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THE ROLE OF SYMBIOSIS IN THE EVOLUTION OF THE BIOSPHERE

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Abstract. The biological systems of all the hierarchy (individuals, populations, ecosystems, biomes, biosphere) by their intrinsic trait of absorbing more and more solar energy, display a tendency of distancing from the state of thermodynamic equilibrium. Biodiversity, by its accelerated growth due to the positive feedback, is the materialization of this trend. Symbiosis, which determines the emergence of new taxa in all ranks – from cultivars to phyla, plays a first rank role in the increase of biodiversity and in the evolution of the biosphere. The human species, through it entire activity, determines the reverse of this action at a global scale.

Résumé. Les systèmes biologiques de touts les niveaux hiérarchiques (individus, populations, écosistèmes, biomes, biosphère), par leur qualité d'absorber l'énergie solaire, montrent une tendance de se distancer de l'état d'équilibre thermodynamique. La biodiversité, par sa croissance accéléré grâce au feedback represente la matérialisation de cette tendance. La symbiose, qui détermine l'apparition de nouveaux taxons de tous les rangs, commençant avec les cultivars jusqu'aux phylums, joue un rôle principal dans l'augmentation de la biodiversité et dans l'évolution de la biosphère. L'espèce humaine, par l'entière activité, determine l'effet contraire à l'échelle globale.

Key words: symbiosis, evolution, biosphere.

Biodiversity is a subject widely debated. There are a lot of discussions but very little is done to preserve it, or even contrary, one may say.

The biological systems are, thermodynamically, in the third state, that is they display a trend to distance from the first state (thermodynamic equilibrium) and from the second state (near thermodynamic equilibrium) (Laszlo, 1987). The condition for achieving this trend is the growth of energy inflow into the system. The essential source of incident energy, the solar energy, is constant and the biological systems uptake just part of it. The gradual increase of the amount of energy *absorbed* by the system is due to activity of the living creatures and is produced due to a positive feedback: the increase of the number and diversity of consumers leads to the increase of absorbed energy, which in turn, stimulates the increase of the numbers and diversity. The proof for this statement is the accelerated pace of the evolution of life on earth.

The trend of increasing biodiversity and thus, of increased energy uptake by the systems, represents the materialization of the trend of the biological systems, of the whole biosphere, to distance from the thermodynamic equilibrium.

I will try to show below the role of symbiosis in this process of biosphere evolution. I am using here the term of *symbiosis* in its original meaning, as it was formulated by Heinrich Anton de Bary in 1878: *cohabiting*, including the whole array of ways – mutualism, commensalism, parasitism, etc.

SYMBIOSIS – FACTOR FOR BIODIVERSITY GROWTH

I will just present a few of the large number of known facts that show the role of symbiosis in the emergence of different rank taxa.

1. *The endosymbiotic origin of eukaryote, a domain* (supra-kingdom), shown by Margulis (1992, 1996). This taxon of the highest rank originates from the endosymbiosis of archaean with bacteria that formed the essential cell organelles: chloroplasts, mitochondria and flagella, probably.

2. *The endosymbiotic origin of some phyla.*

The phylum Pogonophora, by Ivanov (1960), includes two classes: Vestimentifera and Pogonophora as such.

The origin of this phylum has not been cleared, yet. In adult state they don't have intestine, mouth and anus. Vestimentifera live close to hydrothermal springs (vents) on the bottom of the ocean and they have sulphurous bacteria as symbiont. The sulphurous bacteria oxidize H_2S and with the resulting energy they synthesize organic substances. The host lives on these bacteria. The required oxygen is obtained from the ocean water. Some authors consider this animals as being autotroph, independent of solar energy (Malakhov, 1997)[1]. Complex ecosystems develop around these hydrothermal springs, with numerous and varied species (molluscs, crustaceans, fish) some of them symbiont with the same sulphurous bacteria (Vetter,1991; Malakhov,1997).

The Pogonophora class live on the bottom of the ocean down to the greatest depths and they are not conditioned by hydrothermal springs because their symbiont oxidizes the methane and therefore, they are indicator for methane deposits.

