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ECOLOGICAL CRISES AS ORDINARY EVOLUTIONARY EVENTS CANALISED BY THE BIOSPHERE

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Abstract

The main general paradigm which we admit is that there is no biological process beyond the biosphere and, therefore, biological evolution must be regarded first of all as the evolution of the entire biosphere. Evolutionary processes performed at different levels of life organisation are interrelated to each other and to the general biospheric processes.

The evolution of the subordinate units (ecosystems, populations, organisms) is governed by the biosphere. Using both the notion "license" and a license-symbiotic approach, one can explain the evolution of ecosystems, macroevolution (both are the same process studied from different viewpoints), evolutionary changes in populations and organisms. This approach gives also a possibility to define the notion "adaptive zone" as well as to explain Simpson's tempo of evolution and Schindewolf's phylcycles. Taking into account the interconnections between the evolutionary processes at different levels of life organisation, formulation becomes possible of five main principles characterising biological evolution: the principle of sufficient biodiversity of the biosphere, the principle of indefinite specialisation, the principle of an evolutionary deadend for abundant forms, the principle of changing, replaced biotas, and the principle of biodiversity autoregulation.

The biosphere canalises the evolutionary processes by means of either presence or absence of licenses for living organisms. On the other hand, both organism texture and organism physiology which are the results of previous developments are also important canalising factors. All above factors are interrelated due to a feedback, this allowing to speak about autoregulation or autocanalisation in the course of biospheric evolution. Factors independent from the biosphere, e.g., a decrease in the solar radiation rate, play the role of a trigger in speeding up the evolutionary processes canalised by the biosphere. We term the influence of the biosphere on the process of its own evolution as the autocanalisation paradigm which we take as the most general one characterising the development of life on Earth. Hence, out of a number of general statements and mechanisms discussed here, we would like to specially note the following: the paradigm of autocanalisation, an ecocentric concept of macroevolution, a license-ecosystem approach, the hypothesis of embryosphere and, finally, a physico-ecological model of biospheric evolution.

Introduction

Palaeontology provides numerous examples of geologically quick extinction of large groups of organisms which were very diverse before. Such sharp changes displayed on a planetary scale are usually named global ecological crises. They are commonly explained by extraordinary events, in particular by collisions with gigantic meteorites, huge volcanic eruptions, sharp decreases in available solar radiation connected with the Solar system passing through clouds of cosmic dust, etc. Whichever causes, such crises are unequivocal evidences of biospheric evolution [Levchenko, 1993], same as, e.g., the changing gas composition of the atmosphere, the formation of coal-bearing beds, etc.

There is an extremely important view that for the present the biosphere is unique and cannot be studied as compared to any other one. At the same time, we are able to explore ecosystems which the biosphere is composed of. Taking in consideration that the biosphere is also an ecosystem, albeit of the highest structural level, we might hope that, investigating the particular traits of ecosystem evolution, i.e. phylogenesis

[Zherikhin, 1995], and the general patterns that process follows, we could achieve certain success in explaining the direction of the evolution of the biosphere as a whole.

In this article, we attempt to join our previous evolutionary works and concepts to demonstrate their interconnections and also to provide a general picture of biospheric evolution at different levels of life organisation.

Canalising Factors in Biological Processes

Canalisation in biological processes implies certain restrictions to development and evolution. This means that far from any pathway can not be realised because some trajectories are prohibited by the previous development of a system, i.e. by the system's "memory". Sometimes we speak about canalisation by the environment. Moreover, the general laws of Nature, physical ones above all, determine rather numerous main factors of canalisation, all narrowing the field of choice for subsequent change. In this context, stability is an extremely particular case of canalisation when no change is possible due to some restrictions, e.g., morphogenetic ones. A different case is implied when a (bio)system's changes are neutral to its interaction with the environment.

To sum up, we can postulate that there is an "epigenetic landscape" with various types of canalising influence. Using other words, canalisation is the "evolutionary tubes" to which any possible development is reduced. Then the main question for such an approach is, who/what does these tubes build?

One of the traditional viewpoints in answering the above question is quite predeterministic: the laws of Nature determine such "tubes". Yet, in its turn, a biosystem can influence the environment and thus change some of the external factors of canalisation. So we arrive at auto- and self-canalisation of biosystem evolution.

The Autoevolution and Autocanalisation Paradigms

Most of the proposed evolutionary theories, evidently or surreptitiously, use one of two main postulates: the evolution of living beings, and of the biosphere itself, ever proceeds due to endogenous or exogenous causes. The factors canalising the evolutionary process may be discussed in both above cases. Yet almost all more general hypotheses explaining the appearance of these factors and their alterations with time are rather incomplete. The hypothesis of autoevolution (Lima de Faria, 1988) is an exception. It may be regarded as a modern interpretation of the ideas of performing harmony. We propose here another postulate, termed the hypothesis of autoregulated evolution, or, to put it more simply, the paradigm of autocanalisation (Levchenko & Starobogatov, 1994; Levchenko, 1995). According to it, canalising factors include the environment which is not invariable with time but depends just on the evolution of both the biosphere itself and the organisms it is composed of. In other words, when analysing biospheric evolution, we must take into account two main types of canalising factors combined: those which are independent from the biosphere (the laws of non-living nature, including astrophysical and geological factors) and those dependent on the vital activity of the biosphere, e.g., transformations of the gas composition of the atmosphere. The latter group of factors is the environment's "memory" as well as both structure and function of the organisms living inside the biosphere (Starobogatov & Levchenko, 1993). Certainly, sometimes such influences of living matter proper on its environment can be very slow, as was, e.g., the case when the oxygen atmosphere first appeared and finally changed virtually all the pathways of biological evolution. Nonetheless, the cause-consequence relation via the environment between the beginning of an evolutionary process and its subsequent development was present there (Zavadsky & Kolchinsky, 1977). Hence the biosphere seems to have expanded its own boundaries, this way subordinating and organising its own environment (Zherikhin & Rasnitsyn, 1980; Zherikhin, 1980).

