "experimental evolution," but rather assesses the evolutionary-ecological responses of populations of different species to similar development conditions.

POPULATION-ECOLOGICAL EXPERIMENTS IN VIVARIUM AND NATURE

Population-ecological experiments in laboratory conditions and/or in nature as the second direction of research in the mainstream of the experimental approach of evolutionary ecology imply the following aspects. Long-term tracking of populations in natural conditions based on their monitoring and periodic removal of individuals is essentially little different from similar monitoring in laboratory conditions. The differences in the technique of collecting material consist in the fact that, in nature, objects must be caught at a certain time in the corresponding biotopes, but in uncontrolled climatic conditions of the environment. In artificial conditions, the conditions for the development of individuals must be similar but can also be strictly controlled by the experimenter. The combination of both techniques of population monitoring, i.e., parallel analysis of individuals of the same age from natural populations and laboratory groups derived from them, allows us to obtain the most interesting and meaningful results in the fields of both evolutionary and population ecology, since in laboratory conditions all interspecific (cenotic) interactions are removed, intrapopulation interactions are simplified, and an excess of resources is provided, which models a completely different ecological environment for individual development than in natural conditions.

The advantages of monitoring natural populations (e.g., animals) are that individuals are in a natural environment, there are intrapopulation and cenotic interactions (competition, predator pressure, epizoot-

ics, etc.), nutrition is usually varied and complete, but food is not regularly excessive and requires constant searching. The composition of food can be established in a field experiment, using isotopic or molecular genetic methods. Since natural conditions are an uncontrollable factor, it is necessary to collect material over a long period of time in order to detect similar natural situations. The selection of comparable synecological situations in the natural environment is somewhat difficult, although theoretically possible with long-term monitoring [63, 73]. In cases where it is necessary to evaluate the morphogenetic response of different biotypes (according to V. Johannsen) or structural-functional groups (SFGs) [57, 63] in a population to certain environmental conditions in the expectation of their widest range, there is no need to select similar conditions. It is only necessary to ensure the receipt of synchronous and syntopic samples representing the biotypes and morphs being compared [57].

Following the logic of the experimental approach in the mainstream of evolutionary ecology, we carried out a natural experiment on mutual (reciprocal) resettlement of representatives of remote colonies of the northern vole (*Ellobius talpinus* L.) from the Orenburg and Chelyabinsk oblasts [74]. The peculiarity of the experiment was that the Orenburg animals are brown in fur color (brown morph), and the northern ones are black, i.e., melanistic (black morph). This made it possible to trace the fate of the migrants by the color of the animals during periodic total catches with the subsequent return of individuals to their former family colonies. During the experiment in nature, only the southern Orenburg migrants survived in the north of the Chelyabinsk oblast. The experiment lasted 3 years. It was expected that after a small number of generations the brown migrants would become closer to the black ones in their morphological features, but the experiment turned out to have a different result [74].

Using geometric morphometrics methods, we analyzed the variability of the lower jaw shape and found that the variability ranges of the same-aged aboriginal brown and black animals of different populations do not overlap and are located in different areas of the morphospace. The variability range of the migrants shifted slightly in relation to the range of the original brown Orenburg grouping, retaining some of the jaw shape features that are characteristic of the parent population, but this shift did not lead to its convergence with the range of black aboriginal animals. The latter indicates, on the one hand, the genetic specificity of both original populations and the ability to restructure morphogenesis in introducers, on the other. It was also found that the dispersion of the ordinates of individuals within the variability range is nonrandom and is characterized as overdispersion. Meanwhile, in both aboriginal samples, dispersion was random. The phenomenon of overdispersion of coordinates in the group of migrants can be interpreted as an

increase in the fan of morphogenetic responses and the scope of modification variability in the descendants of Orenburg individuals in a new habitat in the north of the species range. Thus, the experiment in nature made it possible to identify the unequal morphogenetic response of representatives of different populations to the same conditions, the possibility of rapid (in a small number of generations) morphogenetic restructuring with the formation of new compromise morphological features that allow introduced species to exist in a new biocenotic environment, being surrounded by another population.

