

The Role of Econes as Elementary Population-Coenotic Groups in the Integration of Evolutionary and Ecological Processes

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Abstract—A population-coenotic concept of an econe, an elementary structural-functional group (SFG) in a coenopopulation, is proposed. An econe has binary properties, since in real time it simultaneously manifests itself as part of the coenopopulation and as part of the local community, i.e., acts as an elementary population-coenotic structure, the individuals of which are phenotypically homogeneous and simultaneously perform certain population and coenotic functions. The role of econes in micro-, meso-, and macroevolutionary processes is considered, and based on this the possible evolutionary-ecological integrative mechanisms of rapid micro- and macroevolutionary processes in the Anthropocene are estimated. The new concept of econes allows one to integrate the processes of micro-, meso-, and macroevolution based on the recently revealed mechanisms of transgenerational inheritance of stress-induced epigenetic changes that parameterize certain rearrangements of morphogenesis. Since all processes (micro-, meso- and macroevolution) of changes in econes in coenopopulations occur in real time, but with varying degrees of efficiency, it is theoretically possible to approach the prediction of the onset of regional biocoenotic crises by comparing the morphogenetic reactions of econes of sympatric species of communities to favorable and unfavorable development conditions, caused by a combination of climatogenic, anthropogenic, and biotic factors.

Keywords: econe, coenopopulation, taxocene, epigenetics, morphogenesis, microevolution, macroevolution

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INTRODUCTION

Evolutionary ecology originated in the middle of the last century [1–4], but evolutionary aspects of ecology proper began to attract the attention of researchers more and more only in recent decades [5–9]. This is mainly due to the fact that numerous examples of rapid microevolutionary changes were found at historically characteristic times [10–12] a significant part of which is due to the action of climatogenic [13] and anthropogenic [14] factors. Interest in rapid microevolutionary changes has intensified after the discovery in recent decades of the phenomenon of epigenetic inheritance, i.e., transgenerational inheritance of stress-induced changes in epigenetic DNA profiles that affect rearrangements of morphogenesis [12, 15, 16]. This led to the formation of the concept of extended evolutionary synthesis (EES) [17–19], based on a special understanding of the role of epigenetic inheritance in rapid microevolutionary processes [20–22].

The terms microevolution and macroevolution are associated with the names A.N. Severtsov [23], Yu.A. Filipchenko [24, 25], and N.V. Timofeev-Ressovskii [26, 27], and the problem of the relationship between micro- and macroevolutionary processes, despite the almost century-old existence of this concept, is still

the subject of constant discussions and is still far from being solved [7, 28–30]. Many evolutionists traditionally attribute the processes of microevolution exclusively to intraspecific changes (mainly genetic) at the level of populations and larger intraspecific groups [3, 4, 22, 23, 27, 31, 32]. It is generally accepted that macroevolutionary processes have a long duration and are associated with the evolution of supraspecific taxa [4, 33–39]. Many authors [40–44] believe that macroevolution cannot be reduced to a simple prolongation of the microevolution process and its mechanisms and must have its own laws and manifestations. The opposite view is also known, when it is argued that the mechanisms of micro- and macroevolution are largely the same, differing only in the length of time [4]. It should be noted that E. Abouheif [45] considered it necessary to single out an intermediate level, the mesoevolutionary process (mesoevolution), i.e., parallel evolutionary changes in closely related species. The term mesoevolution was previously proposed by other authors [31, 46, 47], but Abouheif understands it to be a special situation associated with developmental, genetic, and epigenetic mechanisms that allow species close in origin to change in a similar way, i.e., in parallel, using the same developmental mechanisms and the same genes with the main effect in response to

the action of certain environmental changes [45]. I believe that the understanding of the relationship between micro- and macroevolution as evolutionary-ecological processes is largely determined by the identification of integration interactions between the population and coenotic levels of organization of biosystems [9, 48, 49].

The term coenopopulation was originally used in botanical practice [50–52], denoting a coenotic fragment of a population of a particular species, which is part of a local biocenosis. We proposed to use the term coenopopulation for relatively sedentary and sedentary animal species, for example, some species of insects, rodents, and insectivorous mammals [53, 54]. Individuals that make up coenopopulations differ in age, sex, belonging to seasonal generations, metamorphosis phases, functional morphs, and other structural and functional groups (SFGs). Based on this alone, it seems that the coenopopulation cannot be the smallest elementary group at the junction of population and coenotic processes in biocenoses. Within coenopopulations, elementary SFGs are: universal groups of homogeneous individuals, simultaneously (in parallel) performing certain population and coenotic functions. There is a need for a terminological designation of such structures. The role of such an elementary SFG, which simultaneously performs intrapopulation and coenotic functions, is quite suitable for econe.

The concept of econe was proposed by G. Heatwole [55], but was initially interpreted very broadly, from intrapopulation groups to closely related species. This term, apparently due to its broad interpretation, led to discrepancies and was not accepted by contemporaries. However, in the 21st century econe, with its author being mentioned, was again included in scientific use by P.V. Ozerskii [56, 57], and later I.A. Vislobokova [58].

Objective—To consider conceptually the role of econes in micro-, meso- and macroevolutionary processes and, on this basis, to evaluate the possible evolutionary-ecological integrative mechanisms of rapid micro- and macroevolutionary processes in the light of regional biocenotic crises predicted in the Anthropocene [14, 59, 60], [41, 61–64].

THE ECONE AS A STRUCTURAL FUNCTIONAL GROUP (SFG) OF COENOPOPULATIONS

The concept of econe was used by P.V. Ozerskii in the niche concept, citing the definition of the term given by G. Heatwole [55] for characterization of the “species or any component of a species (such as a life cycle stage, age class, morph, or sex), whose members share the same resource use patterns and the same niche characteristics, while differing from other such components or species” [55, p. 18; cited according to

[65], p. 5]. According to Ozerskii [56, 66], the econe is an elementary population structure, a part of individuals in a population that have a specific phenotype and niche. We must agree with Ozerskii that the term econe can be used not so much for species, but mainly to characterize the structuredness and diversity of a particular population. As a matter of fact, the econe as part of a coenopopulation corresponds to one or another SFG (see above).