Autocanalisation of Biospheric Evolution

If we postulate that any biosystem can influence some particulars of the laws of its environment at least locally, and also if we take that this biosystem possesses some features of accidental behaviour or, using a different terminology, free will, then we are obliged to admit that it is life that builds the above "evolutionary tubes" for own future. According to such an autocanalisation approach, we face a system containing both the

biosphere and its environment as a whole, with the feedback between their parts that determines many important particulars of biospheric evolution throughout biosphere existence.

One of several viewpoints possible in principle, which also may be named paradigms, implies that there is no living process or life itself beyond the biosphere. We accept this because there is no proof whatever that the biosphere ever disappeared or re-appeared some other time and place (Vernadsky, 1980). Then we are forced to admit that the evolution of life on our planet is just the evolution of the biosphere, as well as of the organisms and ecosystems it is composed of, under the effect of the on-going autocanalising mechanism. Hence, natural selection may be regarded as a process ruling over the ecosystems and populations of the biosphere. This strictly determines the canalising influence of the biosphere on the evolution of living beings. Such a situation may be explained in other words as an aspiration of the realised ecological niches of species populations to correspond to the ecological licenses of the ecosystems (Levchenko & Starobogatov, 1986a, 1990).

Licenses

The notion "ecological license" was first introduced by G(nther [1949] but it was defined quite vaguely as the conditions of external and internal environments permitting some evolutionary factors to act: "Es wird von auftretenden und an sich lebensfähigen Mutanten in kleinsten Populationen auch der Zufall (ohne Beteiligung der Selection) günstigstenfalls nur die durchzusetzen vermögen, die von den gegebenen ökologischen Bedingungen für die betreffende Art gerade noch zugelassen werden: damit wird die Annahme eines weiteren Evolutionsfaktors nahegelegt, den wir weiter oben schon gestreift und als den der "ökologische Lizenz" bezeichnet haben." (op. cit., 1949, p. 45).

Many years later, this notion has been revived (Levchenko, 1984a, 1990a, 1993a; Starobogatov, 1984, 1985; Levchenko & Starobogatov, 1986a, 1990), yet as taking in consideration the following factors: (1) position in space and time, (2) role in matter and energy flows, and (3) position in the gradient of external factors the ecosystem offers to or provides for the populations or organisms existing there.

This description of a "license" resembles the meaning of "empty or free ecological niches". However, no "empty niche" can be defined, because the ecological niche has to be described by its definition (Odum, 1986) using such notions as environment of species or species population dwelling in this niche. When the niche is empty (free, species-free), no-one knows the particulars of its environment.

Some Theoretical Aspects of Ecosystem Evolution

The basic theoretical notions concerning the evolution of ecosystems have been outlined in numerous papers (e.g., Odum, 1959, 1986; Razumovsky, 1981; Starobogatov, 1984; Levchenko, 1984a, 1988, 1990a, 1993a; Hutchinson, 1985; Levchenko & Starobogatov, 1986a, 1986b, 1990; etc.). As can be seen from Odum's (1986) definition of the ecosystem, one which is particularly widely accepted now, the problems of ecosystem subdivision and demarcation are interconnected with the problems of their study and, hence, any subdivision is quite subjective. One of the most widely used approaches which we adhere to and would like to emphasise is that organisms and ecosystems are systems with symbiotic interrelations between their components. In order to avoid a misunderstanding, note that we include into an ecosystem not only the organisms proper but also all the matter that participates in the processes of ecosystem matter circulation.

This reasoning has led us to the formulation of a license-symbiotic model (Levchenko & Starobogatov, 1986a, 1990; Levchenko, 1993), now modified into a license-ecosystem approach (see also below). According to it, the ecosystem is understood as a mutually determinate complex consisting both of the organisms associated by relations based on the kind of symbiosis ("ecobiosis") and the non-vital environmental (for the organisms) components that participate in the cycling of matter and in organizing of flows of energy. Each trophic level has a specific aggregate of environmental conditions, that is, a license, whereas each population has a fundamental (potentially possible) and a realised ecological niche (Fig. 1)

