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RELATIONSHIP AND INTERDEPENDENCE OF SUCCESSION AND EVOLUTIONARY PROCESSES IN THE DYNAMICS OF THE EARTH'S LIVING COVER

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The transformation of the living cover (biocoenotic self-regulation) can be performed by changing the species composition of communities, as well as through the acquisition of specific adaptations of populations. Both the succession of species and evolutionary transformations are due to the transformation of ecological niches. Since the emergence of new forms is always accompanied by the elimination of an enormous number of individuals, evolutionary processes are uneconomical compared to succession. Population structure of the species provides a species-specific flux of living material between different ecosystems. This contributes to limiting the evolutionary processes by succession, which is accompanied by a significant economy of living matter in the biosphere.

Keywords: ecological niche, evolution, succession, living matter, population, taxonomic richness.

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Introduction. Deep qualitative changes in the organization of the living cover are the result of the flow of succession or evolutionary processes. Many researchers have paid attention to the generality of the driving forces and mechanisms of ecological succession and organic evolution [2, 3, 9, 10, 16, 34]. Both succession and evolutionary processes are different sides of biocoenotic self-regulation and are carried out by natural selection. The end result of both processes is the formation of the most balanced and sustainable ecosystems that differ from the original ones by more economical use of energy at all trophic levels. However, the evolutionary path of shaping ecological niches means the appearance of corresponding new genetically fixed adaptations, whereas the path of succession is based upon the use of existing options.

The purpose of this paper is to theoretical analyze the interdependence of succession and evolutionary processes and their role in the transformation of the living cover, inter alia, in enhancing its taxonomic richness.

Assumptions. Elementary units and most important links in evolutionary transformations and successional changes are considered to be populations [7]. The population of each species occupies a particular ecological niche of a biocoenosis (the G.F. Gause principle). Under the pressure of life [4], each population tends to make a fuller use of available resources and to expand its ecological niche.

There is a view that in the absence of concrete species the functional field suitable for occupancy of space can be partitioned into niches in an arbitrary manner, so the notion of a potential niche does not make sense [12]. However, the adaptive capacity of each of the existing species is limited by its ecological valence (i.e. genetically fixed norm of reaction). The limits of changes of genotypes at the change of habitat are largely predetermined, which follows from the law of V.I. Vavilov (homologous series in hereditary variation). Theoretically, the division into niches the area of the formation of any ecosystem is possible on the basis of the adaptive capabilities of all modern species. In this respect we can talk about potential niches, which can be effectively utilized by various species.

The imbalance of production processes and the degradation of organic matter in natural ecosystems [1] causes the appearance of substrates (energy sources) yet not used by living organisms. During ecological succession, as in the development of the biosphere as a whole, the potential resource base for most species increases, because changes in species composition of ecosystems complicate the niche structure and the appearance of new species in the community opens up additional possibilities for the next invasion [15, 34].

Transformation of ecological niches in the dynamics of the living cover.

Various transformations of econiches, including their appearance, splitting and disappearance can be divided into two main parts: restriction (extension), and shift. From the standpoint of the concept of G.E. Hutchinson, the restriction (extension) can be regarded as a change in the parameters of the realized niche, and the shift - a transformation of the fundamental niche. The restriction (expansion) of the niche reflects changes in the volume and accessibility for the population of the resource base, which is expressed primarily in changes in its density, productivity and spatial structure. The shift of the niche defines new potential use of resources through the acquisition of appropriate adaptations, i.e., in this case, the change of genetically determined limits of tolerance of the species. This is accompanied by signs of an evolutionary shift of the population, which is taking over a potential niche [20]. The width of the niche of a population in the biocenosis can be considered as the ratio of the realized niche to fundamental niche and the shift - as a notional value of the inverse proportion of the overlap of the initial and transformed fundamental niches.

In the case of the change the conditions of existence of a population the shift in niche might start with its restrictions. But with the rapid approach to the limits of tolerance for a population the organisms will be doomed to extinction, and its niche may be partitioned by other species or disappear at all. If the population is approaching the pessimal zone at a rate comparable with the rate of change of generations, the probability of a niche shift will increase sharply.

The restriction (extension) and the shift are mutually reinforcing aspects of the transformation of the niche structure of biocoenoses. The actual change in the role of population in them may be caused by a narrowing and shift its niche and is the resultant of two components.