Recently Vislobokova [58], mentioning the work of Heatwole [55], proposed a different concept of the econe, considering it as an elementary fundamental unit of evolving paleobiospheric space-time, i.e., understanding the econe as the evolutionary unity of a species and its ecological niche. The author of this concept rightly believes that “species do not invade ecological niches and do not move to other niches (as is sometimes assumed), but change along with the niche” [58, p. 8]. This understanding of the species and its ecological niche was previously expressed by other authors.

We emphasize, however, that according to Vislobokova, the term species niche as a whole corresponds to the concept of a fundamental niche (FN), and the author simplifies the phenomenon of a realized niche (RN), stating that “In nature, a realized niche corresponds to a fundamental niche” [58, p. 8]. In our understanding, the RN of a species does not fully correspond to the FN, it is extremely dynamic, changeable, can differ significantly in characteristics even in neighboring adjacent localities, and even more so in different parts of the species range, and depends on local factors of the biotic environmental, anthropogenic, and climatogenic influence. Changes and modification fluctuations in the adaptive parameters of a RN do not always lead to evolutionary rearrangements, but sometimes, under long-term climatic and landscape trends, they can provide an accumulated orthogenetic effect of evolution (then the species will actually change along with the niche).

In this review, we will not consider the history of ideas about the ecological niche (EN), which wander from one report to another, as well as past and current theories of EN, since these aspects are well represented in publications. Recently, we also considered them in a special review [67]. Let me just remind you that J. Grinnell [68], as early as the beginning of the 20th century, who proposed the concept of EN as a specific habitat, introduced this term “to designate the basic unit of distribution within which a given species is kept by its structural and instinctive restrictions ...; in the same territory there cannot be two species that would occupy a completely identical ecological niche for a long time” [68, cited according to [69], p.120]. The spatial interpretation of EN according to Grinnell gave rise to a persistent idea of an unoccupied or “free niche” [70, 71]. At the same time, it is often mistakenly believed that another species can occupy a free

niche. Until now, there are disputes about whether EN is a property of a species or a cenosis, since niches are not relevant outside the population and community [see. 72].

Traditionally, an EN reflects the properties, capabilities, requirements, and responses of a species, being a category determined by the species itself, and not by a characteristic of the habitat [58, 65, 67, 73–75]. Free niches do not exist, but there are conditions and free resources that species can master when they form the necessary adaptations, i.e., RNs. The disappearance or extinction of a species inevitably leads to the disappearance of its attribute, the niche, in the community. The cenosis “grants” to the coenopopulations of syntopic species “ecological licenses” (ELs), potentially accessible habitats, including the necessary conditions and resources that can really be free or partially used by other species. Initially, the term EL was proposed by K. Günter [76], but a more meaningful interpretation was later given by V.F. Levchenko and Ya.I. Starobogatov [73, 77]: EL successfully solves the collision of a potentially “free niche,” replacing it with a “free license,” serves as a potentially accessible or “free” part of the habitat that an already existing or emerging ecological niche of a species can master (occupy). In the evolutionary-ecological sense, speciation as the initial elementary act of macroevolution is associated with the transformation of the entire ecosystem, i.e., the new species must either physically displace the competitor species or form a new modified niche [77]. Therefore, the role of the community in speciation is very important [41].

The econe concept by Vislobokova [58] differs significantly from the primary interpretation of the term by its creator Heatwole and other authors. The econe described in the article is an attempt to introduce into paleobiology and neontology a special additional interpretation of the EN of species as elementary paleobiological and paleogeographic evolving units, simultaneously experiencing both the pressure of the surrounding abiotic and biotic environment and exerting an active influence on it. We believe that the use of the term econe is permissible, but, in our opinion, it is not rational, since the concepts of “phyla” and “phratry” already imply the performance of the same functions of elementary paleobiological units of the evolutionary process. Given the correct position of Vislobokova about the inseparable unity of the species and its ecological niche, which is similar with the opinion of a number of other authors [67, 73, 77], then the use of econe here is probably a redundant term.

I believe that the term “species” in this understanding of a single whole with its ecological niche and range remains a traditional and quite operational concept for ecology, paleoecology, and paleogeography and does not require replacement by “econe.” At the same time, of course, the structure of econes is specific for each species. In all coenopopulations of the

species, the diversity of SFGs (econes) is usually represented by a similar set. Each econe is specialized, i.e., performs certain functions both within the population and in the group of coenopopulations of sympatric species of the community. In this sense, each econe at the species level, as an SFG common to it, is in a certain sense universal. However, in different localities (biotopes) inhabited by a species, a particular econe will show some features (intraspecific variability) since there are no two absolutely identical ecological parts of the globe, so the requirements for EN in each locality will inevitably be different. It is only theoretically possible to expand the concept of econes to the level of a species, but at the same time it will immediately cease to be an econe but will become a former econe, which received an EL, became an ecomorph/biomorph, and then a species, extending its new “species” features to individuals of all conspecific populations. At the same time, a different population-coenotic structure of econes for a new species and community will be formed at the same time.

In line with evolutionary macroecological ideas, the interpretation of the species-econe proposed by Vislobokova [58], is extremely interesting, but is admissible only at a level close to a genus or tribe within the framework of the macrotaxon and its evolution. The latter requires the creation of special terminology for these phyletic levels, which are higher than the intraspecific one. As such concepts, I propose to introduce eidoecone at the level of the species, which corresponds to that described by Vislobokova, and a macroecone can be considered at the macrotaxon level. I believe, however, that the original concept of an econe by Heatwole [55] basically corresponds to the hierarchical level below the species. At the same time, indeed, it is of key importance for understanding the mechanisms of both micro-, and meso- and macroevolutionary processes. Actually, this is what we will try to substantiate further.