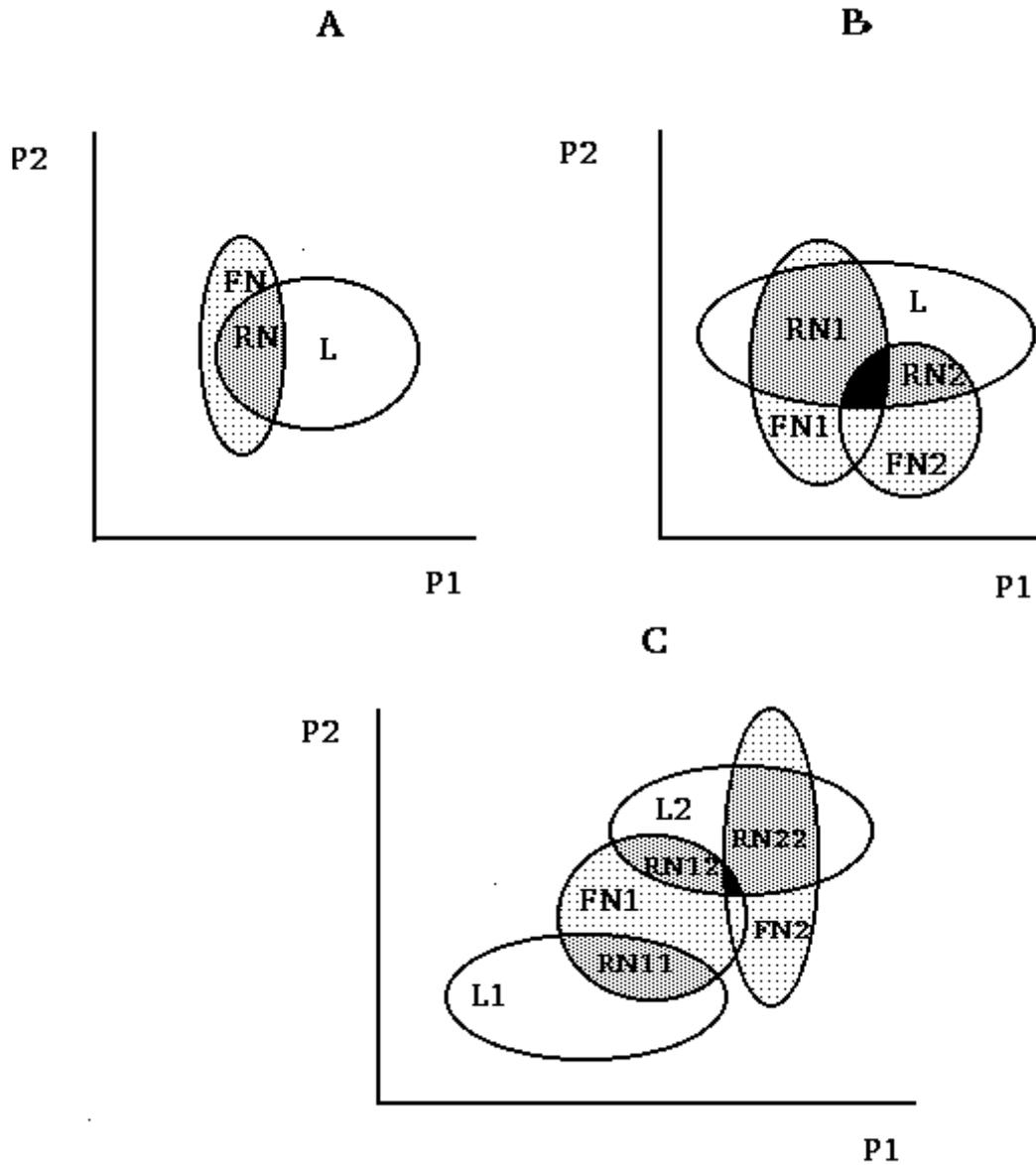


Fig 1. The interrelations between the fundamental niches of species (FN), realised niches of populations (RN), and licenses (L) in the field of external factors (P1 and P2); realised niches are shaded (after Levchenko, 1993a).

A realised niche, RN, never exceeds the licence extent, L, with an overlap between the fundamental niche, FN, and L. Within a licence, a population and/or several competing populations can be found as models of a simple and/or a complex ecosystem, respectively. A simple ecosystem is conservative to evolutionary changes, because the constancy of its internal environment as well as the presence of morphogenetic and morphofunctional limitations on evolution stabilises species composition but, in its turn, a constant species composition stabilises the conditions of the ecosystem's internal environment. So a feedback is evident, one stabilising evolutionary change and forming an ecological homeostasis. Description of the main characteristics of a complex ecosystem approximates the description of those in a simple one, if we ignore both competition between species populations within licenses and autofluctuating processes, but consider group-realised and fundamental niches of the licenses. Then all living being existing at any trophic level of an ecosystem will be understood as some united population executing some functions which are necessary for the ecosystem.

By the evolution of ecosystems we mean an irreversible change in their main characteristics, specifically licenses. Successional changes are non-evolutionary (Levchenko & Starobogatov, 1990), because they are of local restoration and/or cyclic character. In an invariable environment, an ecosystem "strives" toward an evolutionary stasis by preserving the license and group-realised niches. This is just a consequence of ecobiosis relations within it, as well as morphofunctional and morphogenetic restrictions to the phyletic evolution of its constituent populations. Nevertheless, this does not mean that microevolutionary processes are impossible when licenses are invariable. It seems quite reasonable admit an ecologically neutral

evolution in licenses that is confirmed in particular by simulation experiments (Levchenko & Menshutkin, 1988).

Ecosystem Evolution Versus Micro- and Macroevolution

Hence, as noted above, all living organisms on Earth do not exist independently of one another. They are interconnected and form separate functional biosystems of various levels, from single- and multicellular organisms consisting of individual, relatively sovereign cells and organs, to ecosystems and the biosphere. Biosystems of lower levels are subsystems of the higher levels. The existence and evolution of biosystems of lower levels are interconnected with the existence and evolution of biosystems of higher levels. Not all independent evolutionary changes at lower levels lead to those at higher levels, and the adverse holds true as well (Levchenko & Starobogatov, 1990; Starobogatov, 1987, 1988; Starobogatov & Levchenko, 1993).

We have already mentioned that microevolution is putting a realised niche in accordance with the license. Such an accord cannot be perfect due to numerous reasons, first of all license variation with time, for example from year to year.

The possible use of free, e.g. new licenses determines the process of speciation: a new species cannot appear when a free license is absent or when the species cannot "take away" the license, at least its part, of an already co-existing species.

Evolution at supraspecific levels, or macroevolution, is very closely related to ecosystem evolution. All variety of explanations of macroevolutionary mechanisms seems possible to reduce to three main concepts: macrogenetic, taxocentric, and ecocentric. The first (Grant, 1985) and the second concepts presume that natural selection is unimportant (it is not more than a "filter" on either genetical experiments of nature), whereas the third, proposed by us recently (Starobogatov & Levchenko, 1993), claims uniformity of the driving forces of evolution at all its levels due to it explains the creation and changes along time for the above "filter". Microevolution makes the realised niches adjusted to the licenses, while speciation leads to the appearance of new niches, both realised and fundamental, and may be described as an elementary act of ecosystem evolution. Both macroevolution and ecosystem evolution are understood here as two aspects of the same process of biospheric evolution, but studied from different points of view. If we investigate the fate of a clade, we deal with macroevolution (phylogenesis); if we study the fate of an ecosystem, we get the picture of ecosystem evolution, or phylocenogenesis (Zherikhin, 1995).

The internal organisation of living beings, first of all their structure, also affects the processes canalising the possible ways of macroevolution. Extinction of higher taxa is interrelated to the destruction of parental ecosystems, as a rule.

