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THE RUSSIAN PARADIGM IN ECOLOGY AND EVOLUTIONARY BIOLOGY: *PRO ET CONTRA*

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Abstract. A peculiar outlook propagated by ecologists and evolutionists was formed in countries of the former Soviet camp over approximately half a century. Its roots can be traced to the microbiologist Winogradsky and the biogeochemist Vernadsky's ideas. The basic theses of this outlook are as follows: life can exist only in the form of a nutrient cycle (=ecosystem); ecosystems are organised systems; the emergence of life on earth was inevitably accompanied by the appearance of the first nutrient cycles; besides species evolution, there exists one more quite independent evolutionary lineage – the evolution of ecosystems which proceeds through individual selection, its direction being predetermined by an ecological community. This system of views was termed the Russian paradigm by Zavarzin in one of his publications in juxtaposition with the Western one, which in his estimation is reductionist and analytical. In this article, I attempt to highlight the Russian paradigm and compare it with the prevailing modern views of Western ecologists and evolutionists as well as with those held in times when the ecosystem conception was all the rage. Works by most of the Russian paradigm advocates convey rather a controversial impression. On the one hand, there is no doubt that the basic theses of this paradigm have an objective basis and that sooner or later Western ecologists and evolutionists will have to acknowledge their principled correctness. On the other hand, these theses and their particular content can be treated only as an outlook, some kind of natural philosophy. It lacks both more rigid formulations and more definite methodological guidelines capacitating scientists to reconstruct the main stages of ecosystem evolution and explain its mechanisms. If present-day Western biology is characterised by somewhat excessive positivism and scientism, its Russian counterpart surely shows their deficit.
Key words: ecology, evolutionary biology, paradigm, ecosystem evolution

Introduction

It is common knowledge that the former USSR was in many respects isolated from the rest of the world. No wonder that in the long run there were specific biological ideas and conceptions formed there. I mean not only the famous lysenkism, but also many other doctrines that have received lesser attention. One of the doctrines that exerted extremely great influence on the development of both ecological and evolutionary thought in this region was Vernadsky's (1926) conception of the biosphere. Although Vernadsky's ideas were well-known and properly evaluated by some Western ecologists (Hutchinson 1970; Odum 1971), they were not so widespread among them as they were in the former Soviet Union. In this country, there are still many people who are convinced that conceptions of this Russian genius should form a basis for the development of a new evolutionary theory: a theory of ecosystem evolution. This heritage of Soviet science was termed the Russian paradigm by Zavarzin (1995), an academician of the Russian Academy of Sciences. In Zavarzin's opinion, this paradigm is much more productive than the Western one, which, according to him, is already exhausted and can no longer yield any new principled solutions.

The aim of this article is to review the essential peculiarities of the Russian paradigm and evaluate it within the context of current problems of ecology and evolutionary biology. I will confine myself to giving an appraisal only of some theses, which I have singled out as essential in this paradigm. Here are some of them: it is necessary to synthesise Darwinism and Vernadsky's ideas; biocenosis and biogeocenosis should be the main objects of ecology and evolutionary biology; life can exist only in the form of a nutrient cycle; biogeocenoses (nutrient cycles) must have come into existence concurrently with the emergence of life on earth; elucidation of the course and mechanisms of the evolution of biocenoses and ecosystems should be the prime target for evolutionists in this phase. I think that world-view attitudes inherent in the Russian paradigm are valuable and could undoubtedly positively contribute to the development of a new doctrine of general biology that would better correspond to the present-day science level. On the other hand, achievements of Western scientists in ecology and evolutionary theory should not be depreciated either, as most of them not only do not contradict, but rather complement the Eastern platform. I will attempt to collate both paradigms and prove that their current dissociation is not beneficial to either of them. I hope that Western specialists will find this article interesting, as nearly all publications by 'Russians' (representatives of the former Soviet camp, to be exact) urging that Darwinism and Vernadsky's teaching should be integrated and attempting to put this idea into practice are released in Russian. In my opinion, it is worthwhile for Western researchers to get acquainted with a slightly different and unusual for them way of doing science and its results. In one of my latest articles published in Russian (Lekevičius 2003), I touched upon the Russian paradigm. However, I am convinced that this topic deserves a separate publication dedicated solely to it.

Is it only an ecosystem that is living?

In Zavarzin's (1995, 1997, 2000) opinion, the origins of the Russian tradition in ecology and evolutionary biology go back to the 19th century, i.e. to the works by the world-famous microbiologist Winogradsky (1856–1953). In his speech, delivered to members of the Imperial Institute of Experimental Medicine in 1896 (Winogradsky 1996; this report was immediately translated into several languages and released as a separate brochure), he proved the idea that long-term existence of life is impossible without microorganisms decomposing inanimate organic matter. In their absence, organic waste would accumulate and plants producing organic matter would soon suffer a shortage of carbon, nitrogen and other substances. As a result of this shortage, they would perish. This would inevitably lead to death of all living beings. The balance between synthesis and decomposition, the process that is opposite to it, must exist in nature. Existence of life is unthinkable without a nutrient cycle. Animate matter is 'the single entity, a gigantic organism'. In his speech, Winogradsky refers to analogous Pasteur's ideas expounded even earlier.

However, Winogradsky's influence on the further development of ecological thought in the Soviet Union was not so significant. One of the possible reasons for that was the fact that in 1922 he migrated to France, where he worked as a department head at the Pasteur Institute till his very death in 1953. Activities of another Russian genius, the biogeochemist Vernadsky (1863–1945) were of much greater importance for the further course of events. The Western scientific community knows him as the creator of the conception of the biosphere. He was the first in science history to ground the idea that life is an extremely powerful geological force which has dramatically transformed the atmosphere, hydrosphere and the lithosphere. In this article, I want to emphasise that Vernadsky (1931, 1940) furthered the viewpoint taken by Winogradsky: life can exist only in the form of a biocenosis, therefore the birth of life on earth must have been accompanied by the emergence of communities and nutrient cycles. Vernadsky seems (Ghilarov 1995) to have been well acquainted with ideas of the outstanding advocates of holism George de Buffon (1707–1788) and Alexander von Humboldt (1769–1859). What is more, he is likely to have followed Humboldt's credo: 'nothing can be considered in isolation'.

Several decades after Vernadsky's death in 1945, the scientist acquired the status of almost a cult figure in the Soviet Union. His name was referred to and his ideas were quoted both in relevant and in irrelevant contexts. To quote Ghilarov (1995), 'this practice can be partly explained, however, by the normative character of Soviet science, and the long tradition of quoting the 'classics' for support of any statement'. It is no wonder that works by this scholar are still thoroughly studied and highly rated in Russia.

The idea that long-term existence of life is possible only in the form of a nutrient cycle or biogeocenosis was discussed in detail after Vernadsky's death and in principle it was approved (e.g. Beklemishev 1964; Kamshilov 1966; Zavarzin 1979). Russian ecologists seem to be still supporting this viewpoint (Zavarzin 1995, 1997, 2000). In this context, the idea that nutrient cycles and biogeocenoses must have come into existence almost concurrently with the origination of life on earth seems logical to many of them.