The econe in the composition of the population is close to the concept of “biotype” by W. Johannsen [78, 79], i.e., an intraspecific (intrapopulation) group of hereditarily close individuals with a similar physiological and/or morphofunctional response to the same environmental factors. The biotype was initially not associated with the similarity of the niches of the individuals representing it, but this content indirectly follows from the definition of the term. Therefore, Heatwole’s econe is morphophysiologicaly synonymous with Johannsen’s biotype and is also suitable for the analysis of intrapopulation morphofunctional diversity. At the same time, the use of the term econe for a group of species with a similar ecological function, as suggested by Heatwole does not seem to be promising, since the term taxocene [7, 80, 81] better reflects the essence of the phenomenon.

A complex of taxonomically related species with similar ecological functions in a community is pro-

posed to be considered as a special type of guild, a taxocene [7, 80, 82, 83]. The term taxocene was used by A. Chodorowski [82], and then picked up by G. Hutchinson [83], who provided the following definition of a taxocene: "These are all groups of species and representatives of supraspecific taxa found in this association" [83, p. 231]. Such a definition was not strict, so the term was sometimes interpreted only as a list of species in a given area. However, in this case, we are absolutely not talking about a comparison of taxonomic lists of species, which was previously justly criticized [41, 84], but about a similar ecological role of their coenopopulations in the community [7, 53, 80]. According to my ideas, a local taxocene is a group of taxonomically close sympatric species of an ecological guild inhabiting a local biocenosis, and not all members of the community. Local taxocenes are represented by syntopic coenopopulations of related sympatric species (belonging to the same genus or, in extreme cases, close families) with similar coenotic functions (coenotic specialization) and relatively close ENs. We emphasize that the similarity of niches in this case cannot be significant, since, by definition, any species cannot have identical ENs, and closely related species, on the contrary, often have different niches in order to avoid competition. Since the local taxocene manifests itself not only as a fragment of the community, but also acts as its functional unit [69], it can serve as a somewhat simplified model of the local community [7, 53]. As an example of a taxocene, one can consider the syntopic population of taxonomically related species of shrews of the genus *Sorex* [53, 85, 86].

Thus, for characterization at the intrapopulation level of the SFG of individuals of a species with similar morphofunctional response and ecological niche, the terms ecene and biotype are potentially acceptable, and at the coenotic level, ecene and taxocene are used, i.e., the concept of the ecene characterizes two aspects at once. In our understanding, representatives of the ecene perform a binary function: on the one hand, they are a certain SFG in the composition of the coenopopulation, and on the other hand, they perform a certain coenotic function of this species, entering as its structural and functional element into the local multispecies community. In other words, the ecene at the same time, and in real time, functions both as part of the coenopopulation and as part of the local community, i.e., acts as an elementary population-coenotic structure.

PHENOME, PHENOTYPE, AND ECENE

The term phenome was originally used by B. Davis [87] as early as the middle of the 20th century and was considered as the sum of the total extragenetic and nonreproductive parts of the cell. In his interpretation, the phenome is the material basis of the phenotype. Phenomics today is a special branch of molecular

genetics at the junction with developmental biology, aimed at the systematic study of phenotype variability on a genome-wide scale [88]. It can be assumed that in the future phenomics will be directed to the analysis of the genetic and epigenetic nature of morphogenetic variability and the actual formation of a phenome attributable to a particular phenotype.

The vague initial interpretation of the phenomenon allows us to try to provide a new definition. A phenome is a set of all properties of an individual that are transformed in ontogeny from a zygote to a senile state, including subcellular, cellular, tissue, organ, morphophysiological, and ethological features that serve as the necessary bioresources to maintain its life and participate in reproduction [67]. On the one hand, a phenome is a probabilistic copy of a unified epigenetic polyvariant development model for a population [89], and on the other hand, it is a historically emerging multifunctional "biotool" that performs the necessary ecological functions in a population and community, mainly trophic, reproductive, and environment-forming.

In the light of epigenetic concepts that suggest a systemic integral formation of a phenome, the phenotype is the result of the manifestation of one of the alternative developmental paths leading to the formation of a class of similar phenomena defined in a morphofunctional sense in a population. The phenotype according to W. Johannsen [90, 91] is rather a group characteristic than an individual characteristic. Therefore, in relation to a specific individual (phenome), the phenotype should be considered as a multidimensional criterion for its classification: assignment of the phenome of a given individual to one or another class of similar phenomes. Such a class of structurally and functionally similar phenomes is the phenotype realized in the process of development. Within phenotypic classes, the phenomes of individuals are largely similar, but morpho-functionally differ from individuals of other similar classes. Each phenotype as a class of structurally and functionally similar phenomes can be considered as a characteristic of a natural SFG within a coenopopulation or population. Each such group, or SFG, performs certain functions to maintain the integrity and stability of the population. Earlier G.V. Olenov [92] proposed alternative types of ontogenies in rodent populations, associated with the acceleration and deceleration of the development and maturation of animals, to refer to different physiological and functional groups (PFGs). In fact, a PFG is an example of an SFG in the form of ecomorphs, subdivided according to the rate and duration of their ontogeny. Representatives of each SFG population will, due to the similarity of phenomes, also have similar ecological niches. Accordingly, each SFG, along with a certain variability of phenomes, will also manifest the specific properties of their ecological niches, as well as the population and coenotic functions they perform. Therefore, the phenotype as a class of similar phe-

nomes at the corresponding stage of ontogenesis characterizes the individuals that make up a certain econe.

POPULATION-CENOTIC NATURE OF ECONES

Systemic coenotic relations provide the most complex hierarchically multi-tiered and multi-species balance between the requirements for the sustainable conservation and reproduction of biological communities, on the one hand, and the structure and function of the phenomes of their species representatives, on the other. This is a historically long iterative process of mutual adjustment (coevolution), which is controlled primarily by coenotic relations and depends on climatic fluctuations and anthropogenic factors. Each species “strives” to extract resources more efficiently, which is expressed in a change in its structure and functioning and vectorizes further directions of historical changes in its phenome. In other words, the species “strives” by changing its primary ecological niche [67], by means of a phenome, to get out of the strict coenotic control. If a species “succeeds” in such a way, then it can change very quickly, and in other cases even become a species with a high macroevolutionary (arogenetic) potential [49, 95, 96]. A high rate of change in the phenome is potentially probable if the leveling coenotic pressure is weakened.