Another example of a natural experiment conducted on a Eurasian scale is the widespread introduction of muskrats in the 20th century to the territory of European countries and the republics of the former Soviet Union. Population differentiation of the species was accompanied by the development of specific adaptations to new habitat conditions. For this reason, the process of muskrat introduction can be considered as an analogue of rapid geographic morphogenesis, and the morphogenetic changes in populations can be used to judge, as a first approximation, the speed and efficiency of the initial stages of microevolution [75]. The consequences of species introduction were studied using age-homogeneous allochronic samples of yearling muskrat from the Kurgan oblast and the Yamal Peninsula, which were collected at the initial (in 1954 and 1955) and late (in 1979−1980 and 1989) stages of species introduction. Geometric morphometrics methods were used to study the variability of the size and shape of the mandibular branch associated with the trophic function. As a result of the canonical analysis of Procrustes coordinates, it was established that the shape of the lower jaw differed in the northern and southern muskrat populations both at the initial stage of introduction and at the end of the 20th century [75]. The greatest and almost parallel transformation of the jaw in both populations was manifested along the first canonical variable, reflecting the manifestation of directed chronographic variability, accounting for 59% of the total intergroup variance. The morphogenetic specificity of the northern and southern populations at different stages of introduction that reflects the manifestation of geographic variability was expressed along the second canonical axis. This variable accounted for 29% of the variance. Thus, as a result of the introduction of the muskrat in the south and north of Western Siberia, significant morphogenetic and functional changes associated with a change in the configuration of the mandibles occurred in its outpost population groups. The chronographic changes in their shape turned out to be similarly directed, indicating the similarity of adaptive morphogenetic changes in the northern and southern populations. The initial range of interpopulation differences remained the same, despite the fact that the configuration of the mandibles in these populations changed. Parallel transformations of morphogenesis

in the northern and southern populations can be explained only by the result of gradual integration of the species into a new cenotic environment. The revealed remote morphological consequences of the introduction of the muskrat can serve as an example of rapid directed microevolutionary restructuring of the morphogenesis of the introduced species populations in new cenotic conditions.

The analysis of natural "experiments" makes it clear that such research relates to experimental aspects in the field of evolutionary ecology. "Experimental" testing of the morphogenetic response of different intraspecific forms to the same environmental conditions differs little from how this would be carried out during laboratory breeding of animals in a vivarium. Since the animals live in a natural environment, their diet is as close as possible to the natural one, which is a certain advantage in relation to a laboratory "experiment."

"Experiments" in vivarium conditions on synchronous maintenance and breeding of laboratory colonies of closely related species for several generations and their subsequent morphological analysis partly resemble "experimental-evolutionary" studies, but still relate to the experimental study of morphogenetic responses in the mainstream of evolutionary ecology. Let us consider an example related to the study of conjugate morphological variability in two sibling species, the common (*Microtus arvalis obscurus*) and East-European (*M. rossiaemeridionalis*) voles, in vivarium conditions. Together with E.A. Gileva and D.Yu. Nokhrin, we conducted a multidimensional comparison of animals from three successive generations of laboratory colonies of both sibling species based on a complex of metric features of the axial skull and lower jaw. The dynamics of the centroid ordinates of the samples in three generations of each species was presented in the morphospace of the first three discriminant canonical functions (about 80% of the intergroup variance). Interspecific differences appeared along the first function, and intraspecific differences were observed between successive generations of both species along the second one. Both species experienced almost parallel unidirectional and significant changes in craniometric features in a series of generations. In just three generations of maintenance in vivarium conditions, parallel morphological rearrangements of the axial skull and lower jaw (not associated with interspecific differences) were observed in individuals of laboratory colonies of the two closely related species. They are not random and are associated with a similar morphogenetic response to the vivarium conditions in which they developed. In this situation, it is difficult to doubt that a rapid, targeted change in the morphogenesis of both species occurred under laboratory conditions, which is due to a combination of modification variability and driving selection. The phenomenon of "natural selection" is usually very difficult to substantiate and prove, but it is