The evolution of ecosystems in the 'Russian' paradigm

The idea of the possibility of synthesising Darwinism and Vernadsky's teaching received a favourable response not only from Soviet ecologists, which is quite understandable, but also from evolutionists. This can be explained by a number of reasons, one of which is that the Soviet Union, in contrast to Western countries, has never boasted a great number of evolutionists prone to treat evolution as a variance of gene frequencies in populations. Having rejected the Western approach to evolution, 'Russian' scientists seemed to have assumed the duty of developing, as a counterbalance, a theory of their own which ought to be based on a national idea. Winogradsky and Vernadsky's scientific heritage seemed to serve this purpose ideally.

Especially critical evaluation of the population genetics contribution to evolutionary biology was made by Shmalhauzen (1969), one of the leading Soviet authorities on evolution. He treated the version proposed by geneticists as a misrepresentation of real evolutionary processes, their caricature and urged scientists to return back to Darwin, to his primary postulates, the veracity of which was, in his opinion, indisputably proved through the efforts of biologists of several generations. Darwinism needs supplementation, but not radical revisioning. The theory of biocenotic evolution should be one of such supplements. It should be added, that Shmalhauzen did great work in an attempt to formulate this theory (see further).

Researchers of subsequent generations seem to have been doing their best to emphasise the singularity of the Soviet school in evolutionary biology. That is what, for example, one of the most popular in its day evolutionary biology textbooks says (Yablokov & Yusuphov 1981, p. 31):

'We happen to be eye witnesses to a new process currently taking place: the synthesis of microevolutionary teaching, biogeocenology, ecology and population biology which is expected to result in establishing *regularities in biogeocenotic evolution* ((italicized by authors) (…). For the time being this chapter on evolutionary biology is not ready. Its preparation is of vital importance for the further development of the evolutionary theory.'

Vernadsky himself paid comparatively little attention to the biocenotic evolution and change of ecosystem (and of all the biosphere) parameters. His numerous disciples set themselves the task of investigating this sphere. For instance, Wilyams (1950), Perelman (1961), Kuznetsov *et al*. (1962), Kovalsky (1963a), Ronov (1964), Kamshilov (1966), Vologdin (1976) and Zavarzin (1984) discussed some stages of the nutrient cycle evolution and arrived at a common conclusion that at the dawn of life these cycles were much simpler and differed from the present ones. They changed becoming more and more complex and global, their impact on the atmosphere, hydrosphere and the lithosphere increasing. Most Soviet researchers, not only the ones referred hitherto, concluded that the evolution of nutrient cycles was accompanied by some undoubtedly progressive in their essence changes in parameters, the most often mentioned of which are the increase in solar energy use efficiency, biosphere biomass and productivity of biogeocenoses, the constant growth of species diversity (see reviews: Chernov 1983 and Kolchinsky 1990).

Generally speaking, these investigations (with rare exceptions) could not boast the rigour of notions and postulates, specific to Western science, or methods which could dispel all doubts about the veracity of conclusions. That is partially understandable, for in those times, just as nowadays, there was a profound lack of fossil material to illustrate certain changes in nutrient cycles as well as reasons behind them. Scientists investigating these problems had only two options: to find such ecosystems among the present-day ones, which within the range of reliability could be treated as analogues of the past ecosystems, and study them or resort to the deductive method. The majority of scientists took the first option (Kolchinsky 1990), although, it seems, there was a great number of researchers who disregarded the scientific method altogether and relied on intuition, not bothering their heads about the validity of conclusions or the possibility of falsification. In the former USSR speculations of this type and 'philosophising' were not treated as an occupation unworthy of a scientist.

Another group of Soviet scientists were busy searching for mechanisms of the ecosystem evolution. As far back as 1946, Shmalhauzen (1968) wrote that the biogeocenosis steers the evolution of the species constituting it. A reversible process takes place as well: selected phenotypes affect the entire biogeocenosis, which in its own turn changes the direction of selection. In other words, coexisting species canalise each other's evolution in the simplest way of (mutual) interaction. Species have to adapt not only to one another, but also to the abiotic environment, which is also constantly changing under the action of organisms. Stabilising selection operates at an ecosystem level also: co-adaptation and adaptation to the abiotic environment being accomplished, the community sustains the established phenotypic arrays rejecting all deviations from the 'norm'. Disturbed balance stimulates the evolution of species, owing to which the former organisation of the biocenosis is restored in some time.

A galaxy of outstanding soviet paleontologists seems to have been interested in Vernadsky's holistic teaching on the biosphere. Some of them were working a short time ago or are still working at the Institute of Paleontology, Moscow. They are: V. V. Zherikhin, A. S. Rautian, A. P. Rasnitsyn, A. G. Ponomarenko, V. A. Krasilov, A.V. Markov (www.macroevolution.narod.ru/syngenesis.htm). Not only do they attempt to reconstruct ecosystems of the past, but they also show an interest in mechanisms of the evolution of ecosystems and the biosphere. There being no possibility of reviewing works of all of them here, I will confine myself only to some of them. For instance, Zherikhin (1978, 1979, 1987) and Rautian (Rautian & Zherikhin 1997) devised the model of ecosystem evolution the essence of which could be outlined in the following way. Neither from functional nor from evolutionary aspects are co-existing species self-sufficient. Their lack of self-sufficiency is especially apparent in climax communities saturated with species. Rates of species evolution in such communities decrease hundreds of times due to stabilising selection, although evolution potency remains unchanged, mutagenesis and recombinations do not disappear. This stagnation may last for millions of years, until it is interrupted by some external forces (e.g. meteorite) or events of inner character. The first case often results in the extinction of species and the appearance of vacant niches, which are occupied after a comparatively fast diversification. The second case is related to the emergence of successful evolutionary innovation via inherited variability. Mutants (recombinants) proliferate withdrawing part of older forms from their niches until relative peace sets in. The latter (peace) should not be understood as the absence of evolution: a slow process of niche comminution and the conquest of utterly new adaptive zones may be taking place.

Basing on my model of 'cascade selection' (Lekevičius 1986) I conclude that only two main evolutionary lineages exist: the evolution of species and ecosystems. The existence of the latter is predetermined by the fact that none species has ever been or is self-sufficient from the viewpoint of functioning. Hence, a separate species cannot be self-sufficient in its evolution either. Life is a hierarchy of functions, encompassing even ecosystem parameters, the most significant of which are those which define the characteristics of a local nutrient cycle and the energy flow accompanying it. The mechanism of both species and ecosystem evolution is the same in essence: individual (Darwinian) selection. The only difference between them is that in the first case the role of selection is performed by constraints which are internal with respect to an individual and a population and by the abiotic environment, while in the second case, by biocenotic or ecosystem constraints which emerge as a result of (mutual) interaction among species within the same community. The gradually strengthening new genetic information crosses the barriers of internal selection, then those of intrapopulation selection and finally, in case of good fortune, selection at a community and ecosystem level. When life conquers the theretofore uninhabited adaptive zone, the first settlers, producers as a rule, create vacant niches for the future detritivores and herbivores, and these, in their own turn, for primary predators and etc. until nutrient cycles and ecological pyramids emerge. The fact of the evolutionary convergence of local nutrient cycles and production (energy) pyramids shows that assembly rules of ecosystems are rather invariant in character. Evolution and the course of ecological succession are likely to be governed by the same rules (Lekevičius 1986, 2002, 2003).