The term econe is not tied to the hierarchy of superorganismal systems and in this universal sense can also be extremely useful. It can simultaneously be considered as an elementary group niche (subniche), which has a certain ecomorphological manifestation for individuals of a given intraspecific (intrapopulation) group [56, 66], and as a structural and functional element of the organization of the cenosis (taxocene). Ozerskii [75] also proposed the term coenoecone: “coenoecones are subdivisions of coenopopulations composed of individuals ecologically similar to each other” [p. 20]. The author of the term intended its use primarily for building consortive relationships at the population level. In our understanding, the coenoecone seems to be a redundant concept and clarification, since the econe itself is already at the same time a coenoecone, performing not only a population, but also a coenotic function. Therefore, the econe is interesting since it is a border elementary SFG that exists in real time and space between two levels of organization of biosystems, population and coenotic.

According to my ideas, the econe (SFG) is an element of population-coenotic interactions and acts as an elementary unit of the coenopopulation and community rolled into one. In the structure of the population and community (taxocene), the econe occupies a certain place, performs a fixed set of functions, and is represented by individuals with similar phenomes corresponding to a given population-coenotic fragment. In this sense, the econe is a link (bridge) between the coenopopulation and the community. In such a binary

interpretation, we seek to expand the concept of econe into two levels of the biological hierarchy, population and coenotic: within the coenopopulation, econe is actually represented as a SFG (biotype), and at the coenotic level, it is part of the species component of the taxocene (“coenoecone” according to Ozerskii).

An econe reflects the structural and functional similarity of a given group of individuals in a population (coenopopulation), but the same individuals at different stages of ontogenesis and, accordingly, morphogenesis can belong to different econes and perform different functions in the community. For example, tadpoles and frogs that emerged after metamorphosis belong to different econes, performing different synecological functions and having significant differences in ecological niches. The same can be said about insect larvae and adults [56]. In this case, the original econe temporarily disappears, and on the basis of the same lasting phenomes (individuals), a new econe with certain properties is formed [56].

In the coenopopulation of shrews of the genus *Sorex*, examples of representatives of different econes are young (of the year) males and females, as well as overwintered (adult) males and females (see Fig. 1). Each of these four econes performs its functions in the coenopopulation and community. Obviously, that econes, for example, econes of young males and females, after wintering, are transformed into econes of adult males and females, but in the spring–summer period, econes of young males and females of the current year of birth coexist for a long time with the econes of adult (wintered) males and females of the last year of birth from generations of parents. We consider males and females of the same age cohort as different econes, but they represent a functional unity relative to other age groups of the coenopopulation, i.e., can be formally assigned to one common econe as part of it, a sub-econe. In the phase of reproduction, sex differences increase and can enhance the functional differences due to the characteristics of the EN of males and females. However, during evolutionary transformations, both sexes, as a rule, show combined general tendencies, allowing them to be considered as changes in one common econe.

Accordingly, one of the alternative paths of development, which led to the formation of the original econe and then to the emergence of a new one, is realized at the next stage of ontogeny as a group of similar phenomes that have a common phenotype. During reproduction, due to the phenomenon of epigenetic transgenerational inheritance [15, 22, 97, 98], this developmental path leading to a given phenotype will be preserved to one degree or another in the epigenetic system of the population and can be realized again under situational repetition of conditions. The individuals that form the corresponding econe have a similar synecological subniche [56], but in terms of development they belong to the epigenetic subcreod [89],

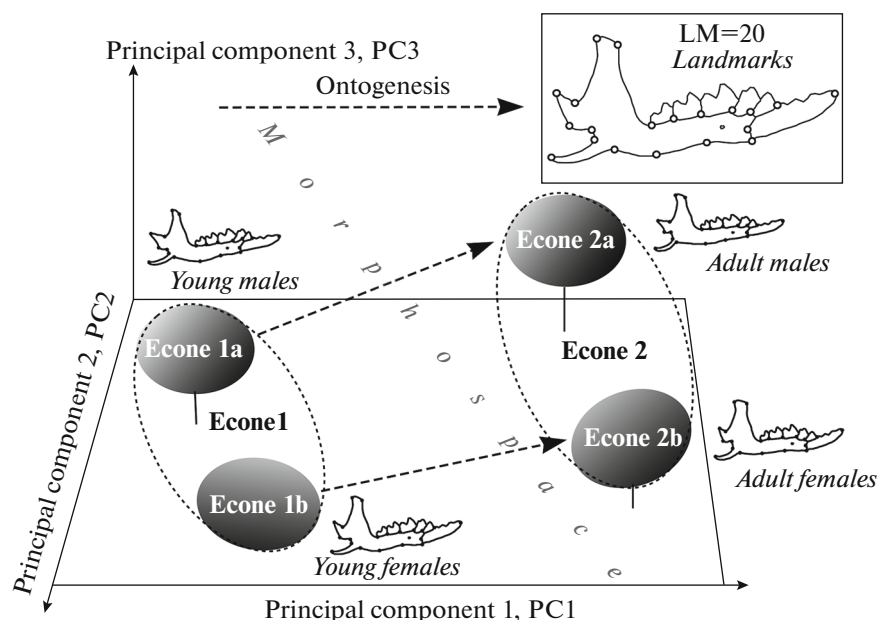


Fig. 1. Hypothetical placement of ellipsoids of dispersion of ordinates of four ecores – structural and functional groups (taking into account their ontogenetic changes) for a coenopopulation of one of the species of shrews of the genus *Sorex* in the general morphospace of the first three principal components PC1–PC3: (1) ecore of young individuals, (2) ecore of adults; (a) male subecore, (b) female subecore.

by which we mean one of the possible alternative options for the main developmental path of an individual (species) – creod (according to C. Waddington [99, 100]).