Some time ago animal communities have been observed in marine reducing mud, symbiont with bacteria that oxidize H_2S (Cavanaugh, 1983).

A new symbiont phylum has been recently described in the domain (supra-kingdom) of Aarchaea. Due to its tiny dimension (diameter of about 400 nm) the phylum has also been named Nanoarchaeota, and the species *Nanoarchaeum equitans* (Huber et al., 2002).

3. *Lichens.* The taxonomic rank of this group is not completely clarified, yet. There are about 15,000 known species resulting from the symbiosis of fungi belonging to a non specified number of species with just 30 species of algae and cyanobacteria (Paracer & Ahmadjan, 2000). They are pioneers of life installation in the most varied conditions.

4. The *land plants.* They do not form a taxon, rather they represent a major constituent of the rank of plants and at the same time one of the decisive factors in increasing the energy input into the biosphere. In a fossil state they are known from the Silurian. Recent investigations support their symbiotic origin between fungi and algae. I cite the opinions of two authors. Lewis (1991), specialist in carbohydrate metabolism in plants and fungi says that the land plants (Bryophyte and Tracheophyte) originate from Charophyte algae living in symbiosis with Zygomycete descending from aquatic ancestors that could interact with Charophyte. "The early land plants were essentially algal-fungal associations in which the morphology of the alga dominated" (p. 296).

Atsatt (1991), starting from the way of nutrition – plants by photosynthesis, fungi by degrading nutrition and absorption – says: "Land plants, and particularly the seed plants, differ from green algae and fungi in combining highly integrated forms of both modes of nutrition, so that in many ways they are effectively photosynthetic fungi" (p. 301).

[1] The autotrophy of Vestimentifera is relative because the ocean water oxygen that they use comes from the phytoplankton photosynthesis, depending thus on solar energy.

5. *The symbiotic origin of species. Co-evolution.* I will cite only two facts from the many known ones. Speciation, due to the co-evolution of *Passiflora* with Lepidoptera Heliconiinae from America. Caterpillars are monophagous eating leaves. Butterflies from each species of Heliconiinae lay just one egg on a plant of a given species of *Passiflora*, which they recognize visually. During the course of co-evolution the plants have evolved chemical and symbiotic defence means: the leaves contain cyanogenic glycosides, they grow excrescences on he leaves that look like butterfly eggs, which keep away the butterflies from laying eggs on those leaves. They developed extra floral nectars that draw ants who attack the caterpillars. Due to these complex relations a strong parallel radiation occurred in both groups, a co-evolution of the species that resulted in cophylogeny, a correlation of plant phylogeny and of their phytophagous. The conclusion of Spencer (1988), specialist in this matter, is significant: the chemistry of the *Passiflora* species changed under the pressure of the Heliconiinae but this change triggered a change of the digestive enzymatic system of the caterpillars.

A similar relation takes place between the toxic plants from the family of Asclepiadaceae and the butterflies from the subfamily of Danainae. The caterpillars eat the leaves that contain heart glycosides and become toxic too, transmitting the toxicity to the adults, which is an efficient mean of defence, particularly against birds. The toxic butterflies are mimicked by some Pieridae species, fully comestible.

6. *Symbiosis and the multiple co-evolution*. An outstanding example are the symbiont relations between the ants from the tribe of Attini, endemic on the American continent and the *basidiomycetes* fungi, family Lepiotaceae grown by the ants. The survey of a large number of ants and of their fungi led to the identification of 553 cultivars (Mueller et al.,1998).

Recent investigations showed that this is a more complex symbiosis. The fungi cultivated by the ants (their only feed) are attacked by a *Escovopsis* micro fungi that is in turn controlled by an antibiotic produced by a filamentous bacteria. Therefore this is a complex symbiotic community in which three members – the ants, the fungi cultivated by the ants and the microfungi, live in relations of mutualism, and the filamentous bacteria, which is a pest. The phylogenetic analysis of this 50 million years-old community shows that it is the product of a tripartite co-evolution of the cultivating ants, of the cultivars and of the parasites (Currie, 2001; Currie at al., 2003).