According to Zavarzin (1993, 1999, 2000), each biocenosis restricts the evolution of the species it comprises in such a way that the established trophic links and the local nutrient cycle are not broken. The well known phenomenon of convergent evolution, i.e. the development of similar characteristics in organisms of different origin due to similar functions performed with regard to the ecosystem, illustrates guite severe constraints at the biocenosis level. It might seem that migration and evolution can produce any combinations of species – biocenoses, yet in real life we can observe only such combinations which functionally are surprisingly alike: the same cycles and similar trophic pyramids exist everywhere. The biocenosis does not select species as such because the origin of species is not relevant to it. All that matters is the function performed by them. This author states that it is the emergence of vacant niches that initiates the evolution of ecosystems which is accomplished when niches are occupied.

Although the contribution of Soviet authors to this field is really great, it is impossible to mention works of many other 'Russian' scientists. Therefore I will present only the general conclusion, which I came to on getting acquainted with them. It seems possible to assert that the issue of mechanisms of ecosystem evolution does not excite much controversy. Nearly all specialists support the view that an individual is to be treated as the principal unit of selection. Hence, Darwin's theory is not incorrect, but it is rather incomplete in the sense that it says nothing about how ecological communities and nutrient cycles are formed and how these structures evolve. There is no doubt at all that self-organisation, i.e. specific functional constraints, is typical of biocenoses. It must be these constraints that play the role of selection which directs the evolution of individuals and species. The task of the future evolutionary biology is to investigate the nature of these constraints.

The Western paradigm in the context of the 'Russian' one

The 'Russian' paradigm originated from the formula 'life can exist only in the form of a nutrient cycle'. Hence, in the beginning, it is expedient to clarify what real and alleged opponents of 'Russians' think about this issue.

The famous specialist in theoretical biology Pattee (1968) wrote:

'There is no living unit which can be considered 'living' without reference to the external environment (...). Biologists should emphasise over and over that 'living' is unavoidably a total ecosystem property and not the property of an isolated collection of macromolecules. It seems to me that the central question of the origin of life is not, 'which comes first, DNA or proteins?', but rather 'what is the simplest possible ecosystem?'.

Some other theorists were of the similar opinion. For instance, Morowitz (1968, 1992) is convinced that the existence of life without a nutrient cycle would be extremely short-termed, as decomposition of inanimate matter is of no less importance for life than biosynthesis. Therefore, even the so-called autotrophs are not self-sufficient from the functional viewpoint. Hence, a nutrient cycle is an indispensable attribute of life. Ulanowicz (1986, p. 61) also believes that separate organisms and species are merely participants in a nutrient cycle which guarantees the long-term existence of all organisms. Thus, their fitness depends on their contribution to the maintenance of the whole ecosystem.

'Darwinists are always speaking of fitness for environment. The biogeochemical cycles in which every living being partcipates are most assuredly a part of any creature's environment. If it were possible to quantify the autonomous attributes of communities, then one's understanding of fitness would markedly improve'.

Undoubtedly, the idea to correlate fitness of an individual or a genotype with a nutrient cycle is not traditional and, as it seems, has no supporters among the advocates of the current version of evolutionary biology prevailing in Western countries.

The idea of a nutrient cycle as an indispensable attribute of life can be easily traced in the conception of the ecosystem (Odum 1971). According to it, all life on earth is organised into self-contained entities, i.e. local ecosystems, in which plants, animals and microorganisms are united by the common result of their activity (a nutrient cycle and the energy flow accompanying it) into one system. None species is self-sufficient from the long-term functioning viewpoint, a nutrient cycle being an indispensable guarantor for the existence of each of them... According to the creators of this conception, autonomous in the full sense of the word is only the global ecosystem or the biosphere.

The ecosystem and the biosphere were treated as the principal objects of ecology by Odum (1971). He even wrote (Ibidem, p. 3) that ecology is 'the study of structure and function of nature'. Such globality can be traced to the holistic approach which is peculiar to the creators of this conception. Adherents of this approach urge scientists to stick to the principle of universal cohesion when dealing with natural phenomena. Odum and his supporters preached down reductionist methodology and recommendations to investigate natural phenomena in isolation. In their opinion, it is impossible because of functional interdependence among separate species.

According to Odum and his supporters, the ecosystem is an organised system capable of self-regulation and self-organisation. These properties of the ecosystem manifest themselves not only through homeostasis at the ecosystem level, but also through the capability of an ecological community to find optimal and suboptimal solutions in the course of succession (developmental 'strategies' – Odum 1969).

In Odum's opinion, these 'strategies' are common for both succession and ecosystem evolution (Ibidem, p. 262):

'In a word the 'strategy' of succession as a short-term process is basically the same as in the 'strategy' of long-term evolutionary development at the biosphere – namely, increased control of, or homeostasis with, the physical environment in the sense of achieving maximum protection from its perturbations'.

Hence, although the formula 'only an ecosystem is living' was not emphasised by the creators of the ecosystem conception and it was not clearly formulated, this idea did exist. In conclusion, it is possible to assert that the Russian paradigm found influential supporters and advocates among the creators of the ecosystem conception. It was by no accident that at the time of reference Vernadsky was 'rediscovered' in the West (Hutchinson 1970; Odum 1971).

However, the domination of the holistic approach in Western ecology was not long-lasting. Upon the termination of the International Biological Programme (IBP) in 1974, the belief that in reality ecosystems exist as discrete structures, was gradually replaced by the opinion that an ecosystem approach is merely a methodological tool, neither better nor worse than others (Golley 1993). The view that ecosystems and the biosphere can be treated as some kind of an integral organism, that transforms and accumulates energy and substances, also lost a great part of its supporters. Holism and synthesis gradually gave way to reductionism and an analytical approach. In ecology this change meant a transition from ecosystems to populations as the main object of ecological research (Krebs 1972). All conclusions having at least something in common with holism, i.e. that life can exist only in the form of a nutrient cycle; that species fulfil certain functions with respect to a nutrient cycle; that all ecosystems become functionally alike (which shows that forces controlling succession and evolution are invariant); that functional interdependence at the ecosystem level generates the evolutionary dependence of species etc. were excluded from the new ecology arsenal as ungrounded or unverified speculations. This outspokenly analytical and anti-holistic view is still prevalent in Western science (Brown 1997; Looijen 1998; Ghilarov 2001; Murray 2001; Mittwollen 2002; Swihart *et al*. 2002).