in this case simply difficult to find another explanation. Another question is what is the substrate of selection in this case, i.e., how are the selected phenotypes formed, and how is such a similar direction of morphogenetic restructuring achieved? It is also unclear what is the mechanism of their fixation and how irreversible are these changes? Since the rate and scale of morphogenetic changes were quite high, the most probable mechanism can be assumed to be the sequential accumulation of "long-term modifications" due to the accumulation of transgenerational epigenetic rearrangements caused by chronic stress in representatives of both species under vivarium conditions. This is in many ways reminiscent of the effect of the appearance and fixation of new modifications in generations due to chronic stress, which was described by C.H. Waddington and called by him the "assimilation of traits" [76–78]. Since the mortality of the animals was low, it can be assumed with a high degree of probability that there were targeted stress-induced epigenetic changes in morphogenesis in representatives of both species, which were accompanied by their transgenerational inheritance [5]. Changes and switches in animal morphogenesis induced by different types of stress and based on the effects of transgenerational epigenetic rearrangements of the genome have been discovered by different authors in different model species [8, 11, 79, 80], i.e., they can actually be a real molecular mechanism of such rapid rearrangements of morphogenesis. The high rate of morphogenetic rearrangements of voles in a vivarium (regardless of their mechanisms and driving factors) indicates a general potentially high phenotypic plasticity [81, 82] of these species, their ability to undergo rapid morphogenetic changes and possible accelerated rearrangements of a microevolutionary nature with a sharp change and/or deterioration in development conditions. Such experiments in controlled and/or uncontrolled conditions can shed light on understanding the nature of rapid morphogenetic rearrangements of different intraspecific forms in a modified environment.

A special place in conducting such conditional natural experiments is also occupied by the analysis of the associated geographic and biotopic variability and the degree of morphogenetic stability of populations when comparing a series of natural samples, taking into account the diversity of local ecological and geographical factors [83], which makes it possible to assess their evolutionary and ecological influence on adaptive changes.

POPULATION-COENOTIC "EXPERIMENTS"

Population-coenotic "experiments" and community monitoring are another direction in the mainstream of experimental approaches in evolutionary ecology. Of particular interest in this regard is the analysis of various forms of conjugate variability in sympatric species not in laboratory conditions (as in the example considered above), but in the natural environment. These may be manifestations of conjugate geographic, chronographic, or biotopic variability in different species of the same community. Parallel analysis of the variability of synchronous samples in sympatric species inhabiting a local biotope corresponds to the above example of parallel study of morphogenetic responses of different forms in the same laboratory conditions. Therefore, the study of syntopic allochronous samples in representatives of sympatric species is a direct analogy of laboratory comparison, which is transferred to natural conditions. The simplest analog of laboratory studies to monitoring observations in natural conditions may be the collection of data on syntopic allochronic samples of sympatric species in the natural environment, which is regularly (annually) carried out in the same season and time period [84]. Therefore, the study of syntopic allochronic samples in representatives of sympatric species is a direct analogy of laboratory comparison, which is transferred to natural conditions, but does not require expenses for the maintenance and breeding of animals or the cultivation of plants.