Evolutionary processes as a mechanism for biocoenotic regulation. The scene for evolutionary process is the biocoenosis [25]. The emergence of new adaptive forms enable to more efficiently use the available resource potential and enhance the balance of metabolic processes, being thus an important mechanism for biocoenotic regulation. The genetic fixation of new initial adaptations occurs on a fairly restricted area. Microevolutionary processes to the level [or scale] of the species are accompanied by a small, compared to the original volume, niche shift. The emergence of new species is determined not only by the degree of geographic and ecological isolation of the source population from those competing with it. The most important condition of speciation is a significant shift of the fundamental niche with respect to its initial settings, in which the optimum zone of the source and the transformed populations do not overlap and both differentiate under the influence of driving, and later on stabilizing selection. It is assumed that the evolutionary transformation of populations takes place mainly in developing ecosystems, which are undergoing succession changes and the replacement of species and, consequently, are subjected to the continuous transformation of the niche structure [18, 25, 31].

The presence of potential ecological niches, in the absence of candidates for them, stipulates the evolutionary transformation of populations [18]. In biocoenotic terms the restructuring of genetically determined characteristics of the population will be accompanied by a shift of its niche. Under the action of the evolutionary shift of the characteristics the transformation of the fundamental niche will occur consequently and the population may be possible to find a more efficient way of the use of resources [17]. By fully overtaking the shifted niches it will have a significant selective advantage, subsequently contributing to the expansion of the occupied realized niche.

For adaptation, acquired in the course of evolution, the population is paying the price set by elimination of poorly adapted genotypes [2, 21, 23]. Already at the beginning of the shift a part of the individuals are eliminated for which changes in living conditions exceed the limits of tolerance. Numerous examples from the practice of pest control, forestry and pathogens suggest that races, resistant to the drugs used, usually occur only after the death of the vast majority of individuals in populations of the constrained species [26, 33].

Many organisms are killed being subsequently exposed to driving selection. It is shown experimentally that the population size is usually in inverse proportion to the intensity of selection [27]. The evolutionary shift of characters increases with the intensity of selection and with increasing population size [22, 30]. As a result of the acquisition of genetic adaptation is a reduction of the population numbers, since the increase in population fitness decreases the survival of the mass of individuals [32]. Considering the problem from the viewpoint of thermodynamics, M.M. Kamshilov [14] assumes that the evolutionary perfection of the species occurs at the cost of the death of a large number of their representatives. Thus, the evolutionary process leading to the emergence and consolidation of new adaptive variants, is followed by the elimination of a large number of individuals of the evolving population and, therefore, is a wasteful way of biocoenotic regulation.

At the same time, the biosphere scale of evolutionary changes is aimed at minimizing and preventing further loss of living matter. For example, the emergence of several syngens (in ciliates), and later the emergence of the two sexes, enhances the likelihood of their meeting (as in higher organisms) and increases the genetic heterogeneity by combinatorial means, without the occurrence of undirected mutation, which is accompanied by a significant loss of living matter.

Succession changes in the mechanism of biocoenotic regulation. Given the free exchange of species, the potential niche will be more fully engaged by respective organisms, having previously appeared in other parts of the biosphere in similar situations. In this case the assimilation and partitioning of ecological niches will be controlled by succession under biocoenotic regulation, while competition for the common resources by species by interspecific selection [3, 9, 11, 13]. These kinds of selection do not lead to the formation of new forms and, therefore, are accompanied by the elimination of much smaller number of individuals than occurs under driving selection [13]. Actually succession processes, which are consistent changes in the species composition can occur only if there is a sufficient number of species in place in the environment, so the potential ecological niches can be realized. Such a mobile reserve, i.e. material for the succession process is created by the population structure of the species. Populations, as part of species throughout its range may be part of a number of different ecosystems, occupying the same type of ecological niche [8]. As a consequence, species-specific living matter, as defined by V.I. Vernadsky [4], under the pressure of life spreads over the surface of the planet, providing interpopulation communication by filling appropriate potential niches. Thus, the potential niches will be realized by representatives of those species that are well adapted to the conditions.