Strategic aims of ecology and ecologists seem to have undergone dramatic changes over the last 30–40 years in the West: previously ecological research attempted at discovering universal ecological laws, later the focus shifted towards the search for ecological patterns, whereas presently the so called mechanistic approach, i.e. attempts to establish mechanisms which result in certain patterns, is all the rage (Murray 2001; Ghilarov 2001; Swihart *et al*. 2002). In E. Odum and his colleagues' opinion, universal laws were expected to be of service to synthesis, creation of the comprehensive theory of ecology. However, present-day Western ecologists not only do not search for such laws, but, it seems, they do not believe that they will ever be discovered (Murray 2001; Ghilarov 2001). According to the first of these authors, at present Western science boasts an abundance of researchers, who tend to diversify the view of the world ('diversifiers'), the number of scientists, who would like and would be able to unify it ('unifiers'), being very small.

All that sets the Western paradigm far apart from the Russian one, which is infested with ideas of synthesis. It is true, that 20–30 years ago a great many of Soviet ecologists and evolutionists (the author of these lines including) optimistically believed that the sought-after universal laws and the comprehensive theory would be discovered in the near future. Today, however, this optimism has abated. The logical simplification of the world and theorisation turned out to be by far a more complicated task than it had been initially expected. One cannot help but wonder that the number of 'unifiers' on the territory of the former USSR is still comparatively great.

Not only holism, but also the understanding that the most fundamental attributes of life are to be searched for at the ecosystem level, in a nutrient cycle, is alien to Western ecologists of the younger generation. As Zavarzin (1995) implies, the refusal by Western ecology to give a nutrient cycle its appropriate status has an adverse effect on the former. These Zavarzin's conclusions should be understood in the following way: Western ecologists of the younger generation do not seem to be clearly asserting that life can exist without detritivores (i.e. without a nutrient cycle), they are not inclined to discuss this issue altogether. Neither do they consider the fact, which in Zavarzin's opinion is bare, that there is an obligatory interdependence or mutualism between producers and detritivores, which is an essential, vitally significant property, and therefore this fact has to be validated as a universal biological law, that will have far-reaching consequences for the would-be theory of biology and evolution.

Yet, even in recent years some of the publications appearing in Western ecological press can be called relics, as their authors adhere to emphatically holistic views. Studies by Fiscus (2001, 2002, see also http://www.calresco.org/fiscus/esl.htm) and Wilkinson (1998, 2003) may be taken as examples of such publications. The first author submits 'the ecosystemic life hypothesis' for public discussion. He is inclined to juxtapose this theory with the dominant in the West 'organismic life hypothesis'. The author believes that his approach to the origin of life and evolution can break the deadlock at which contemporary theoretical biology and ecology are, in his opinion. He states that life can exist for an indefinitely long time only in the form of an ecosystem (a nutrient cycle), which requires two groups of organisms at least – composers (autotrophs) and decomposers. The first group of organisms synthesises organic substances from the inorganic ones, whereas another decomposes organic compounds and returns original substances back to the cycle. Therefore, none of these groups is functionally self-sufficient. Hence, life is symbiosis and interdependence of organisms. In such a form of a nutrient cycle life has existed since its origination on earth. Here the author refers to H. T. Odum's (1970) conceptual model, according to which the separation of production and consumption functions took place before the emergence of life itself (sic!). However, Fiscus seems to know nothing about the representatives of the Russian paradigm and their works.

Another author referred to above Wilkinson (1998) points to photosynthesis and decomposition, i.e. a nutrient cycle, as the most significant ecological processes deserving attention of the majority of ecologists. The analysis of publications by Western ecologists performed by this author shows that their attention, however, is focused on some aspects of ecology of plants and animals, few scientists showing an interest in organisms that ensure a sustained nutrient cycle (fungi, protists and bacteria). In his further publication Wilkinson (2003) is already more categoric. He submits, in my opinion, rather logical arguments to prove that life, in whatever part of the universe it exists, assumes the form of a nutrient cycle because it is only a nutrient cycle that ensures the long-lasting existence of life. At least two guilds are necessary to form a nutrient cycle: autotrophs and decomposers. In the absence of the latter, the substances necessary for biosynthesis would sooner or later come short and autotrophs would perish, the same fate befalling heterotrophs later. (Here the author invokes deductive logics, a thought experiment, because, according to him, no correct crucial experiments have been performed to verify these speculations). A nutrient cycle must have originated on earth almost concurrently with life, both guilds developing and transforming the inanimate environment in their co-evolution.

The position of this author does not differ essentially from what Zavarzin calls the Russian paradigm in ecology. In fact, an attentive reader may notice that Wilkinson's formulations are clearer and he puts forward a greater number of logical and empirical arguments in support of his conclusions. However, Wilkinson (2003) does not refer to any author, be it a Westerner or a 'Russian', who has prior to him asserted that life cannot exist without a nutrient cycle. Such a perfunctory attitude towards the prehistory of the problem causes surprise, having in mind not so outdated views of brothers Odums and their congenial colleagues. But he is, undoubtedly, right to say, that his outlook is unconventional in the context of the contemporary Western theory of ecology and evolution. I would like to add the following to these Wilkinson's conclusions: it must be clear why the formula 'it is only an ecosystem that is living' originated in the Soviet Union, not anywhere else. The level of microbiology has always been very high there: it did not concede to that in Western countries. What is more, Soviet microbiologists seem to have been participating in theoretical disputes over issues of general biology, about ecology and evolution, in particular, more actively than their Western colleagues. Zavarzin might be an exponent of such activity: qualified as a biologist, he was an ecologist and an evolutionist by vocation. When speaking about his influence on public opinion, one should not forget that he was backed by two more leading authorities Winogradsky and Vernadsky. It seems that microbiologists in Western countries were forced to do with a somewhat different status. The famous microbiologists Atlas and Bartha (1998) write that in contemporary textbooks on general ecology the Western reader can find ample material on animal and plant ecology and by far less on the ecology of microorganisms. Microbiologists, as a rule, do not take part in the compilation of these textbooks, as they are debarred from this process. One of the reasons behind it is that previously microbiologists did not impose their will in ecology either. What is more, they employ slightly different methodology and up till now they are prone to treat a nutrient cycle as a fundamental process, without which life could hardly exist. In their opinion, decomposition of inanimate matter is an ecosystemic process not inferior to photosynthesis in significance. Even their viewpoint on inter-species relations and the self-regulation of populations is 'Odum-like' up to this day: they assert that competitors and consumers play a positive rather than a negative role in communities.

The evolution of ecological communities and the biosphere: a Western approach

Let us try to throw some light on the Western viewpoint on the evolution of communities and ecosystems, the topic so vigorously upheld in the East. Proponents of the ecosystem conception tried getting to the heart of evolutionary problems by themselves (Hutchinson 1970; Odum 1971; Patten 1975; Richardson 1977). In their opinion, it is not only species that evolve, but also ecosystems and their parameters. In the course of evolution not only nutrient cycles, but also the structure of communities undergoes changes. Ecological communities evolve together with the inanimate environment, adapting to it and thereby changing it. While evolving life exerts a greater and greater impact on the atmosphere, hydrosphere and the lithosphere. As to mechanisms of such evolution, these authors mainly focused on the so called group selection and coevolution, maintaining that individual or the Darwinian selection also takes place in the ecosystem evolution.