Symbiosis may also determine indirectly the increase of biodiversity by establishing favourable conditions for this process. I will just mention two examples – the rain forests and the coral reefs.

The equatorial forests are prosperous not just because of the warm and wet climate but also due to the symbiont relations, particularly of the angiosperms with various groups of nitrogen-bounding bacteria, of fungi (*mychorrhiza*) and of insects (maybe the most important), which in fact condition the existence of those forests. Indeed, there is no wind in the equatorial area and therefore the insects are the essential pollinators. The wide array of plants caused a wide diversity of the insects specialised in pollinating various plant species. Under these conditions a large diversity of organisms developed at all trophic levels.

A similar phenomenon took place in the coral reefs whose existence is due to the mutual symbiosis of the corals with flagellate algae. A community developed from this association, whose diversity is comparable only to that of the equatorial forests.

The wealth of species in both communities is not due the immigration of species from colder areas, as some biologists say, but to *in situ* speciation, favoured by the diversity of resources, supporting again the idea that diversity gives birth to diversity.

7. *Lateral (horizontal) gene transfer.* At first sight it would seem that this phenomenon has nothing to do with symbiosis. However, if I consider that it results from the cohabitation of species it fits to the original definition of symbiosis. The in depth investigation of the phenomenon is just starting but its large scope and its role in the interspecific relations, in the evolution of taxa from all ranks, in increasing the biodiversity of the entire biosphere is already visible. (Margulis, 1991; Goff, 1991; Woese, 1998; Doolittle, 1999, 2000; Pennisi, 1999; Paracer & Ahmadjan, 2000; Raymond et al., 2002). I will cite just three opinions. Woese (1998) stated that "It is now clear that lateral transfer is more widespread than has previously been appreciated" (p. 6858). Doolittle (2000) considers that "Lateral gene transfer would explain how eukaryotes that supposedly evolved from an archaeal cell obtained so many bacterial genes important to metabolism" (p. 94). Raymond et al. (2000) concluded after the compared analysis of the full genome of 5 groups of photosynthesising prokaryotes that "... horizontal gene transfer has been pivotal in their evolution" (p. 1616).

As it is known so far, the lateral transfer of the genetic information takes place through viruses, plasmids and transposons. I shall get back later to this problem.

These few categories of facts that represent important ways of increasing biodiversity and therefore the input of energy in the biosphere and the general acceleration of evolution, raise several issues of wide interest. Here are some of them.

1. *Origin of the large taxa.* The issue of the manner in which the high rank taxa (kingdom, phylum etc.) appeared was raised when the book of Goldschmidt (1940) appeared. He was against the Darwinian explanation and formulated idea according to which such innovations could appear by systemic mutations which could result in "lucky monsters" that could represent new taxa of higher rank. The dispute continues even today (Nazarov, 1991) when the Darwinian and neo-Darwinian opinions still predominate, according to which the micromutations and the natural selection explain satisfactorily the apparition of taxa of any rank.

2. *Role of the natural selection.* Since the taxa of any rank may appear through symbiogenesis, it might be concluded that natural selection is no longer necessary.

Natural selection is an emergent process of the ecosystem because it is the result of interaction between the three levels of organization – individual, population, ecosystem (Botnariuc, 2003). Natural selection controls (assesses) therefore the compatibility of individuals and populations with the conditions of the given ecosystem irrespective of their origin and manner of formation. I might say that natural selection "smoothes" their structure and functioning. A proof is the well known fact that the populations of the same species from different ecosystems differ (morphologically, as behaviour and even genetically).

Therefore, considering the problem of random mutation plus selection or symbiogenesis, I think that the correct answer is symbiosis plus selection.

3. *Together with the development of neo-Darwinism, Lamarckism* became an outlawed theory, essentially because it admits the hereditary transmission of the traits acquired by the organism during its life, idea which is not admitted by the neo-

Darwinism. The hereditary transmission of symbiosis, as well as of the information acquired during the life time of an organism (lateral gene transfer) are Lamarckian phenomena. This makes some biologists consider that symbiosis represents a neo-Lamarckian mechanism of evolution (Nardon & Grenier, 1991). Symbiogenesis brings thus back Lamarckism into discussion, on a new basis, however.