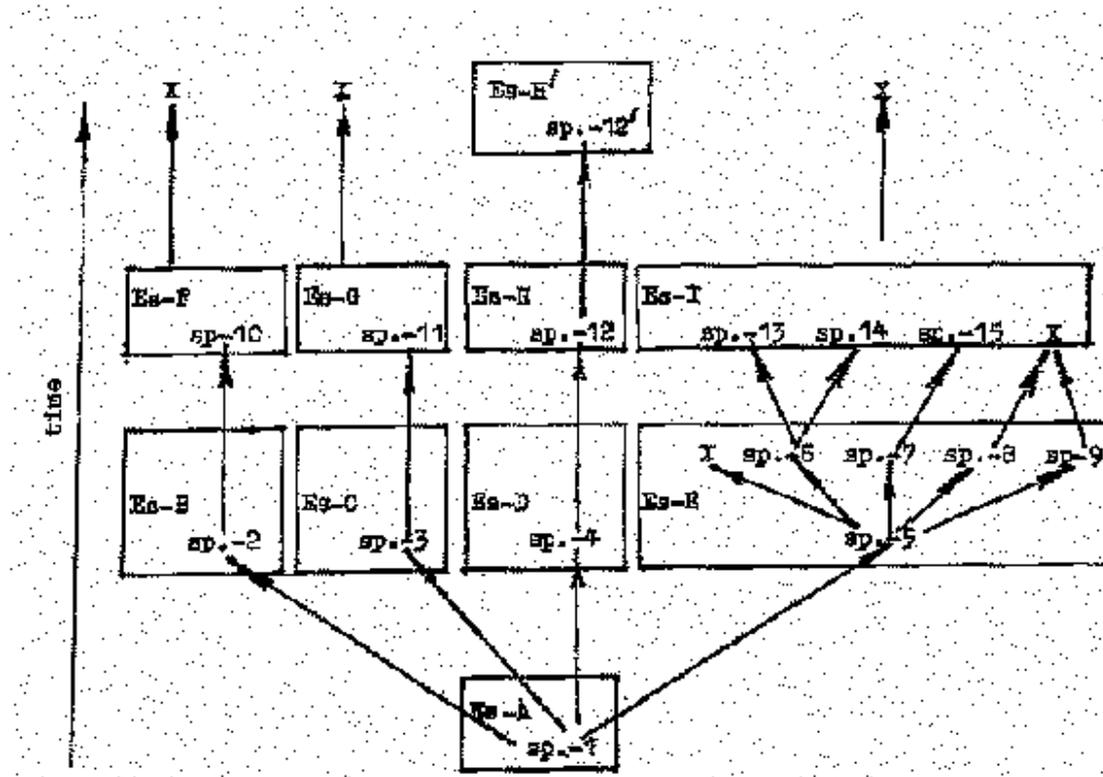
"Tempo and Mode in Evolution"

Below, we shall name any type/stage of ecosystem evolution in accordance with the particular kind(s) of macroevolutionary process taking place during a described evolutionary change.

Ecological niches and, respectively, licenses are changed rather slowly under both divergent and anagenetic types of ecosystem evolution when the ecosystem or some of its parts develop toward a more neat adaptation either to the different physic-geographical conditions existing within its range or to their change with time. Ecosystem change very quickly at both introduction and diversification types of ecosystem evolution when the ecosystem evolves due to either introduction of some species or speciation upon a purposeful introduction into isolated ecosystems, for example in the reason of either "evolutionary inventions" especially under condition of existence of free licenses (as in Lake Baikal and the Caspian Sea). New niches and licenses are formed quickly after the appearance of new species under both latter types of ecosystem evolution (Starobogatov, 1984, 1985; Levchenko & Starobogatov, 1990).

In his well-known work entitled "Tempo and Mode in Evolution", Simpson (1944) proposed his own classification of the rates of evolution. Our license-ecosystem approach (Levchenko, 1993; Levchenko & Starobogatov, 1986a, 1990) allows to interpret that classification in the following way. The ecosystems in Fig. 2 are designated both by icons and the symbols Es-A to Es-I, the species by sp.-1 to sp.-15. We can see that the descendants of a "promising" species sp.-1 first penetrate some ecosystems Es-B to Es-E and then

get transformed in sp.-2 to sp.-5. The process of diversification within Es-E leads to the formation of a species cluster, sp.-6 to sp.-9. When ecosystem evolution is at an introduction and/or diversification type, with both diversity and the rate of evolution increasingly high, we face the so-called tachytelic evolution. Further on, the descendants of sp.-1 evolve slowly together with the ecosystems in which they take part, this time in accordance with a divergent or an anagenetic type of evolution.



Under construction

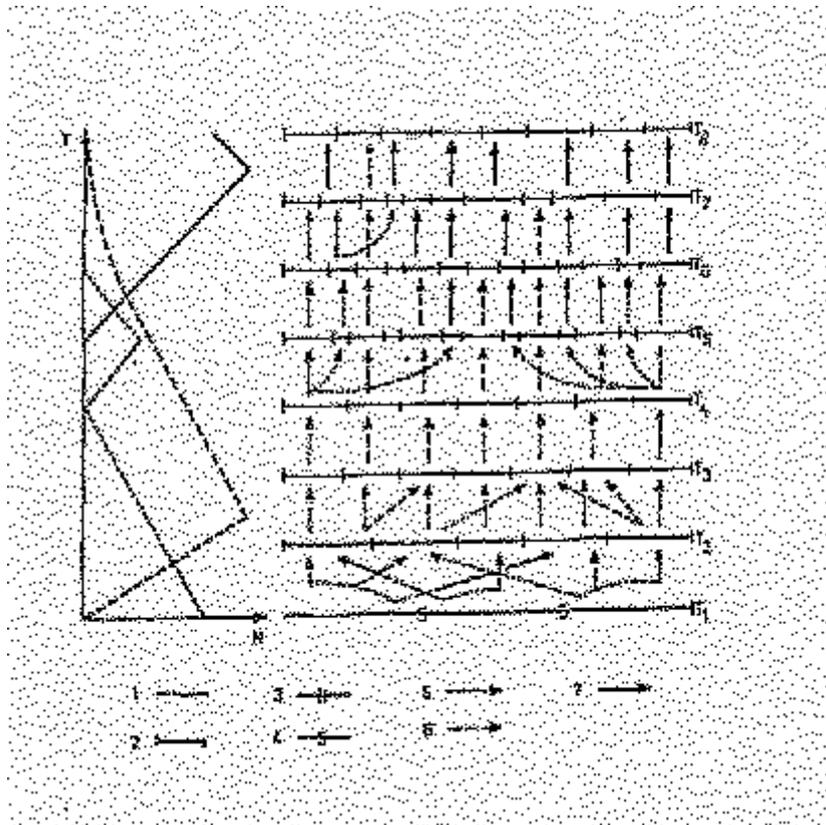
Fig. 2 The fates of descendants of "perspective" species. Rectangles and letters Es (from A to I) -- ecosystems; sp (from 1 to 15) -- species; X - extinction (by Ya. Starobogatov).