One more conception directly related to mechanisms of the ecosystem evolution emerged almost concurrently with the formulation of the ecosystem conception. I bear in mind the idea of coevolution (Ehrlich & Raven 1964), which later turned into a universally recognised theory. This theory sprang up from the investigation into interrelations between flowering plants and herbivorous insects. The gist of this theory is explained in the following way. Almost all plants synthesise chemical substances, the so-called secondary compounds, which make plants inedible or nearly inedible. There may exist hundreds of thousands of such compounds in nature. But herbivores are adapted to these substances. Each species of herbivores feeds on particular plant species whose secondary compounds are not dangerous to it. That is the outcome of the long-lasting coevolution of plants and herbivores. According to Ehrlich and Raven, the process of coevolution starts with mutation or recombination of plants due to which they start synthesising a new secondary compound. Insects hitherto feeding on these plants lose part of their food resource, as it becomes not palatable. Meanwhile, plants get into a new adaptive zone, thus getting a chance of spreading and diversifying freely. That is followed by adaptive radiation, in the course of which the initially single mutation or recombination turns into an attribute of a group of species. However, herbivores also react to the newly arisen situation, as they also mutate and recombine. Thus, after some time, variants capable of overcoming defence barriers of the new plants emerge in their populations. Maintained by selection, these variants spread fast, a new wave of adaptive radiation (this time in insect populations) starting. This wave ebbs away only when the whole adaptive zone is occupied, i.e. when all plant species acquire their specific herbivores. In such a way, the growing plant diversity stimulates the increase of biodiversty at the level of herbivores, the reversible positive impact being also probable. In the authors' opinion, coevolution is a widespread phenomenon: not only plants and herbivores consuming them, but also prey and predators, hosts and their parasites coevolve. It is possible to assert that all organisms of the local community: plants, animals and microorganisms are adjusted to one another as a result of the long-running coevolution.

The concept of the ecosystem advocated by Odum and his supporters has, undoubtedly, impacted on the development of the coevolution theory, the reversible impact being recorded also (Odum 1971; Patten 1975). The latter author treats ecosystems merely as 'coevolutionary units'.

It is obvious that coevolution breeds coadaptation. But in what does coadaptation manifest itself? Advocates of this conception are prone to think that coevolution means not only an acquisition of consumers, but also a subtler adjustment between the exploiter and the exploitee, which is achieved through selection, prompting moderate consumption. It is understandable, as in the end the ruthless exploiter punishes himself. Hence, the assumption that there must exist a negative feedback stabilising these systems seems reasonable. Such a mechanism (or maybe only one of them) seems to have been really detected (Pimentel 1968). The author investigated it thoroughly by experiment and termed it genetic feedback.

The concept of coevolution is quite well supplemented by the model of adaptive radiation which was developed by Stanley (1973). Presently this model is unjustifiably forgotten. According to Stanley, only autotrophs (mainly blue-green bacteria and later unicellular algae) and detritophages existed throughout nearly all the Precambrian, herbivores and predators still not existent. Hence, there were vacant niches, which in this particular case can be treated as unexploited biomass. Sooner or later this situation was to bring about the emergence of consumers of this resource. These must have been flagellates, the ranks of which were later joined by the first multicellular filtering animals. In their own turn, the latter formed a vacant adaptive zone open to the would-be predators. Finally, other trophic levels made their first appearance in the Cambrian in a similar manner, one group of organisms inducing the evolution of the other ones. The emergence of higher trophic levels stimulated the diversification at lower levels even more (here Stanley refers to Paine's experiments with a community of benthic invertebrates, that are well known to ecologists). According to the author, this process was rather rapid, as a 'self-propagating mutual feedback system of diversification between trophic levels' was formed. All vacant niches having been occupied, the work of this system was suspended, evolution decelerating.

Boucot's (1978) observations about conditions predetermining the rate of evolution were similar. According to him, evolution proceeds rather rapidly until communities get saturated with species. However, the assembly of communities being accomplished, directional selection turns into the stabilising one and evolution slows down considerably. New species can set in only by supplanting those that are older from the evolutionary viewpoint.

The theory of coevolution does not envisage any other form of selection but the individual or the Darwinian one. Group selection can be referred to only when coevolution leads to the obligatory interdependence of species (rigid mutualism) and species join a spatially integral entity. However, according to the definition, such an entity automatically turns into a discrete individual, and thus it is subordinate to the ordinary Darwinian selection.

Hence, it is possible to think that, according to this theory, the interaction of species performs another role, i.e. the role of constraining and directing factors. In other words, the selector's function in the process of selection of individuals is performed by the community, i.e. other species with which the given species has trophic or other relations. It is possible to conclude from the publications of the authors referred to above and those of Valentine (1968), Bock (1972) and Endler (1986) that communities and ecosystems evolve via selection of individuals, there being no other way for their development.

Bock (1972) classifies all forms of interspecies interaction into two main ones: competitive and exploitative interaction. The first one leads to the displacement of part of the forms or divergence, while the second one to coevolution and preservation of all the interactors. The author comprehends selection not as differential survival and analogous reproduction, but rather as selection forces. He searches for them in interspecies interaction first of all. Competition is indispensable for the evolution of communities. Due to it, old and energetically less effective forms are replaced by the new ones, which are capable of using energy resources more effectively.

Another group of researchers was interested not so much in intimate biological mechanisms as in the interaction between life and the inanimate environment in the course of evolution, in the coevolution of biota and the environment (Cloud 1968, 1972, 1974, 1976, 1978; Walker 1977, 1980). These authors were quite well acquainted with works by Odum and his supporters and they applied the ecosystem conception in one way or another when interpreting evolutionary processes. Their investigations yielded conclusions of lasting value, which are still significant. Having no possibility of reviewing all works by these authors, I will mention only some of them. Walker (1980) attempts to reconstruct ecosystems of the past in a truly original way, i.e. using the deductive method. Initially he introduces axioms, the 'guiding principles':

Substances move in cycles;

Nutrient cycles are leaky (part of substances constantly leak from cycles and are conserved);

Satisfied creatures do not change (The author's metaphor implying that organisms are not prone to reclaim new resources unless there is a shortage of substances and energy);

Organisms are greedy (The metaphor implying that organisms are prone to increase their total biomass at any cost).

In the author's opinion, these principles are sufficient to deduce the main stages and mechanisms of the evolution of ecosystem metabolism (nutrient cycles), although conclusions arrived at in such a way will undoubtedly be rough. The author's article surveys the period from the appearance of life and the first nutrient cycle till the emergence of cycles of contemporary type. The paper is furnished with schemes-models. He concludes in the following way: 'Earth's early history may have been characterised by coevolution of microbial metabolism and atmospheric composition. Metabolic developments affected the composition of the atmosphere and the resultant changes in the atmosphere stimulated the evolution of new metabolic capabilities'.

Due to its holistic approach and methods applied, this publication by Walker stood out of other works similar in content. In the course of time, its curiosity seems to have increased even more.