4. *The importance of the real knowledge of biodiversity* and of its role in the evolution of biosphere brought new vigour to the research into systematics and phylogeny. The in depth study of these domains became possible due to the progress in the molecular biology of both present and fossil (molecular paleobiology) organisms.

The results obtained so far revealed the necessity and possibility to review the general phylogeny and the evolution of biodiversity. Variants of global molecular phylogenetic trees appeared composed by comparing the ribosomal RNA that determines protein synthesis.

Difficulties appeared, too. Their general cause is the lateral gene transfer, much more widespread that it was recently considered, as mentioned at pct. 7.

Some scientists consider meaningless the attempts to build the molecular phylogeny because the lateral gene transfer was generalized during the early stages of life evolution. The branches of the global phylogenetic tree are actually anastomotic so that the tree looks rather like a reticulate structure with complex connections between various branches (Woese, 1998; Doolittle, 1999, 2000).

It results that the genomes of the present day organisms are a mosaic of genes with varied origin, not just from one single form. Therefore, the ribosomal genes too, do not reflect the true history of the phylogenetic relations. There even are suggestions of "uprooting" the molecular phylogenetic tree and returning to the phylogeny based on the investigation of entire organisms, the classical phylohgeny, therefore. It is clear that polyphylly becomes the dominant trait of the evolutionary process. Monophylly and cladistics are now questioned, therefore (Margulis, 1991).

5. A last aspect is the *effect of biodiversity on ecosystems*, particularly on the their stability and productivity.

The classics of ecology, Elton, Odum, McArthur, claim that the complex ecosystems having a wide biodiversity are more stable and more productive. The most convincing examples are the equatorial forests and the coral reefs.

In a recent analysis of the debates on the relationship between diversity and stability McCann (2000) confirmed the conclusion of the ecologists: "... the results indicate that within an ecosystem, diversity tends to be correlated positively with ecosystem stability" (p. 231).

The role of the functional redundancy of species must be added to the role of biodiversity in keeping the stability as Odum (1983) noticed. The efficiency of diversity and its positive role on stability and productivity was shown experimentally (Tilman et al., 1996).

I think that to the functional redundancy as factor of stability, we must add the fact that it is accompanied by the structural diversity. For instance, all the phytoplankton species and the macrophytes provide by photosynthesis the food for the entire community of a lake throughout the year, but the *quality of the food* (primary production) differs from species to species, which stimulates the increase of consumer diversity, which increases ecosystem stability.

What does the agricultural practice say? Two aspects must be ascertained here. The subsistence agriculture shows clearly that poly-culture yields more biomass than mono-culture. The problem is different with commercial agriculture which gives a higher production. But the stability of the crop and the increase of the yield are obtained at a high cost: fertilizers, large amounts of herbicides and insecticides, because mono-cultures on wide areas favour the mass spread of pests. Other adverse effects are soil and water pollution, including water table pollution, lower biodiversity on wide areas.

The importance of the problem is clear, as well as the disputes in which, unfortunately, politics dominate science many times.

In conclusion I will try to answer briefly the question on the role of humans in the evolution of biosphere. There is a lot of literature on the consequences of human activity on the environment. I will single out some of the most important effects.

The global population is obviously the key factor to the whole problem: it will reach 9 billion by 2050, from the current 6.2 billion.

Man activity, armed with the modern science and technology, by its global effects on the biosphere, is comparable only with the strongest forces of nature. It affects adversely all the conditions of existence and evolution of biodiversity and of the whole biosphere.

Two categories of activities play an essential role: *pollution* of the environment (atmosphere, water, soil) and *overuse* of the resources, mainly of the biologic ones.

The pollution of atmosphere with gases, some of them with greenhouse effect, is the main cause for global warming, which together with forest clearing and overgrazing lead to desertification of wide areas on all continents and a subsequent loss of biodiversity. The strong warming of the atmosphere in deserts changes the continent-ocean relations, influences the air currents, increase the frequency and strength of hurricanes, the transport of dust, sand and even pathogens on very long distances. The wind influences the surface ocean currents. In other words the relations between biomes are affected. Forest clearing accompanied by overgrazing caused the extinction of a large number of species, strips the soil, enhances soil erosion, open the way to floods. Acid rains fall from the atmosphere full of nitrogen and sulphur oxides with a lethal effect on the land flora and fauna.