There is one more very common case: horotelic evolution. As a rule, this type of evolution is brought about by events (after tachytelic evolution) just like those described above. Then most of the ecosystems (together with the descendants of sp.-1) become extinct (marked by X), and only one or a few ecosystems manage to survive (Es-H' together with its relict sp.-12'). Finally, the rate of evolution of the clade is very slow here, hence bradytelic evolution.

Using such an approach, it is possible to interpret also Schindewolf's (1950) phylcycles, i.e. the "youth", "maturity" and "old age" of a taxon. If we try to relate some clade and a taxon to the bottom of the scheme in Fig. 2, when the diversity rises quickly (such a procedure may well hold true for some real succession of events), we can notice that the bottom shows the taxon's youth, the middle part its maturity, and the top its older age.

Endogenous and Exogenous Factors Affecting Ecosystem Evolution

Endogenous factors and, first of all, redistributions of resources and energy are of importance throughout quickly changing ecosystems. This becomes evident from a recently developed scheme (Fig. 3) which demonstrates that poorly specialised, generalist forms can play a significant role in the process of substitution of long-specialised groups by new ones. The dotted lines and arrows indicate generalists, the dashed lines and arrows the specialists of an older formation, whereas the solid lines and arrows the newer specialists. The abscissa is time, the axis of ordinates is diversity. As can be seen from Fig. 3, a continuous specialisation of older specialists leads to the formation of "ecological lacunas", i.e. free licenses not used by specialists but suitable for generalists. The latter stepping in, the diversity of such forms grows along with a decreasing complex of older specialists, followed by a rising variety of newer specialists. The dynamics of diversity is shown on the lefthand side of the scheme.



Under construction

Fig. 3. Scheme of the evolution of a community and its biodiversity. 1 -- amount of resources; 2 -- licenses (adaptive zones); 3 -- unused licenses (interzonal lacunas); 4 -- inevident demarcation of licenses; 5 -- poorly specialised biological forms (generalists); 6 -- specialised taxa of an older formation; 7 -- specialised taxa of the new formation; T -- geological time, N -- biodiversity (after Kalandadze & Rautian, 1992).

Strictly speaking, the structure of the organisms which is the result of their preceding evolution also renders a canalising effect on their further development (Starobogatov, 1988). Such effects restrict the set of licenses which can be used by the representatives of a clade or taxon. For example, among such most ancient, primarily sea-dwelling and co-ordinate phyla as the Arthropoda and the Echinodermata, the former has managed to conquer virtually all environments since the last 550 million years, whereas the latter taxon has failed to colonize even fresh waters during the same period of time. This has happened so, because the Echinodermata has never had/developed an apparatus performing an osmoregulatory function. Using a similar reasoning, Simpson's (1944) notion of the adaptive zone of a macrotaxon can be redefined as a certain set of licenses which can be used by representatives of the higher taxon during the whole time of its existence.

Concerning exogenous impacts, global abiotic factors function as triggers for big reorganizations of ecosystems ("ecological crises", or "catastrophes"). The reorganizations are associated with the appearance of (under new conditions) progressive clades. This is confirmed by the fact that, in the same environments, some taxa become extinct, some other suffer significantly or insignificantly, some do not suffer at all, some flourish, with all possible intermediates involved.

Evolution of the Biosphere as an Integral Biological System

As already emphasised above, there is no biological process beyond of the biosphere. One of the main consequences of this paradigm is that biological evolution must be regarded first of all as only and solely the evolution of the biosphere, because if some ecosystem or population were fully independent from the others, it would be impossible to claim the biosphere as a single whole. Certainly, some evolutionary changes of ecosystems, populations, organisms and genotypes advance relatively independently, and we term such evolutionary processes as ecologically neutral evolution. Yet in any event these are subordinated and controlled immediately by the biosphere as the only integral body creating all the complex of environments and, consequently, canalising factors.

Although we adhere to the opinion that full independence of any ecosystem except the biosphere does not actually exist, it is necessary to note that the probability of settling of organisms is restricted, and their penetration into/from other ecosystems is likely only from/into spatially neighbouring ecosystems, as a rule. The routine existence of ecosystems and their evolution depend both on abiotic and biospheric factors. During the extinction of older ecosystems and species, abiotic factors can play the role of triggers. On the other hand, many important changes are the result of settled progressive representatives of some clades. A general trend observed lies in diminishing the relative amount of both energy and matter offered to the other ecosystems and/or buried as geological deposits, thus resembling the process of differentiation.

Hence, the evolution of the biosphere is directed in some ways opposite to the processes observed at subordinate levels, sometimes slowing down, sometimes speeding up. The existence of changing endogenous factors serves as proof of autocanalisation which is a consequence of that life controls certain features of its own evolution. Autoregulatory processes determine both trend in and combination of canalising factors and at the same time, in accordance with the principle of feedback, these processes are determined by the above canalising factors. All this leads to the idea that the process of biospheric evolution is similar in some traits (e.g., autoregulation and tendency) to the process of ontogenetic development (see also below). Such a similarity can be discussed only in relation to the evolution of the biosphere but not as regards the evolution of numerous changes in ecosystems, populations, organisms or genotypes. Moreover, this similarity is certainly not full. In particular, ontogeny's final goal is to achieve the construction of adult organisms with definite morphological and physiological characters; on the contrary, the evolution of organisms is devoid of any final goal except acquiring a more perfect adaptation to the environment.

Some Evolutionary Principles of Biodiversity

As can be seen, all evolutionary processes occurring at different levels of life organisation are interrelated to each other and to panbiospheric processes. Above, we have already discussed the following general statements: (1) the paradigm of autocanalisation, one which may be conventionally called also as "life within the biosphere only", or, for short, the biospheric paradigm; (2) an ecocentric concept of macroevolution; and (3) a license-ecosystem approach. In addition, we have briefly outlined some evolutionary mechanisms in relation to those statements. But how are they all associated with the processes of speciation?