Anti-holistic thinking (not only in ecology) becoming more and more prevalent, the conviction that the ecosystem conception has to be integrated with the theory of evolution grew weaker and weaker. The collection of articles under the editorship of Schopf (1983) devoted to the generalisation of the main achievements in the recostruction of the Precambrian ecosystems seems to have been the last large publication to display holistic spirit. Later paleonthologists and evolutionists returned back to less intricate, as it may seem, topics. It is true, that one can still find publications in the Western scientific press (Behrensmeyr *et al*. 1992) devoted to the analysis of data on the evolution of certain 'ecosystems'. However, these publications, as a rule, do not deal with nutrient cycles, ecological pyramids, functional convergence of ecosystems, interaction between the biosphere and inanimate spheres. As it was possible to anticipate, sooner or later reduction in ecology was to develop into evolutionary biology. And so it did. It seems to me, that, in the West, the term 'ecosystem' has lately developed into a nice metaphor, the original meanings of which are remembered just by a handful of ecologists of the elder generation mainly. Thus, at present the phrase 'the evolution of ecosystems' evokes slightly different associations to Westerners and the creators of the ecosystem conception or the representatives of the Russian paradigm.

And still it would be hardly right to assert that Western evolutionists have abandoned holistic approach for good and all. Diversity of opinions inevitable under the conditions of sufficient liberalism hinders conformism, which seems to have become total. Here I would like to point out two publications which, in my opinion, exceed the borders of what has been defined by Zavarzin as the Western paradigm in the science of evolution. The author of one of them is the already referred to Wilkinson (2003), who argues that a nutrient cycle is the most fundamental ecological process, that, unfortunately, receives too little attention.

In his opnion, the formation of cycles in the geological past was very simple (p. 173):

'Life forms evolved to utilise a wide range of novel resources, lignin, cellulose and petroleum hydrocarbons. If a resource appears in the environment, then it seems organisms will evolve to use it.'

For instance, the Paleozoic saw the appearance of plants that synthesise lignin, but as there were no organisms capable of decomposing the compound for some time, it accumulated in detritus. In the opinion of the author, ligneous plants were on the verge of extinction and were saved from it by lignin-decomposing fungi and bacteria which emerged after some time. In my view, the author's position and the final conclusion about the necessity of a cycle are logically impeccable (substratum appears first and after that enzyme), yet he calls his final conclusions speculations. Surprising fidelity to the Western tradition of doing science! It is even more surprising that he refers to empirical data on the coevolution of ligneous plants and lignin-decomposing fungi generalised by Robinson (1990).

Another publication, which undoubtedly falls out of the contemporary Western context, is the article by Leigh and Vermeij (2002). Both authors (the first one is an evolutionist and the other one a paleonthologist) are renowned as perfect specialists in their fields, therefore their approach cannot be ignored and treated by opponents as an insignificant misdemeanour. In essence, they accept Odum's conception of the ecosystem and propose proceeding even further: in their opinion, functioning and evolution of natural ecosystems are similar to those of capitalistic economic system, or at least to the functioning and evolution of capitalistic economics as imagined by Adam Smith, the outstanding economist-theoretician of the 18th century. This scientist proved the idea that state institutions must not interfere in economics: driven by personal initiative and competition, this economic system controls itself. Dishonest producers and traders punish themselves, as the market of free labour and goods has quite a great number of efficient mechanisms of self-regulation. Leigh and Vermeij believe that in ecosystems, just like in Smith's economics, it is only the governing body that is missing. Hence, individual selection should suffice to ensure the evolution of the ecosystem. Individuals are selected, but it is not only they that evolve: evolution covers the whole ecosystem, its global parameters (productivity, species diversity, etc.). The organisms, which replace weaker competitors, are most probably distinguished for the ability to use energy and material resources more efficiently. As this process is universal and constant, the evolution of species and also of the whole ecosystems is directed towards higher efficiency.

One more trend showed up in the evolutionary biology of the West 30–40 years ago. Its growth seems to have separated the Western paradigm from the Russian one for long. For the representatives of the new trend the fundamental issue was units of selection. By analogy with evolution, that covers not only individual, but also group and even ecosystem parameters, the process of selection is also multilevel, i.e. it also embraces individuals, groups (families, demes, species), communities and even ecosystems. Wynne-Edwards (1962) and Lewontin (1970) were among the first scientists to air such views, which were further developed by Gould (1982, 1998), Wilson and Sober (Wilson 1980; Wilson & Sober 1989; Wilson 1997) and quite a number of other evolutionists (see Keller 1999).

Gould uses the term the hierarchical theory of selection to define his views. In his opinion, Darwin mistakenly thought that natural harmony and species peculiarities are the by-product of selection at individual level. It is sheer and unjustifiable reductionism. It would be more logical to assume that individual traits evolve via individual selection and species characters via species selection. In addition to the hitherto mentioned units of selection, the author distinguishes genes, demes and clades. Wilson and Sober term their conception the multilevel selection theory. Its basic difference from Gould's theory lies in the following: the evolution of ecosystems is impossible without a specific mechanism: selection of communities. Those local communities 'that function well as a unit contribute differentially to the next generation (...). Traits can therefore spread, not by virtue of their advantage within local communities, but by virtue of the advantage that they bestow on their local community, relative to other local communities (...). When natural selection operates at the community level, all of the species in a local community become part of a single interacting system that produce a common phenotype' (Wilson 1997, p. 2020, 2024).

Both Gould, Wilson and Sober resort to various empirical data to ground their ideas, but still most Western evolutionists seem to doubt the reality of supraindividual selection or believe it to perform only an episodic role in evolution. Whatever the case, these ideas are widely discussed in contemporary scientific and even non-scientific press and they receive more attention than, for instance, coevolution... One of the reasons behind such popularity is that for a long time leastwise Lewontin and Gould have been considered unquestionable leaders of the American school of evolutionists. In this article it is necessary to stress that, to the best of my knowledge, these authors, likewise Wilson and Sober and their numerous disciples, have never attempted to reconstruct past ecosystems or to explain the mechanisms of ecosystem evolution: they have never set themselves such an aim.

Conceptions of between-species and between-communities selection substantially clash with the Russian paradigm in evolutionary biology. As it has been mentioned already, Russian authors are not apt to give up Darwinian positions, they do not find various ideas of supraindividual selection impressive. Meanwhile, coevolution and suchlike conceptions win much stronger approval, as they complement the view created by Russian scholars quite well (Ghilarov 2003).

Discussion

Differences between the two paradigms under discussion can be specified in the following way (Table 1). I would like to warn the reader in advance that to emphasise their contrasts, conclusions presented in the table may be somewhat biased. There are quite a lot of ecologists and evolutionists not only in Western countries but also in the present-day Russia, who do not follow long-established traditions and current conjuncture. Therefore a researcher attempting to marshal such a variety of difficult to classify opinions and conceptions, which is typical of the present-day theory of ecology and evolution, is inevitably doomed to face justifiable criticism.