Apparently, the occupation of potential niches by their respective populations in the absence of competition occurs only under the control of balancing selection at its lowest pressure, when the number of mutations in the population is small and the elimination of individuals is insignificant. The analysis of invasions of an array of species, described in detail by Charles Elton [26], confirms this assumption. The filling of potential niches can be accompanied by replacement of one species by another in the course of competition for the same niche. This changes the ratio of parts of the niche occupied by different populations, expanding to full employment for one of them, and at the same time, tapering to zero the employment for the other. Since the competitive displacement of individuals in the struggle for existence means their immediate replacement by representatives of other species, it is expected that for a constant source of available energy per unit of biomass of eliminated individuals there should be an equal number of surviving organisms, i.e. cumulatively as a result of the process there will be an elimination of about half of the individuals of both competing species. The relative stability of the total biomass of competitors, which is observed in experiment [6, 7], is defined by the constant character of the energy flow at the site of the trophic network, that is, corresponds to the overall width of the employed niche. These processes are accompanied by changes in the width and do not shift the niches. In general, the substitution of some species by the restriction of the niches of others within the ecosystem is compensated by the expansion of others, and the total elimination of the species is much less than in the case of the shift of niches.

The interrelation of evolutionary and succession processes in the development of the biosphere. The development strategy of the biosphere is not only an increase in differentiation of living matter in the course of development of habitat space, but also in increasing the mobility of the body of previously established forms. The high mobility and group migration between very distant habitats characteristic of evolutionarily advanced groups of organisms contribute to the rapid employment of potential niches for readily adapted forms. In the course of the development of the biosphere the number of species has been increasing. In the early stages of evolution the forming of new species had an explosive nature [15]. In connection with the enhanced use by living matter of new energy sources and habitats a dramatic increase occurred in the diversity of potential niches. Accordingly, growing numbers of species employing them occurred, in addition they had more sophisticated methods of dispersal.

But, as often as many new applicants for a variety of niches appear, there is an increase of the probability that all classes of similar niches may be occupied by rather well adapted to them organisms, i.e. limitations of evolutionary processes are imposed by succession and, therefore, there is slowdown to further growth in the number of species. Apparently, the interrelation of succession and evolutionary processes is a regulator of the intensity of speciation and supports it within certain limits at each stage of development of the biosphere.

Groups (taxa) of organisms that have a significant migration capacity or have special dispersal abilities, as a rule, have relatively smaller numbers of species (evolutionary diversity) since succession processes dominate over evolutionary during the occupation by them of new habitats. The number of known species of microorganisms is considerably inferior to that of mesoorganisms (insects, etc.), but exceeds the number of macroorganisms (vertebrates). This, by V.D. Fedorov [24], is a consequence of the proportionality of the rate of change of different habitats and the rate of change of ecological niches. On the other hand, it is possible that a smaller variety of microorganisms compared with mesoorganisms is due to the high efficiency of their distribution in the passive form of dormant stages, which allows the quick employment of existing types of potential niches, keeping them from developing in an evolutionary way. The high mobility and organization of the home ranges of higher animals are more conducive to limit their speciation.

The economy of living matter at the biocoenotic level. Thus, the transformation the niche community structure (biocoenotic regulation) can be performed by shifting niches (through evolutionary transformation of populations), and by changing species (leading to a change in the width of niches in the process of their employment). Moreover, the succession processes responsible for the availability of potential niches for invasion of alien species may limit evolutionary phenomena. The evolutionary path of establishing community structure prevailing in the specific conditions (for isolated large ecosystems, the occupation of new habitats, etc.) is accompanied by the appearance and subsequent elimination of a huge number of less fit (or poorly adapted) organisms [2, 19, 28] and, therefore, is an uneconomical way to occupy new niches and perform biocoenotic self-regulation. While perishing in the struggle for existence, the components dead individuals can be used by heterotrophic communities, it has no significant effect on the processes considered, as in the food chain, according to the Lindemann rule, there will be approximately a 10-fold (in energy terms) loss of biomass. Consequently, the restriction of evolutionary processes by succession leads to the economy of living matter at the biocoenotic level and contributes to its preservation in the biosphere.

Conclusion. Self-regulation of ecosystems, as well as the development of the living cover in general, should be viewed as a dialectical process, including two opposite sides: succession and evolution. Both the succession of species and evolutionary transformations are due to the transformation of ecological niches (their narrowing or shift). The evolutionary emergence of new forms is always accompanied by the elimination of an enormous number of individuals, so, in the sense of loss of living matter, evolutionary processes are very wasteful compared to succession. However, the general vector of evolutionary change is to prevent the loss of living matter within the biosphere.

The transformation of the living cover (biocoenotic self-regulation) can be performed by changing the species composition of communities, as well as through the acquisition of specific adaptations of populations. Moreover, succession processes in the absence of spatial or environmental barriers may limit evolutionary processes that are accompanied by significant cost of living matter. Population structure of species not only provides the fixation of general adaptive changes of the species, but also provides a species-specific flux of living material between different ecosystems, which contributes to limiting evolutionary processes by succession.

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