A good example of conducting a population-cenotic experiment in natural conditions is the assessment of the consequences of creating an "ecological vacuum" through local deratization and subsequent monitoring of the restoration of species components in a local rodent community [85]. In this case, situations that occur during non-selective elimination of animals, such as a flood or fire, were modeled in nature. Based on this material, using geometric morphomerics methods, we analyzed the morphogenetic changes in the shape of the lower jaw in two closely related sympatric species bank vole (*Clethrionomys glareolus*) and northern red-backed vole (*Clethrionomys rutilus*) during the restoration of their syntopic cenopopulations after non-selective elimination. The "ecological vacuum" was created through total deratization in order to reduce the epidemic risk in a hemorrhagic fever outbreak in the southern taiga of Udmurtia in a logging zone [85]. The model simulated the situation arising during the spring non-selective elimination of local rodent coenopopulations and communities and their subsequent restoration. When analyzing the variability of the size and shape of the lower jaw during the restoration of the local rodent population, both similar parallel morphogenetic changes and species-specific ones were revealed. Species differences were found in the change in the intragroup morphological diversity index (*MNND* [86]) of the lower jaw shape in the dominant species, the bank vole and the subdominant species competing for territory, the northern red-backed vole. Different morphogenetic responses of closely related vole species when filling the "ecological vacuum" can be considered as a result of a decrease in the level of competitive relations for the subdominant species and the effect of a compensatory increase in the morphological diversity of

the dominant species under conditions of low density and incompleteness of the community composition, thanks to the "compensation principle" of Yu.I. Chernov [87].

In the opposite situation, sympatric species, the pygmy wood mouse (*Silvaemus uralensis*) and the bank vole (*Clethrionomys glareolus*) belonging to different families, but historically living for a long time in the same territory in the same rodent communities in the Orenburg oblast, showed unidirectional parallel changes in the shape of the lower jaw, which are characteristic of the corresponding phases of population dynamics, but are not associated with interspecific differences [88]. Parallel changes in the shape of the jaw of different species at different population sizes indicated a similar change in the trophic functions of both species in the cenosis at different population phases, i.e., probably a common modification change in morphogenesis for representatives of the local community, which is of a functional-cenotic nature.

Similar studies using geometric morphometrics methods and mandibular morphofunctional indices were conducted on populations of two sympatric species, *Sylvaemus flavicollis* and *S. sylvaemus*, in France [89], which also revealed similar responses of these species to the same conditions. A similar comparison of syntopic populations of sympatric white-footed mice *Peromyscus truei* and *P. californicus* in the mountains of California (United States) revealed differences in the shape of their mandibles and morphofunctional mandibular index, which revealed some divergence in their trophic niches [90]. Similar ecomorphological comparisons of the responses of syntopic sympatric snakes [91] and lizards [92] made it possible to assess the different adaptability of the compared pairs of closely related species to local conditions.

At high numbers, conditions are favorable for most species that form the community (even a change of dominants may be observed); at low numbers, subdominant species on the contrary almost completely disappear, being obviously less adapted to a given environment than dominants. An increase in the relative proportion of dominant species with a decrease in the total number of rodents must be compensated for by a redistribution of their functional cenotic load. Therefore, the rearrangements of the morphogenesis in dominant species can be of a targeted functional-compensatory nature (the possibility of this was previously indicated by Yu.I. Chernov [87]), when they perform additional functions in the community instead of subdominant species. Thus, simple parallel monitoring of sympatric species allows us to evaluate the evolutionary-ecological mechanisms of interspecific interactions and the nature of synecological coevolutionary rearrangements of morphogenesis in the community.

Additional ecological load on the community due to local technogenic pollution of the environment, i.e., a kind of forced natural "experiment," makes it possible to obtain estimates of the stability of the morphogenesis in sympatric dominant and subdominant species in an ecologically altered impact environment. It becomes fundamentally possible to identify the directions and speed of morphogenetic transformations under chronic influence of certain technogenic pollutants, to determine the general and specific morphogenetic responses of the species components of the community.