The above expressed ideas and data presented in this table seem to support Zavarzin's (1995) view that differences existing between the two camps have reached the rank of a paradigm. It can be added that before this divergence, which is not more than 30 years old, the Western paradigm did not differ from the present-day Russian paradigm much. As it is known, in those times fruitful and bilateral exchange of ideas and results took place, grandiose joint projects (I have in mind the International Biological Programme, first of all) were run... Later cooperation between the East and the West declined, divergence of paradigms being one of the possible reasons (or maybe even one of the outcomes). However, most probably there are some sounder rea-

Table 1. Comparison of the Russian and the present-day Western paradigms in ecology and evolutionary biology.

Approach to...	Russian paradigm	Western paradigm
ecosystems	Ecosystems are organised systems; they must be the main object of ecology and evolutionary theory. It is only an ecosystem that is living (holism).	Ecosystems are not organised systems. Only a population can be the main object of ecology and evolutionary theory. Life is an attribute of separate individuals and species (partism).
universal laws and possibilities of developing a unified theory	There are universal ecological and evolutionary regularities; the construction of a unified theory can and should be started immediately.	The existence of universal ecological and evolutionary regularities is problematic; for the meantime the construction of a unified theory is an unreal prospect.
origin of life	The emergence of life on earth was concurrent with that of nutrient cycles.	The issue of the emergence of nutrient cycles should not be correlated with that of life origination.
evolutionary lineages	There are two main evolutionary lineages: the evolution of species and that of ecosystems	The main evolutionary lineage is phylogenesis, i.e. the evolution of species. Ecosystems as units do not evolve.
mechanisms of evolution	It is individuals that are selected. The role of selection is performed by constraints of functional character, which emerge in the course of interaction of system's elements.	If species and ecosystems evolve, there must exist selection of entire species and ecosystems. This presumption has not been confirmed yet.
possibility of forecasting evolution	A certain extent of direction is characteristic of evolution. Hence, it is partly predictable.	Evolution has no clear direction. It is unpredictable and coincidence-driven.
investigation methods	Both verbal and conceptual models are acceptable at the present stage of ecology and evolutionary theory. The problem of falsification is overemphasised.	Mathematical methods and experiments should be given preference in ecology and evolutionary theory. One of the basic requirements is the possibility of falsification.

sons behind this approach divergence and non-cooperation. One of them is radically different traditions of scientific methodology: all natural sciences in the West have been saturated with positivism and scientism for a long time, an experiment and/or mathematical modelling being integral parts of any investigation.

In the Soviet Union positivism as a scientific ideology was little known even to scientists, it was not propagated and practised widely. This might be the reason why even nowadays 'Russians' unlike Westerners are less prone to rely on mathematical models in search for truth or why they do not consider extended ratiocination, which Westerners would treat as mere fruitless speculations or in the best case verbal (i.e. shoddy) models, to be unacceptable. The Western scientific tradition requires rigidity and precision wherever it is possible (even a biologist has to reason like an engineer). Any phenomenon, that a researcher takes an interest in, must be studied within the phenomenological context and the context of mechanisms concurrently. Dealing with it in the phenomenological context only means speculating. Every conclusion must be grounded empirically, i.e. on facts, or on theory, i.e. deduced from unambiguously formulated premises. These rules, so natural to Westerners and therefore seldom referred to, may seem to the majority of 'Russian' biologists too strict and restricting the freedom of opinions, associations, methods and fantasy, which is so important to every scientist. Access to Western scientific journals for the majority of 'Russian' authors is not easy partly because of the fact that, in the opinion of Westerners, 'Russians' do science 'not according to the rules'. It is a fact, that some authors, the above mentioned Zavarzin among them, publish their works both in Western and Eastern journals. However, articles, which on crossing the barriers of Western reviewing are published, are distinguished for positivism, whereas this can hardly be said about the articles by the same authors published in their mother-tongue.

'Russians' are less meticulous in doing science. Despite all the problems evoked, this manner of doing science has some advantages. They are especially conspicuous in those fields, which are sometimes referred to as frontier science, i.e. where ignorance preponderates cognizance. The evolution of ecosystems is just the case. Here, even verbal models and 'speculations' come in useful. However, a more rational way out, I think, is qualitative or conceptual modelling, which may be later on supplemented with quantitative or mathematical modelling. There are a few examples of such modelling: it was employed by some investigators of ecosystem evolution. Part of them also followed the deductive method (Walker 1977, 1980; Lekevičius 2002, 2003).

In my opinion, the vulnerable spot of the Russian paradigm in ecology and evolutionary biology is its philosophical rather than constructive character. I am almost sure that sooner or later Westerners will concur with the presumption that life can exist only in the form of a nutrient cycle; that the emergence of life was almost concurrent with that of nutrient cycles; that ecosystems should be the main object of ecology; that the evolution of ecosystems is the main object of evolutionary biology at the present stage. But are the existing differences in approach to the world well worth such efforts? In my opinion, these general in character ideas owing their origin to Vernadsky have been reiterated for too long: it is time they were formulated in a more precise language and were applied, let us say, in the development of new methodology, suitable for the reconstruction of the past ecosystems and on the basis of this methodology the search for new concrete mechanisms was initiated. Regrettably, but it is this work that is not going smoothly. I do not intend to say that since Vernadsky's times nothing has been done, but the results, in my estimation, are rather modest. One of the possible reasons behind such inefficiency is that the majority of authors considering themselves as representatives of the Russian paradigm are not inclined to take an interest in achievements of their Western colleagues, who are carrying out the same work in fact: their works are undeservedly too seldom discussed and even more seldom are used for synthesis. Thus, the baby is thrown out with the bath water. Isolation and segregation of the two paradigms, sometimes arrogance and tendentious contraposition, deliberate veiling of opponents' advantages do not do and probably will never do any good. On the contrary, exchange of ideas would be to advantage of both sides, as both paradigms under discussion have positive elements.

I would distinguish the theory of co-evolution as an undoubtedly positive element from the Western paradigm first of all. In my opinion, this theory is the greatest achievement of Western evolutionists in the second half of the 20th century. At that time it seemed to many scientists (and not devoid of substance) that mechanisms of the evolution of ecosystems would be soon unriddled. An absolutely novel evolutionary doctrine, which was expected to clarify the evolution not only of species, but that of biodiversity and ecosystems also, was in the air. The world of science had expectations that the course or at least the main stages and driving forces of the co-evolution of the biota and the atmosphere, the biota and the hydrosphere and the lithosphere would be soon clarified. It is quite probable that a significant part of evolutionists and ecologists of that time as well as their colleagues in the East lived in similar hopes. Regrettably, these hopes have not come true. And it was not faults of the conception of co-evolution that were to blame for that. The most probable reason behind that was the replacement of holistic thinking by partism and the shift by ecologists and evolutionists to a more detailed investigation of separate species. The investigation of evolution of communities as separate entities was postponed for the future.