Creod and subcreods are regulated by an epigenetic system of threshold restrictions, which recursively defines the entire range of permissible development programs and subprograms [89, 101]. A separate subcreod leads to the formation of similar individual phenomes and is one of the possible ways for the probabilistic implementation of a single polyvariant program for the development of individuals in a population, “population ontogenesis” [89]. If we consider the ecore as an SFG (or biotype), then all individuals of this group, i.e., genetically close and exhibiting similar or identical physiological and morphogenetic responses to certain environmental conditions, have not only similar properties of the genome and epigenome, but also a certain phenotype, a similar phenotypic response (life trajectory of development).

In this regard, of particular interest is the evolutionary-ecological problem that has been intensively developing in the last decade, based on the concept of intrapopulation variability of life cycles (life-history variability) and pace-of-life syndrome (POLS) [93, 94]. It is assumed that within a population there is a certain potential range of life cycles, life trajectories, which may differ in the time of onset of ontogenetic stages and the manifestation of ecological and functional features that allow individuals of this population to quickly adapt to changing environmental condi-

tions. Previously, we have already given [92] an example of “ontogenetic morphs” of rodents with different speeds and life spans, PFG. Certain life trajectories [93, 94], which at different stages of ontogeny lead to the formation of phenotypically defined ecores within a coenopopulation, ensure not only its stability, but also, due to diffuse coevolution, when interacting with coenopopulations of other species, the community iteratively polishes and enhances the stability of its functioning in general.

In the light of recent discoveries in epigenetics [22, 97], it should be expected that, along with the molecular genetic variability of individuals included in the ecore, they have the ability of mobile transformation and transgenerational inheritance of altered epigenetic profiles (DNA methylation, rearrangement of mobile genome elements, etc.), which determine the implementation of certain life trajectories historically accumulated by the population as potential adaptive modifications. What has been said above about the nature of the ecore is in good agreement with ideas about the variation in the life cycles of individuals and contributes to their further theoretical development.

ECONE AND MICROEVOLUTION

If we consider the role of ecores in microevolutionary rearrangements of populations and coenopopulations, then it will mainly be reduced to a change in the performance of the structural and functional role of a given group of individuals in maintaining the stability of their population grouping under changing

conditions. Each econe performs a certain role in the coenopopulation to ensure its functioning. Changes that occur in econes during microevolutionary rearrangements in a coenopopulation and/or population may primarily affect the course of their morphogenesis, including changes in the size, shape, and design of individual morphostructures – merones (according to S.V. Meyen). Changes in morphogenesis are mainly due to changes in “normal” habitat conditions, including changes in climatogenic, trophic, and topical factors (resources). In the latter case, the topical factors should include the properties and sizes of habitats (biotopes) traditionally suitable for the species, as well as the diversity of microbiotopes (microenvironments) – microhabitats [102].

After catastrophic natural impacts (drought, flood, fire, hurricane, windfall, volcanic processes, etc.), a significant part of habitable biotopes may disappear, and in their place will appear unsuitable or even mostly unsuitable for life habitats. In such cases, five main response scenarios are possible for the species: (1) do not change anything, continue to live for some time in a changed unfavorable environment, experiencing severe stress, and gradually die out; (2) go in search of new suitable territories; (3) having reduced the abundance, occupy and use the remaining suitable sites (microrefugia), waiting for their restoration; (4) master new previously inaccessible resources by changing behavior, but exist in adverse conditions; and (5) rebuild morphogenesis in a direction that allows the formation of morphostructures that make it possible to use other natural resources (lengthen the beak, increase size, change body proportions, etc.), which will reduce stress and adapt to a new environment.

During the first stage at a chronic climatogenic process, for example, a general warming of the climate, the econe of a particular species can change morphogenesis due to the historically established pool of modifications (“extract” the developmental modification option that most individuals have, which is necessary under given conditions). With further climate change, on the basis of this modification, with the creative support of selection, a series of intermediate variants of morphogenesis modifications induced by stress-induced epigenetic rearrangements will gradually form. At a certain moment, with a directed change in the environment, the normal regulation of development can be disrupted (all the main subcreodes will be exhausted), and in response to this, a chaotic search by organisms for a suitable path of development will increase, which will lead to multiple aberrations, morphoses, and deformities (according to I.I. Schmalhausen). It is likely that certain aberrant paths of development will turn out to be adequate to the new environment and, with the assistance of selection, there will be a process of changing the previous norm of development and synthesizing (“planishing”) a new norm according to the key model of

M.A. Shishkin [103] within the framework of his epigenetic theory of evolution (ETE).

In accordance with ETE, the irreversibility of epigenetic changes should be due to the fact that the transformation of a specific path, the trajectory of development (in our understanding, subcreode), will inevitably affect other paths (deform them to one degree or another), which will not allow returning to the original state of the epigenetic system in the future. Therefore, epigenetic rearrangements will not be able to become reversible in the future due to the multiplicity of changes that have occurred in the system. Potentially available modifications, i.e., already present in the pool that has historically developed in a population/species, upon the onset of environmental conditions provoking them, will not be able to reproduce exactly in the phenomes, as it was during their formation. In this sense, the modification response may be approximate, but it will be able to manifest itself not singly, but massively in many representatives of a given population/species, which will ensure its rapid selective “finishing” to the required state if the change is beneficial to the population and enhanced by selection.

Such a model is in many ways reminiscent of the hypothetical mechanism of the principle of “organic or coincident selection” by D.M. Baldwin, K.L. Morgan, and G.F. Osborn, independently formulated by three authors in 1896. According to this principle, modifications (Baldwin [104] called them accommodations) are the basis for the formation of new evolutionary changes. The mechanism of organic or coincident selection, later called the “Baldwin effect” consists of the replacement of modifications with hereditary changes similar in phenotypic expression. Brian Hall [105], one of the founders of evolutionary developmental biology “Evo-Devo,” devoted a review article to the Baldwin effect, in which he emphasized the seriousness of the arguments in its favor in the light of modern ideas about the nature of phenotypic plasticity.