Forest eradication has very complex consequences. Plants assimilate carbon dioxide and release oxygen. The forests are therefore a source of oxygen and a huge storage area for carbon. The disappearance of the rainforests, which are cleared with increasing speed (the current speed is about 1 million square kilometres over 5-10 years), leads not just to the extinction of about 50% of the total plant species, but also to an accelerated increase of the carbon dioxide concentration in the atmosphere, which speeds global warming and thus the drastic depression of biodiversity.

The chemical pollution from agriculture, and not just from it, has essentially the same effect. Herbicides decrease plant biodiversity. Insecticides destroy some pests but also many plant pollinators. Many pests adapt quickly and become resistant to insecticides, they replicate in mass and produce actual invasions, often with catastrophic consequences, in agriculture, in spreading diseases, disorganizing the proper functioning of the ecosystems.

An increasing number of species is spread by airplanes, ships (in the ballast water) and by land, often causing considerable damages, epidemics, epizooties, disrupting the organization and functioning of large ecosystems, all this resulting in a significant decrease of biodiversity.

The chemical pollution of the oil and water and the household wastes affects even the ocean water. An alarming example is the death of the corals, the so-called coral whitening, due to the symbiont algae death. The reef ecosystems comparable in biodiversity with the equatorial forests, also disappear rapidly.

The balance of these processes presented briefly is as follows:

1. Global warming
2. Altered relations between the biomes
3. Altered essential biogeochemical cycles (C, N, S)
4. Disruption of the functional structure of the biosphere
5. Global, accelerated decrease of biodiversity
6. The essential consequence of these processes is the lower energy input followed by a slower distancing from the thermodynamic equillibrium and even the reverse process.

No doubt, the humans are the most intelligent species but it seems that intelligence doesn't always imply wisdom. *Homo sapiens* became an aberrant species.

ROLUL SIMBIOZEI ÎN EVOLUȚIA BIOSFEREI

REZUMAT

Sistemele biologice de toate nivelele ierarhice (indivizi, populații, ecosisteme, biomi, biosfera) prin caracteristica lor de a absorbi energie solară, au tendința de a se depărta de starea de echilibru termodinamic. Biodiversitatea, prin creșterea sa accelerată datorată feedbeck-ului pozitiv, reprezintă materializarea acestei tendințe. Simbioza, ce determină apariția de taxoni noi de toate rangurile - de la cultivari la filumuri, are rolul principal in creșterea biodiversității și evoluția biosferei. Specia umană, prin întreaga sa activitate, are un efect contrar la scară globală.

LITERATURE CITED

ATSATT, P. R., 1991 – Fungi and the origin of land plants. Pp. 301-328. *In*: L. Margulis, R. Fester (eds.) Symbiosis as a source of evolutionary innovation. The MIT Press. Cambridge, Massachussets, London.

BOTNARIUC, N., 2003 – Evolution of supraindividual biological systems. Edit. Academiei Romane. (in Romanian)

CAVANAUGH, C. N., 1983 – Symbiotic chemautotrophic bacteria in marine invertebrates from sulphid-rich habitats. Nature, 302: 56-61.

CURRIE, C. R., 2001 – A community of ants, fungi and bacteria. A multilateral approach to studying symbiosis. Annu. Rev. Microbiol., 55: 357-380.

CURRIE, C. R., B. WONG, A. E. STUART, T. R. SCHULTZ, S. A. REHNER, U. G. MUELLER, G. SUNG, J. W. SPATAFORA, N. A. STRAUS, 2003 – Ancient tripartite coevolution in the Attine Ant-Microbe symbiosis. Science, 299: 386-388.

DOOLITTLE, W. F., 1999 – Phylogenetic classification and the Universal Tree. Science, 284: 2124-2128.

DOOLITTLE, W. F., 2000 – Uprooting the tree of life. Scientific American. February: 90-95.