As to hierarchical and multilevel approaches (I have in mind works by Lewontin, Gould, Wilson and Sober, first of all), my attitude towards them is dual. On the one hand, these approaches focus our attention on those aspects of evolution, that once were part of Darwinism, even its essence, but later were undeservedly ignored in Neodarwinism. I mean, 'struggle for existence'. This Darwin's conception appealled to external limiting factors, i.e. to evolutionary trends. 'Struggle' being excluded, there was no measure of fitness, dissociated from reproduction, or references to evolutionary development directions left. The theory became an excessively tautological scheme propagating the idea that evolution is just a play of coincidences (Gould 1994; criticism of this approach see e.g. Lekevičius 1986, 2002). Such a turn of the evolutionary thought embodied in population genetics did not receive much approval in the former Soviet Union and increased the gap between the two paradigms even more. The hierarchical and multilevel doctrines propose to take an interest not only in inner mechanisms (genetic variation, developmental constraints, selfish behavior of genes) but also in factors that are external with respect to an individual and a population. The latter may have a not lesser significance for the process of evolution, that of communities and ecosystems in particular. That is quite a rational and substantiated approach. It is true that the proposal of the authors to put demes, species and communities on the list of selection units seems rather doubtful to scientists, not only to the representatives of the Russian paradigm. And if the authors made the system of their propositions more rigid and less confusing, this proposal would raise even more doubts.

I think that the hierarchical/multilevel doctrine loses out because it is dissociated from those theoretical constructs and models, which were worked out by specialists of the general systems theory working in the field of biology (Simon 1962; Mesarovic 1968; Whyte *et al*. 1969; Novoseltsev 1978; Malherbe *et al*. 1979). These authors discussed quite in detail the hierarchy of organisation levels in the animate world both from the viewpoint of structure, function and control. I believe that only upon the elucidation of the functioning mechanism of that grandiose complex, which is called life, we will be able to say something essential about how it could evolve. Unfortunately, Gould, Wilson and Sober, as far as I understand, do not follow this logic and ignore many of the essential features characteristic of the hierarchy of biological systems. Therefore, their doctrine loses a significant part of its potential value. For instance, it is not clear from their doctrine whether there is only the hierarchy of structures or whether there is that of functions and that of control as well. What is more, what is the range of the functional hierarchy? Does it range up to an individual? a population? a community? a nutrient cycle? Our approach to evolutionary mechanisms depends on the answer to these questions: if it turns out that, for instance, the hierarchy of functions and control ranges up to a nutrient cycle, as 'Russians' assert, the conclusion about two evolutionary lineages and not one, as still many scientists in the West maintain, becomes inescapable (Table 1). The whole theory of evolution would automatically and radically change too. The role, that is at present assigned by Westerners (Gould among them) to accidental factors, would also considerably decrease, as any organisation and control are bound up with coordination, i.e. with constraints and forces, which probably may be invariant from the viewpoint of time and space.

In my view, the biological systems theory gives at least preliminary answers to the question about selection units too: individuals are the most likely candidates for the main units of selection because the degree of integration of their subsystems is extremely high, much higher than that characteristic of demes, populations and communities. The hierarchy of functions may be characteristic of the community level also, but in its intensity and the mode of control it is a radically different hierarchy. It allows species not only to compete, but also to accumulate properties beneficial to certain species only. On the other hand, accumulation of such ('selfish') properties is possible, although to a lesser degree, at subindividual levels, meiotic drive and 'selfish' DNA phenomena testifying to that. The originator of such an approach to selection units was Rosen (1967; see also Lekevičius 1986).

Among Western ecologists and evolutionists there are those, who clearly understand that the present-day ecology and the theory of evolution are facing a severe crisis. It is interesting to note that the way out from this deadlock is searched for within the same framework of positivism.

In his newly released book Lewontin (2000) criticises manifestations of both reductionism and its opposite holism in biology for not answering the cherished hopes. He sees the way out in Three C's: catastrofe theory, chaos theory, and complexity theory. I am convinced that such a passage seems unexpected and unjustifiable

to the majority of supporters of the Russian paradigm, including me. How so: so many times were ecologists and evolutionists (and probably Lewontin himself) disappointed with methods borrowed from other sciences and adapted to biology and now again they are being offered mathematical instruments as a panacea devised by others and for other purposes! Is it possible to expect the final product of this to be something else and not formal and rough analogies between a biological phenomenon and some physical or chemical process? My long experience prompts me that the development of biological methodology is a matter of concern of biologists themselves: nobody can devise it but we ourselves. We need a methodology that would be an effective tool of logical simplification allowing to preserve essential properties and inherent specificity of biological objects. It is not methods at our disposal, that should dictate investigation objectives and tasks, as was the case up to now, but rather on the contrary, the peculiarities of a research object should determine the choice of both particular methods and methodology. I believe that Lewontin himself, who concluded his book with the following programme sentence, understands that perfectly:
'Progress in biology depends not on revolutionary new conceptualisations, but on the creation of new methodologies that make questions answerable in practise in a world of finite resources'.

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Rusiškoji paradigma ekologijoje ir evoliucinėje biologijoje: *Pro et contra*

E. Lekevičius

Santrauka

Buvusio tarybinio lagerio šalyse per maždaug pusę šimtmečio susiformavo savita ekologų ir evoliucionistų propaguojama pasaulėžiūra, kurios šaknų reiktų ieškoti mikrobiologo Winogradsky ir biogeochemiko Vernadsky pažiūrose. Štai šios pasaulėžiūros pagrindinės tezės: gyvybė gali egzistuoti tik medžiagų ciklo (= ekosistemos) pavidalu; ekosistemos yra organizuotos sistemos; kartu su gyvybe Žemėje turėjo atsirasti ir pirmieji medžiagų ciklai; be rūšių evoliucijos egzistuoja dar viena pakankamai savarankiška evoliucinė linija – ekosistemų evoliucija; pastaroji vyksta dėka individualios atrankos, kurios veikimo kryptį užduoda ekologinė bendrija. Vienoje iš savo publikacijų akad. Zavarzin šią pažiūrų sistemą pavadino rusiškąja paradigma ir priešpastatė ją vakarietiškai, kurią jis laiko redukcionistine ir analitine. Šiame straipsnyje bandau išryškinti rusiškąją paradigmą ir palyginti ją su vyraujančiomis vakariečių ekologų ir evoliucionistų pažiūromis, kokios jos buvo ekosistemos koncepcijos triumfo laikais ir pastaruoju metu. Peržvelgus daugelį rusiškosios paradigmos propaguotojų darbų, susidaro gana kontraversiškas įspūdis. Viena vertus, beveik neabejotina, kad pagrindinės šios paradigmos tezės turi objektyvaus pagrindo, anksčiau ar vėliau jų principinį teisingumą teks pripažinti ir vakariečiams ekologams bei evoliucionistams. Kita vertus, šias tezes bei konkretų jų turinį galima traktuoti tik kaip pasaulėžiūrą, savotišką natūrfilosofiją. Jai trūksta tiek griežtesnių formuluočių, tiek ir konkretesnių metodologinio pobūdžio nuostatų, leidžiančių rekonstruoti atskirus ekosistemų evoliucijos etapus bei paaiškinti tokios evoliucijos mechanizmus. Jei Vakaruose šiuo metu pozityvizmo ir ypač scientizmo biologijoje yra gal kiek per daug, tai „Rytams“ jo, turbūt, gerokai trūksta.

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