Let us consider in this regard the results of studies [84] conducted in the zone of the East Ural radioactive trace (EURT) in the Chelyabinsk oblast using the example of allochronous samples from syntopic colonies of the pygmy wood mouse (*Sylvaemus uralensis*) and the northern red-backed vole (*Clethrionomys rutilus*). The methods of geometric morphometrics [93] and the canonical analysis of Procrustes coordinates were used to reveal the conjugacy of the chronographic variability of the lower jaw shape of the vole and mouse in the EURT zone [84]. Interspecific differences were revealed along the first canonical variable, and a significant parallel shift of the centroids of the impact samples and their dispersion ellipsoids relative to the control ones was revealed along the second axis in both sympatric species. Such a parallel shift of the impact samples in both species can be unambiguously interpreted as a manifestation of unidirectional technogenic variability in them. The morphological differences between the samples of the pygmy wood mouse from the impact and control sites were almost twice as great as those in the northern red-backed vole. Consequently, the sensitivity and morphogenetic reactivity of the mouse to the action of the chronic radiation factor turned out to be higher than that of the vole. According to the intragroup morphological diversity (*MNND*) indices, it was established that the control groups of both species had a random distribution of ordinates, while the impact groups of each species had a significant overdispersion of ordinates. Therefore, we can talk about the expansion of the fan of ontogenetic trajectories in the EURT territory and an increase in intragroup morphogenetic diversity in the impact groups of both species. Individuals in the control areas have a normal course of morphogenesis, and the implementation of morphogenetic subprograms in them is random. The results indicated a high coevolutionary potential of the species [57], when a similar morphogenetic response was manifested in syntopic and synchronously obtained samples of sympatric species in a wide range of fluctuating conditions.

Thus, the population-cenotic approach to the study of variability and morphological diversity using geometric morphometrics methods allows us to detect, in natural conditions, manifestations of destabilization of morphogenesis in populations of individual sympatric species that form the core of the community. The analysis shows that in syntopic groups of sympatric species, parallel technogenic variability can

manifest itself at the level of both populations and communities. The results can serve as a basis for organizing and conducting morphogenetic monitoring of natural populations and communities in natural and technogenically altered environmental conditions. They also demonstrate the methodological advantages of the population-cenotic approach we are developing to the study of variability and diversity of species components of communities using geometric morphometrics methods, providing the possibility of their morphogenetic and evolutionary-ecological interpretation [57].

CONCLUSIONS

The Turesson–Schwartz methodological principle allows us to compare the range of implemented modifications in different intraspecific forms and related species, to assess the mutual degree of their evolutionary-ecological divergence, and to come closer to assessing the similarity of their ecological requirements for the environment and ecological niches based on the variability of morphofunctional features. The principle allows us to apply a special aspect of experimental research in the mainstream of evolutionary ecology, assessing the morphogenetic responses of cenopopulations of closely related sympatric species to natural, anthropogenic, or simulated (e.g., trophic, temperature, radiation, etc.) changes in development conditions. The development of experimental research in the mainstream of evolutionary ecology can be presented in three main directions, which include the assessment of the evolutionary divergence of forms during development in similar (controlled) conditions, population-ecological experiments in laboratory and/or natural conditions, as well as population-cenotic "experiments" in evolutionary synecological studies and monitoring of local fragments of communities.

The approaches and results of laboratory as well as natural uncontrolled and partially controlled experiments described above allow us to conclude that the experimental aspect of research in the mainstream of evolutionary ecology can be the applied scientific tool that will allow us to further approach the prediction and quantitative modeling of rapid transformations in populations and communities. Since geometric morphometrics makes it possible not only to separately study the variability of both the size and shape of objects, but also allows for morphogenetic interpretation of the differences revealed, it can be used as the main working tool for assessing the direction and degree of stability of the coenopopulation morphogenesis in sympatric species under different conditions.

The proposed experimental aspect of research in the mainstream of evolutionary ecology based on the Turesson–Schwartz principle can potentially make a significant contribution to solving not only regional but also global synecological problems associated with identifying signs of biotic crisis phenomena that humanity will inevitably have to face in this century.

ETHICS APPROVAL
AND CONSENT TO PARTICIPATE

The review article does not contain studies involving animals in experiments performed by the author, which complies with the decision of the Bioethics Commission of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences (Protocol no. 13 as of November 1, 2022).

CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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