GOFF, L. J., 1991 – Symbiosis, interspecific gene transfer and evolution of new species: a case study in the parasitic red algae. Pp. 341-363. *In*: L. Margulis, R. Fester (eds.). Symbiosis as a source of evolutionary innovation. The MIT Press. Cambridge, Massachussets, London.

GOLDSCHMIDT, R., 1940 – The material basis of evolution.Yale University Press, New Haven.

HUBER, H., M. J. HOHN, R. ROHEL, T. FUCHS, V. C. WIMMER, K. O. STETTER, 2002 – A new phylum of Archaea represented by a nanosized hyperthermophyllic symbiont. Nature, 477: 63-66.

IVANOV, A. V., 1960 – Pogonophora. Fauna URSS, nr. 75. Moskwa, Leningrad. Edit. Academiei URSS. (in Russian)

LASZLO, E., 1987 – Evolution. The Grand Synthesis. New Science Library Shambhala Boston and London.

LEWIS, D., 1991 – Mutualistic symbiosis in the origin and evolution of land plants. Pp. 288-300. *In*: L. Margulis, R. Fester (eds.). Symbiosis as a source of evolutionary innovation. The MIT Press. Cambridge, Massachussets, London.
MALAKHOV, V. V., 1997 – Vestimentifera – autotrophic animals. Sorosovski obrazovetelnyi jurnal, 9: 18-26. (in Russian)
MARGULIS, L., 1991 – Symbiosis and Symbionticism. Pp. 1-14. *In*: L. Margulis, R. Fester R. (eds.). Symbiosis as a source of evolutionary innovation. The MIT Press. Cambridge, Massachussets, London.
MARGULIS, L., 1992 – Biodiversity: molecuar biological domains, symbiosis and kingdom origin. Biosystems, 27: 39-51.
MARGULIS, L., 1996 – Arachaeal eubacterial mergers in the origin of Eukerya: Phylogenetic classification of life. Proc. Nat. Acad. Sci. USA, 93: 1071-1076.
McCANN, K. SH., 2000 – The diversity-stability debate. Nature, 405: 228-433.
MUELLER, U. G., S. A. REHNER, T. R. SCHULTZ, 1998 – The evolution of agriculture in ants. Science, 281: 2034-2038.
NARDON, O., A. M. GRENIER, 1991 – Serial endosymbiosis theory and Weevil evolution: the role of symbiosis. *In*: L. Margulis, R. Fester (eds.). Symbiosis as a source of evolutionary innovation. The MIT Press. Cambridge, Massachussets, London.
NAZAROV, V. I., 1991 – Ucenie o macroevolutii (The theory of macroevolution) Moskwa, Nauka.
ODUM, E. P., 1983 – Ecology and our endangered life-support system. Sinauer Associates, Inc. Publishers Sunderland, Massachusetts.
PARACER, S., V. AHMADJAN, 2000 – An introduction to biological associations. Second edition, Oxford University Press.
PENNISI, E., 1999 – Is it time to uproot the tree of life? Science, 284: 1305-1307.
RAYMOND, J., O. ZHXYBAYEVA, J. P. GOGARTEN, S. Y. GERDES, R. F. BLANKENSHIP, 2002 - Whole-genome analysis of photosynthetic prokaryotes. Science, 298: 1616-1619.
SPENCER, K. C., 1988 – Chemical mediation of evolution in the Passiflorae-Heliconius interaction. *In*: J. C. Spencer (ed). Chemical mediation of evolution.
TILMAN, D., D. WEDIN, J. KNOPS, 1996 – Productivity and sustainability influenced by biodiversity in grasslands ecosystem, Nature, 379: 718-720.
VETTER, R. D., 1991 – Symbiosis and the evolution of novel trophic strategies: thiotrophic organisms at hydrothermal vents. Pp: 219-24514. *In*: I. Margulis, R. Fester (eds.). Symbiosis as a source of evolutionary innovation. The MIT Press. Cambridge, Massachussets, London.
WOESE, C., 1998 – The universal ancestor. Proc. Natl. Acad. Sci. USA, 95: 6854-6859.

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