Based on the above statements and mechanisms as well as on the fact that evolutionary change in the environments require a constant change in living beings, we propose the following general principles (Levchenko & Starobogatov, 1995).

- (1). The principle of sufficient biodiversity of the biosphere. Biodiversity at each trophic level is necessary for support of a stable functioning of ecosystems in altering environments. If this is so, some species within an ecosystem are capable of lying at the beginning new evolutionary lineages.
- (2). The principle of not full, non definite specialisation. Only species displaying no hard restrictions to evolutionary change can serve as supply material for further evolution.
- (3). The principle of evolutionary dead-end for widespread forms. The main role in ecosystems and in the biosphere as a whole is played by abundant species well-adapted to the environment and thus specialised but, as a rule, such species fail to serve as material for further evolution.
- (4). The principle of changing, replaced main biotaxa. Abundant taxa are replaced first of all in response to globally changing external factors. The necessary levels of biodiversity are maintained during such times of change by a rising number of new abundant specialist and older generalist species.
- (5). The principle of autoregulation of biodiversity in the biosphere. The biosphere "strives" for supporting the level of biodiversity necessity under the inconstant conditions on the planet.

The Hypothesis of Embryosphere

Impossibility for biotic processes to be carried out beyond the biosphere warrants the recognition that life must have originated simultaneously within the whole biosphere, albeit probably not as global as today. From such a standpoint, this brings about some reflections.

Several evolutionary principles are applicable to organisms, to ecosystems and to the biosphere, the latter as the highest level of ecosystem hierarchy. Among these, there are (1) the principle of evolution of functions, which is intensification of the processes providing some function of the individual functional systems within a single biosystem; (2) the principle of increasing multifunctionality of separate subsystems of organisms or ecosystems; (3) the principle of overbasis, i.e. new functions do not replace previous but superimpose over older ones and subordinate them (Levchenko, 1990a). Just the same principles are applied also to embryonic development. Based on the above, we can surmise that the initial biosphere must have been a self-preserving, undifferentiated system which may be compared to a single primitive organism developing like an embryo by means of differentiation. This process has been in effect during the entire period of biosphere development, with rising complexity and hierarchies of processes and structures, the appearance of organisms and simple ecosystems up to more complicated cenoses. For this reason, perhaps the primary biological organisms known to us as microfossils were not fully independent. Instead they could simply have served as some functional fragments/elements of an embryosphere, i.e. a primitive biospheric system, like the cell constructed of organelles. This is the hypothesis of embryosphere (Levchenko, 1993a, 1993b). It is also noteworthy that we use the traditional term "evolution" as applied also to the process of development of the biosphere.

A Physico-Ecological Model of Biospheric Evolution

As yet one of the logical consequences of some already presented statements, first of all that biological evolution must be regarded as panbiospheric, global, a model of physical evolution of the biosphere has been put forth by (Levchenko, 1984b, 1990b, 1993a; Levchenko & Starobogatov, 1986a).

An increasing flow of energy passing through the biosphere is understood here as the latter's physical evolution. At the earliest, Proterozoic stages, physical evolution could have been associated with improving the chemical mechanisms of photosynthesis, with the advance in chlorophylls. At later, Phanerozoic, stages, physical evolution might have become connected with an increase in photosynthetic surface, i.e. leaves and other photosynthetic organs. Apparently, the growing energy flow through the biosphere leads to some amplified complexity of biospheric organisation, in particular to the creation of new life licenses. These changes are interconnected also with the well-known progressive evolution of many biological forms (Krasilov, 1986; Levchenko, 1984, 1990b, 1993a; Levchenko & Starobogatov, 1986a, 1986b).

To explain biological evolution as a consequence of the physical evolution of the biosphere, a general model has been developed (Levchenko, 1984, 1993a; Levchenko & Starobogatov, 1986a). This model implies that each biosystem "strives" for functioning without decrease in the energy flow passing through itself; it is only such biosystems that are self-preserving under changing environmental conditions. This means that any temporary drop in the amount of energy received through some "energy channel(s)" of a biosystem must lead to its looking for new (path)ways of energy acquisition and, ultimately, to the appearance of new, additional energy channels. In case of failure, the biosystem is bound to die. Hence, each interruption of the energy input promotes a biosystem's physical evolution. Simultaneously, this results in the creation of new canalising factors for subsequent evolution in response to the development of new/novel adaptations and, respectively, morphogenetic restrictions.

In general, the physical evolution of a biosystem may be described by the following equation:

$$G(N) < J_0 + \text{Sum}_{1,N} (J_k)$$

where $\text{Sum}_{1,N} (J_k)$ is the algebraic sum of J_k from 1 up to N , $G(N)$ is the energy flow passing through the biosystem after N interruptions, J_0 is the initial rate of energy flow passing through biosystem, J_k is the amount of decrease in energy during the interruption with number k . If J_k is proportionate to $G(K)$, i.e. $J_{k+1} = J_k(1+b)$, where b is the relative decrease in the energy flow (this being the case of the biosphere), then $G(N) \sim J_k(1+b)^k$.

To show that the last equations correctly describe the evolution of the biosphere, it is necessary to prove that under invariable conditions the physical evolution of ecosystems and of the biosphere stops, and interruptions, i.e. the situations when the productivity of photosynthesis decreases, give rise to more effective producers. The former is easy to understand taking into account that the biosphere, ecosystems and their representative fragments are symbiotic biosystems which constrain the evolution of species in some

directions. In complete ecosystems, a constant internal environment as well as the morphogenetic and morphofunctional restrictions permit only a non-final, i.e. aimless and undirected, evolution (Eigen, 1971) of species where ecological characters of populations are preserved. This leads to stabilised internal environmental conditions, i.e. an ecological homeostasis. Successional change is non-evolutionary, as explained above. In case of interruptions, the equilibrium in interrelations between the trophic levels is broken, and more efficient producers start having advantages in selection. As a result, irreversible changes in the population abundance and characters of successive circle occur. In some way, this mechanism resembles those proposed by Eldredge & Gould (1972) and Krassilov (1986). It is noteworthy that the origin of new producers may occur earlier, then achievement of their prosperity. If an environmental change is so considerable that it becomes impossible to maintain a suitable rate of energy flow, then a crisis takes place (Levchenko, 1992, 1983a; Levchenko & Starobogatov, 1986b).