Each developmental trajectory leads to a specific phenotypic state, a series of phenomena similar in size, shape, structure, and function. Each individual can implement almost any developmental trajectory, but with a certain probability specified by the epigenetic landscape of the population [89, 101]. Subcreodes are usually realized in the phenomenon with a lower probability than the main creode [89]. The epigenetic landscape of a population [101] determines for each individual the main set of invariant developmental trajectories. At the same time, innovations and differences between phenomes can occur within the same phenotype due to somatic effects and stress-induced changes in the epigenome.

Microevolutionary restructuring at the level of the econe should affect not only the econe itself and the coenopopulation in which it is realized, but also the

entire population (usually a series of coenopopulations of the same species). As a result of the microevolutionary restructuring of morphogenesis, the population development system will acquire a potential possibility under the conditions of a certain biocenosis, i.e., in a coenopopulation inhabiting a particular biotope, to be realized in the form of a certain variability (in the understanding of Darwin) a new modification as a phenotype or a set of closely related phenotypes corresponding to an econe. Acquired phenotypic traits will only become a microevolutionary event when they can potentially be reproduced in the phenome under certain conditions by all individuals of a particular econe in a given population. In other words, until the population's epigenetic system integrates a new developmental modification into the general pool of potential modifications, the microevolutionary process is not yet complete.

The econe, being at the same time a coenotic structural and functional unit, the coenoecone [75], of a specific local community occupying a certain biotope (facies), directly or indirectly receives a regulatory signal from the community about the need to switch to the use of one or another resource that is excessive for it. After successful rearrangements of morphogenesis and behavior, which make it possible to partially use a resource new to the coenopopulation, the econe will thereby "send" the community a request for an ecological license [77], a potential "right" to further perform a new function in the cenosis, expanding its EN. A new modification of the phenomenon acquired in this way will gradually accumulate in the coenopopulations of a given biotope, spreading in the population as an invariant of the ability to switch the development of any of its individuals whose ontogeny proceeds in a particular type of biocenosis. After incorporating this morphogenetic trajectory into the system of "population ontogeny" [89, 101], with the creative support of selection, it is fixed in the modification pool of the population, which acts as a "mobilization reserve" of variability.

Such morphogenetic changes can occur relatively quickly during epigenetic rearrangement and their further transgenerational inheritance [15, 97]. In this way (so far hypothetical), new morphogenetic features of the population can be formed on the basis of the econe in response to initial abiotic or coenotic signals. The fixation of changes stimulated by the abiotic environment and cenosis in the developmental system of individuals of the entire population will mean the implementation of microevolutionary changes, a change in the attitude of the population to a new set of environmental resources and conditions (see S.S. Shvarts [4]). It is obvious that this restructuring of the "morphoniche" [67] will inevitably change in a certain way the fundamental and realized ecological niches of individuals in the population. In turn, this can provide an increase in the size of the transformed population and strengthen the role of the species in the community.

The latter can potentially lead to esogenetic (in the understanding of V.V. Zherikhin [41]) phylocoenogenetic changes. The rearrangement of the morphogenesis of the coenopopulation of one species can then stimulate response changes in another (or others), i.e., lead to their mutual microevolutionary and at the same time diffuse coevolutionary changes [10] of a macroevolutionary nature.

The above-described hypothetical case of an adaptive change in morphogenesis and/or behavior, which, as a modification, gives an advantage to individuals of a particular biocenosis compared to individuals that developed in another type of biocenosis, may turn out to be preadaptive when the population masters other living conditions in time and/or space. In the future, under new similar conditions, this modification can become the basis for further adaptive morphogenetic transformations in a certain direction, simultaneously channeling both the microevolutionary process and the initial stages of phylocoenogenesis (as special genesis according to Zherikhin [41]).

Rapid microevolutionary events can take place over several decades [10, 106] and occur during the initial assimilation of new conditions by a species, when the target community into which its outpost population has penetrated has not yet had time to regulate the population dynamics of the species and its coenotic role. Under conditions of strict coenotic regulation, rapid changes are likely to be difficult or impossible. In the absence of strict regulation by the biotic community, domesticated species under artificial selection are able to very quickly change their specific morphophysiological characteristics and form many breeds, the range of diversity of which significantly exceeds the range of interspecific differences [107].

Similar rapid microevolutionary changes occurred with the outpost populations of the muskrat when it was introduced into the territory of the former Soviet Union in the 1930s–1960s [106]. We found that significant morphological differences between the northern and southern populations of muskrats in Western Siberia arose one to two decades after introduction (from the same population), and over a half-century period, parallel unidirectional morphofunctional changes occurred in both southern and northern muskrats [106]. The first (population) changes were associated, most likely, with modification rearrangements of morphogenesis in the conditions of the southern and northern regions of Western Siberia, their further adjustment to local conditions, and fixation of the result achieved through selection. The latter point to the gradual incorporation of the species into a new coenotic environment and are accompanied by directed parallel changes in morphogenesis. An analysis of the intergroup variability in the shape of the foraging structure, the muskrat mandible, which reflects the population micro- and coenotic macroevolution-

ary aspects of changes in morphogenesis, revealed their different directions in the general morphospace [106]. Therefore, it can be assumed that first there were population transformations (of a microevolutionary nature), and then (almost simultaneously) and coenotically determined parallel changes in morphogenesis (of a macroevolutionary nature) for northern and southern muskrats.

Consequently, the ecores of the same name in the muskrat coenopopulations in the north and south, during the first stage of introduction, under weak control from local communities, almost simultaneously acquired different morphogenetic features that changed the functional trophic capabilities of animals. In fact, there was a rapid multidirectional change in morphogenesis in the southern and northern populations on the basis of the type of pool (spectrum) of potential modifications available in the "historical memory." The fixation of these modifications reflects the population aspect of changes in ecores in their floodplain intrazonal groups, and the further long-term process of parallel morphogenetic changes in the north and south reflects the coenotic aspect of directed morphofunctional transformation of ecores.

ECONES AND MACROEVOLUTION

S.S. Shvarts was convinced that macroevolution, like microevolution, is determined and regulated by ecological causes. He also believed that there were no grounds for opposing micro- and macroevolution, since "... Evolution is a single process of progressive assimilation of the arena of life by organisms" [3, p. 168]. Further, he clarified that "evolution is a single process of progressive adaptation of organisms to the environment, which consists of improving the use of vital resources with the lowest energy costs and in the progressive expansion of life over the land and water areas of the Earth" [3, p. 169]. Thus, it was about the evolutionary restructuring of ENs, which are attributes of individuals, populations and species, and therefore, are transformed both during the microevolutionary process and during meso- and macroevolutionary changes. These circumstances do not exclude different time scales and special ecological laws in the implementation of two evolutionary processes, micro- and macroevolution, which are largely dictated by communities during the formation of species and taxocenes. Similar conclusions, although based on slightly different initial ideas, were previously made by D. Erwin [42]. The complexity of the problem, in addition to the above, also lies in the fact that the processes of microevolution primarily affect rapid population changes in the morphogenesis of specific species, while meso- and macroevolutionary transformations are probably carried out in the process of longer co-evolutionary interactions between species components of cenoses.

Can the ecore become the basis for the formation of a new species? In my opinion, there is a positive answer to this question, as evidenced by the results of studying the rapid sympatric formation of flocks of cyprinids and cichlids in African lakes [108–110]. It is sufficient to emphasize that individual forms, for example, representatives of the *Labeobarbus* of Tana Lake, in their origin, are ecores: first ecomorphs, and then ecospecies within one species, *Labeobarbus intermedius*. Recall that a "flock," or, as it is also called, a bunch of species, is a kind of community of morphologically different and ecologically specialized sympatric ecospecies (the term "ecospecies" belongs to G. Turesson [111]), which are genetically almost homogeneous, i.e., in the traditional sense of genetics, they probably cannot yet be considered species. However, for one reason or another, they do not interbreed and steadily retain the features of morphogenesis and ecological specialization in a series of generations even when they are jointly grown in the same aquariums in the laboratory, i.e., look like "good" species from the point of view of zoologists and ecologists [110].

In this case, from different ecores of *Labeobarbus* of the Nile, a similarity of a community was sympatrically formed, uniting two conditional taxocenes, non-fish-eating and predatory fish-eating ecospecies. The processes of sympatric microevolution, then coevolution, and simultaneously macroevolution occurred almost in parallel, and their total duration was only 15,000–17,000 years [109]. As a result, 15 specialized ecospecies (ecomorphs) of *Labeobarbus* emerged. During this time, small errors and changes in DNA nucleotide sequences, which are usually used to estimate molecular distances between species, have not yet accumulated, and formally all flock ecospecies belong to the same ancestral species [109], which are currently alive today. Therefore, ecores can also become the basis for the implementation of macroevolutionary events based on microevolutionary mechanisms within a population of a genetically single species.

With the natural process of diversification of *Labeobarbus* in Tana Lake, perhaps over the next 300 000–500 000 years, similarities of two *Labeobarbus* genera could form, the taxonomic level of which could be confirmed by molecular genetic methods. Accordingly, in Tana Lake, after the specified period of time, two full taxocenes of non-fish-eating and predatory *Labeobarbus* species, which acquired the properties of biological (reproductive) isolation, could be found.

Based on the foregoing, it can be assumed that the ecore, being an elementary population-coenotic SFG in the outpost coenopopulation, is the main driver of rapid microevolutionary changes. At the same time, even in the absence of effective spatial isolation, it is then quite capable of becoming the basis for the formation of ecomorphs and, in the future, ecospecies

(biomorph), since it simultaneously performs coenotic functions (it is a coenoecone according to Ozerskii) and is regulated by the existing and emerging community. Therefore, simultaneously with microevolutionary changes at the population level, an econe, which has become an ecomorph (or a potential biomorph, a life form), can later become an element of the mesoevolutionary process, i.e., the parallel formation of species components not only of a supraspecific macrotaxon, but also of macroevolutionary restructuring of taxocenes.

Another example of the formation of biomorphs in a relatively short time is a complex of closely related species and forms of Darwin's finches [112, 113], originating from a common ancestor, a small group of founders, accidentally introduced from the nearest mainland by a storm wind. A sharp change in habitat conditions caused a stress-induced burst of epigenetic and morphogenetic variability, and weak regulation and control by the community allowed selection to creatively quickly "synthesize" new ecomorphs, eco-species, and then species of finches with different capabilities based on increased biotopic and chronographic variability. when extracting resources [112].

We have repeatedly noted situations of compensatory changes in morphogenesis, which provide the entire coenopopulation or its individual morphs (econes) with the formation of altered morphostructures, which make it possible to compensate for the temporary absence of closely related species in the community, performing certain functions for them [9, 54, 114]. This possibility of temporary compensation and replacement of one bioinstrument species by another has been historically debugged in communities and, as a rule, "programmed" in the modification pool of potential morphogenetic trajectories of coenopopulations against the background of regular and multidirectional fluctuations in the abundance of species and taxocenes.

If certain changes in the environment persist for a long time and are regularly repeated, then within the population (coenopopulation), representatives of individual econes can massively develop and quickly fix stress-induced changes in epigenetic profiles that correlate with a certain restructuring of morphogenesis due to the possibility of their transgenerational inheritance [15, 16, 97]. On their basis, potential biomorphs are formed, which allow further reduction of the already weakened control and regulation on the part of the community (this is the mechanism for granting an ecological license to a species), providing the possibility for rapid evolutionary changes. The latter makes it possible to maintain and even increase the population size under pessimal conditions, as well as to develop new resources that are not available to other species at the expense of biomorphs. Therefore, the appearance of biomorphs leads to an increase in the

macroevolutionary (arogenetic) potential for both the species and the community.