The palaeontological data confirm this approach and allow to presume that the oscillations of the Earth orbital parameters as well as the periodical decreases in the carbonic acid flow rate from the entrails of Earth are important external causes for interruptions on the biospheric scale at least since the Phanerozoic. The former factor seems even more important than the latter one. The orbital oscillations are several dozen thousand years in periodocity, evoking changes in the duration of the seasons and the freezing in higher latitudes. Some of them redistribute also the rate of the solar radiation at all latitudes. All important calculations with using of astrophysical data concerning oscillations of solar radiation are presented in detail in book (Levchenko, 1993a), chapters 4 & 5.

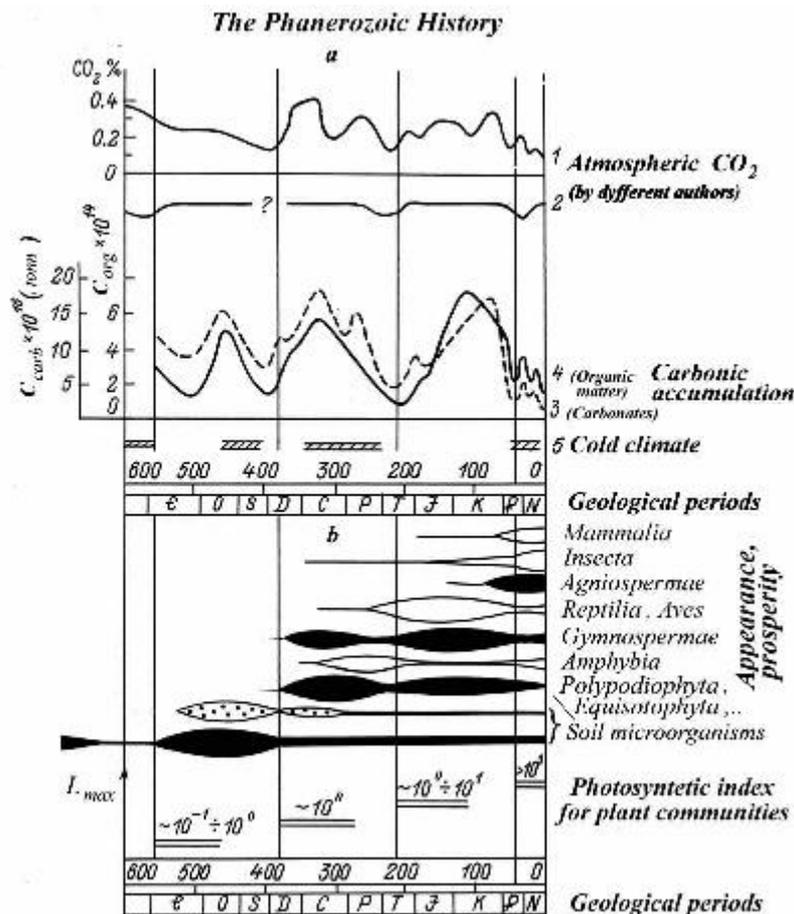


Fig 4. The Phanerozoic history of the biosphere by different authors (after V.Levchenko, 1993a).

The geological data testify that gas eruption from the entrails is not constant but occurs about every 200 million years. A decreased CO₂ flow may be considered an interruption as well, being of importance for photosynthesis. The palaeontological record demonstrates that the beginning of each wide spread of the most important terrestrial plant macrotaxa (the Devonian, the Triassic, the Cenozoic) is always associated with the end of the preceding epoch of gas eruption decrease (Ronov, 1976; Budyko, 1984). The above equation describes those factors correctly. Wide spreadings of new animal macrotaxa seem to display an about twice lower periodicity, i.e. ca. 100 million years. The origin of new progressive vital forms appears to have taken

place 100-200 million years prior to their prosperity, as a rule (Levchenko & Starobogatov, 1986a, 1986b; Levchenko, 1992, 1993a).

Some Conclusions

If some ecosystem or population were independent from the others, it would be impossible to claim that the biosphere is a single whole. Therefore, we emphasise that there is no biological process outside the biosphere. As one of the main consequences of this paradigm which might be conventionally formulated as "life within the biosphere only" is that biological evolution should be regarded first of all as the evolution of the entire biosphere.

The existence of changing endogenous factors is the proof of autocanalisation which is a consequence of that life controls certain features of its own evolution. This leads to the idea that the process of biospheric evolution is similar in some traits (e.g., autoregulation and trends) to ontogeny.

Evolutionary events at different levels of life organisation are interrelated to each other and as well as to panbiospheric processes. Out of several general statements and mechanisms discussed above, we would like to specially note the following: the paradigm of autocanalisation, an ecocentric concept of macroevolution, a license-ecosystem approach, the hypothesis of embryosphere and, at last, a physico-ecological model of biospheric evolution.

Hence, our working definition of life is as follows: life is a biospheric, self-supporting, energy flow-based process of maintenance of well regulated structures with low levels of entropy in altering environments. The model of embryosphere development using the mechanism of physical evolution is reduced from such a definition. Therefore, we distinguish two main patterns of the "flow of life" on Earth (Levchenko & Starobogatov, 1986a; Levchenko, 1992, 1993a). The first one is predetermination of the physical evolution of the biosphere or, in other words and even more strictly, the development of the biosphere from primitive chemical processes -- embryosphere -- up to the modern biosphere. The second pattern lies in some non-predetermined phenotype realisations of biological evolution (ecologically neutral changes in many biological forms in the course of biological evolution, autocanalisation). So we can see from above that ecological crises within the framework of our approaches are just ordinary evolutionary events of biospheric evolution autocanalised by the biosphere itself under the inconstant exogenous conditions on the planet.