CONCLUSIONS

Thus, the econe should be considered as an elementary unit of a supraorganismal biological organization simultaneously in a coenopopulation and a community (taxocene), capable of providing the initial stages of micro-, meso-, and macroevolutionary changes. Due to its binary function, performed in the coenopopulation and the community, the econe has, on the one hand, the potential for rapid adaptive changes in the developmental system of the coenopopulation, and on the other hand, it receives a "signal" (license) from the community about the presence of a new potentially available set of resources and the possibility of its exploration. The presence of pre-adaptive properties (a pool of modifications) allows the econe to actively use this signal in the form of a new resource and change the morphological and functional capabilities of the phenome for its effective development.

A sharp acceleration of the adaptive process, associated with the need to restructure morphogenesis, can occur when conditions of climatogenic, anthropogenic, and biotic (invasive) nature change, which can become threatening for the further existence of the population of this species. In these cases, one or several econes can provide the necessary rapid restructuring of morphogenesis in the direction of expansion and/or changes in the morphoniche of the coenopopulation [see 67], compensating for the resulting lack of resources. As a result, new morphofunctional features can become the first step towards microevolutionary transformation and at the same time to further macroevolutionary rearrangements of morphogenesis, providing a certain direction of speciation in the phylocoenogenesis process [41].

Feedbacks in econes ensure the unity of the evolutionary-ecological process, which in parallel affects both ecological and evolutionary phenomena, i.e., actually sets the parallelism of the driving mechanisms of micro- and macroevolutionary rearrangements, which are carried out simultaneously, but with different intensity and on different time scales. Probably, mesoevolutionary processes are also built into these feedbacks on the basis of evolutionary-ecological mechanisms of interactions between econes, coenopopulations, and communities [45, 49, 67].

Thus, there are theoretical grounds for assuming that micro-, meso-, and macroevolutionary changes can begin in parallel as a population-coenotic adaptive change in the econe in the coenopopulation. Perhaps Shvarts [3], who insisted that "...Microevolution and macroevolution are a single process" [3, p. 173] was partially right. However, our point of view is still somewhat different from the position of Shvarts. Par-

allel and almost simultaneously occurring micro- and macroevolutionary processes based on changes in the morphogenesis of ecores are subject to different evolutionary-ecological mechanisms of transformation: populational and coenotic. Therefore, in the phenotypes of ecores, different aspects of adaptive morphogenetic transformations, developed in parallel for both population and coenotic levels of biotic interactions, can be combined in a compromise. In other words, populational and coenotic requirements for micro- and macroevolutionary changes in morphogenesis, as a rule, can be unequal and multidirectional, but on the whole, functionally compromise and mutually balanced, increasing the overall viability of the transformed phenomes of the corresponding ecores at both levels of biological organization.

It is the ecores, as structural and functional groups within the coenopopulations of closely related sympatric species of the community, that are able to provide integration interactions between the population and coenotic levels of biosystem organization in the process of rapid evolutionary changes. Due to the possibility of transgenerational inheritance of stress-induced epigenetic rearrangements, proven in recent decades, rapid real-time changes in ecore morphogenesis are possible, which contribute to the formation of microevolutionary changes. On the other hand, ecores, as interacting SFG of coenopopulations, species components of communities, based on the same mechanisms of rapid epigenetic changes, are able to provide mutual diffuse coevolutionary rearrangements that determine the direction of macroevolutionary changes and phylocoenogenesis of the community as a whole. The “beneficial” changes picked up by the community, for example, the instrumental improvement of foraging morphostructures that allow additional utilization of its excess resources in the community, can provide not only more favorable living conditions for the coenopopulations of individual species or their SFG, but also the ecological balance of the communities. At the taxocene level, the mutual adjustment of ecores and coenopopulations of its species on a historical, rather than geological, time scale can provide conjugate coevolutionary changes in the same way, which will determine the parallelism of further adaptive radiation, which has a mesoevolutionary character.

The MS theorists [32, 116, 117] considered sympatric speciation to be an unlikely and difficult to implement phenomenon. In recent years, examples of sympatric speciation in the world literature have multiplied due to the understanding of the reality of the epigenetic mechanisms of initial evolutionary changes [12, 16, 17, 97, 109, 115]. Based on recent evolutionary theories, ETE [89, 101, 103, 118, 119], as well as the concept of extended evolutionary synthesis (EES) [17, 19], based on the stress-induced and transgenerationally inherited transformation of the epigenetic system that parameterizes the processes morphogenesis, the

evolutionary role of sympatric speciation began to be actively revised [67, 113, 115, 120].

As we noted above, the rapid formation of new ecores as special biomorphs and ecospecies has a real confirmation based on the example of African cichlid and cyprinid fish flocks, as well as Darwin’s finches. These examples confirm the reality of rapid sympatric speciation based on the diversification of ecores and serve as a prototype of the initial stages of sympatric micro-, meso- and macroevolution, which occur almost simultaneously in coenopopulations and communities (taxocenes) but are simultaneously implemented at different levels of organization: intrapopulation, species, and coenotic.

In conclusion, we note that ecores, which first became biomorphs, and subsequently ecospecies, and finally phyletic species, can continue their phyletic evolution, leading to an increase in taxonomic rank and the level of evolutionary divergence. Ecores can really transform and expand to the species norm, i.e., form eidoecores, changing the EN of the new species, and then potentially becoming macroecores and to determine the features of the macroecology [121] of new macrotaxa. In this regard, our ideas may well be combined with the paleoecological and evolutionary-ecological concept of the ecore developed by Vislobokova [58].

The population-coenotic concept of ecore proposed by us makes it possible to substantiate the possibility of integrating the processes of micro-, meso-, and macroevolution on a historical time scale, based on the phenomenon of transgenerational (soft) inheritance of rapid stress-induced epigenetic changes that parameterize certain rearrangements of morphogenesis. Due to the fact that all evolutionary-ecological processes (micro-, meso- and macroevolution) of ecore changes in coenopopulations occur in real time, but with different efficiency, it is theoretically possible to approach modeling and predicting the onset of regional biocenotic crises due to rapid epigenetic rearrangements caused by combination and intensity of influence of climatogenic, anthropogenic, and biotic (invasive) factors.

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