References

- Budyko M.I. (1984) Evolution of the Biosphere. Ghidrometeoizdat: Leningrad (in Russian).
- Eldredge N. & S.J. Gould (1972) Punctuated equilibria: an alternative to phyletic gradualism. - Models in Paleobiology. San Francisco: 82-115.
- Eigen M. (1971) Selforganisation of Matter and the Evolution of Biological Macromolecules. Springer-Verlag: Berlin, Heidelberg, New York.
- Grant V. (1985) The Evolutionary Process. New York.
- Gunther K. (1949) (ber Evolutionfaktoren und die Bedeutung des Begriffs "'kologische Lizenz" f(r die Erkl(rung von Formenerscheinungen in Tierreichs. - Ornithologie als biologische Wissenschaftl. 28 Beitr(ge als Festschrift zum 60 Geburtstag von Erwin Stresemann (22 November, 1949). Heidelberg, C. Winter-Universit(tsverlag, 23-54.
- Hutchinson G.E. (1965) The niche. An abstractly inhabited hyper-volume. - The Ecological Theater and the Evolutionary Play. New Haven: 26-78.
- Kalandadze N.N. & A.S. Rautian (1994) A heuristic model of the evolution of a community and its taxonomic and ecological biodiversity. - Biodiversity: Approaches to Investigation and Preservation. St. Petersburg: 65-80 (in Russian).
- Krassilov V.A. (1986) Unsolved Problems of Evolution. Vladivostok (in Russian).

- Levchenko V.F. (1984a) Internal links and conservativeness of structures in ecosystems // Methodological Problems in the Evolutionary Theory. Tartu: 22-23 (in Russian).
- Levchenko V.F. (1984b) A physical model of the evolution of biosystems (in Russian). - Zhurn. obshch. biol., 45: 158-163 (in Russian).
- Levchenko V.F. (1988) A physico-ecological model of biospheric evolution. - V. I. Vernadsky and Modern Science. Leningrad: 28-30 (in Russian).
- Levchenko V.F. (1990a) Evolutionary ecology and evolutionary physiology: what do they have in common? - Zhurn. evol. biokhim. fiziol., 26, 4: 342-347 (in Russian).
- Levchenko V.F. (1990b) A physico-ecological concept of biospheric evolution. - Proc. 7th Int. Symp. "Simulation System in Biology and Medicine". Praha: 59-63 (in Russian).
- Levchenko V.F. (1992) Directedness of biological evolution as a consequence of biosphere development. - Zhurn. obshch. biol., 53: 58-70 (in Russian).
- Levchenko V.F. (1993a) Models in the Theory of Biological Evolution. St. Petersburg (in Russian).
- Levchenko V.F. (1993b) The hypothesis of embryosphere as a consequence of the principles of modelling. - Dokl. Ross. Akad. nauk, No. 2, 317-320.
- Levchenko V.F. (1995) Evolution of the biosphere and the origin of life. - Proc. Int. Symp. "Ecosystem Evolution". Moscow: 52-53.
- Levchenko V.F. & V.V. Menshutkin (1988) Simulation of macroevolutionary process. - Zhurn. evol. biokhim. fiziol., 23, 5: 668-673 (in Russian).
- Levchenko V.F. & Ya. I. Starobogatov, (1986a) Two aspects of the evolution of life: physical and biological. - Physics: Problems, History, Persons. Leningrad: 102-142 (in Russian).
- Levchenko V.F. & Ya.I. Starobogatov Ya.I. (1986b) Evolution of ecosystems and global ecological catastrophes. - Important Biotic Events in the History of Earth. Tallin: 44-45 (in Russian).
- Levchenko V.F. & Ya.I. Starobogatov (1990) Successional changes and the evolution of ecosystem (some problems of evolutionary ecology). - Zhurn. obshch. biol., 51: 619-631 (in Russian).
- Levchenko V.F. & Ya.I. Starobogatov (1994) Autoregulation in the evolution of the biosphere. - Biodiversity Dynamics with Time and Space. St. Petersburg: 30-32 (in Russian).
- Levchenko V.F. & Ya.I. Starobogatov (1995) Factors of the diversity formation of subspecific taxa. - Proc. Workshop "The Factors of Taxonomic and Biochorological Diversity". St. Petersburg: 43 (in Russian).
- Lima de Faria A. (1988) Evolution without Selection: Form and Function by Autoevolution. Elsevier: Amsterdam, New York.
- Odum E.P. (1959) Fundamentals of Ecology. W.B. Saunders Co.: Philadelphia & London.
- Odum E.P. (1986) Ecology. Moscow (Russian translation).
- Razumovsky S.M. (1981) Patterns in the Dynamics of Biocenoses. Moscow (in Russian).
- Ronov A.B. (1976) Volcanism, carbonate accumulation, life. - Gheokhimiya, 8: 1252-1277 (in Russian).
- Schindewolf O.H. (1950) Grundfragen der Palaontologie. Stuttgart.
- Simpson G.G. (1944) Tempo and Mode in Evolution. Columbia University Press: New York.

- Starobogatov Ya.I. (1984) Ecosystem evolution. - Methodological Problems in the Evolutionary Theory. Tartu: 70-72 (in Russian).
- Starobogatov Ya.I. (1985) The Problem of Speciation. - Results from Science and Technology. General Geology. Moscow, vol. 20 (in Russian).
- Starobogatov Ya.I. (1987) Causes for the particulars of macroevolution. - Towards a New Synthesis in Evolutionary Biology. Praha: 214-216.
- Starobogatov Ya.I. (1988) On the correlation between micro- and macroevolution. - Darwinism, History and Present State. Leningrad: 138-145 (in Russian).
- Starobogatov Ya.I. & V.F. Levchenko (1993) An ecocentric concept of macroevolution. - Zhurn. obshch. biol., 54, 4: 389-407 (in Russian).
- Vernadsky V.I (1986) The Biosphere. - Selected works. "Nauka" Publ.: Moscow, vol. 5 (in Russian).
- Zavadsky K.M. & E.I. Kolchinsky (1977) The Evolution of Evolution. "Nauka" Publ.: Leningrad (in Russian).
- Zherikhin V.V. (1987) A biocenotic regulation of evolution. - Paleont. zhurn., 1: 3-12 (in Russian).
- Zherikhin V.V. & A.P. Rasnitsyn (1980) A biocenotic regulation of evolutionary processes. - Macro- and Microevolution. Tartu: 77-81 (in Russian).
- Zherikhin V.V. (1995) Towards a general theory of community evolution. Proc. Int. Symp. "Ecosystem Evolution". Moscow: 48.