
Directed Evolution of the Biosphere: Biogeochemical Selection or Gaia?*

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At the end of the nineteenth and the beginning of the twentieth centuries, a few Russian scientists proposed an inter-related hypothesis on the coevolution of life and the environment. Because political, linguistic, and cultural barriers between Russia and the rest of the world existed through most of the twentieth century, many of their concepts are not well known in Western science. The synthesis of their works presented in this article leads to the concept of directed evolution of the global ecosystem. Similar to the influential Gaia hypothesis, this concept predicts evolution of the global ecosystem toward conditions generally favorable for organisms. Unlike the Gaia hypothesis, however, the directed evolution in works of Russian scientists results from the superposition of "micro-forces" controlled on local and regional scales by the universal criterion of biogeochemical selection. **Key Words:** biogeochemical cycles, biosphere, directed evolution, Gaia.

Introduction

It has been suggested that the Earth's biosphere consists of not only genetically related organisms, but organisms connected closely to each other through a complex web of biogeochemical cycles that integrate all living things in the single entity named Gaia (e.g., Lovelock 1988). The major premise of Gaia is its ability to change the environment in a direction favorable for life (the concept of "strong Gaia"), or at least to support the environment within limits suitable for life ("weak Gaia") (Kirchner 1991). With the employment of the simple heuristic model Watson and Lovelock (1983) demonstrated how the hypothetical biosphere Daisyworld, which consists of only two species—high-albedo white daisies and low-albedo black daisies—responds to changes in solar luminosity. According to their model, the population of black daisies declines, while the population of white daisies increases with increased solar luminosity. These changes result in the stabilization of Daisyworld temperature due to increase in planetary albedo. In Lovelock's opinion, this example should demonstrate the central feature of Gaia: the ability to regulate the environment and keep it within the limits suitable for the majority of organisms.

Although modeling of the environment is a widespread scientific approach, governing equa-

tions of simple mathematical models often reflect the subjective opinion of the modeler and not the objective reality. The Daisyworld model, for example, did not take into account possible adaptation of black daisies to higher temperatures, evolution of gray or other-colored daisies, and so on. Therefore, this kind of mathematical exercise cannot be considered as proof of Gaia.

At the same time, the hypothesis of strong Gaia has an intriguing axiom. In strong Gaia, organisms and their environment evolved to a modern state, not by simple chance, but mainly through directed efforts of the same organisms. Although it is difficult to find any simple explanation, the fact of this evolution seems to be consistent with many paleogeographic and biogeochemical studies (e.g., Volk 1998).

It is well known, for example, that over geologic time communities of organisms, as well as individuals, have become more complex and diverse. This has happened mainly because abiotic and biotic environments have become increasingly patchy over time—"[G]eodiversity and biodiversity have both increased" (Huggett 1997, 299). In some cases, the leading role played by organisms in the increase of geodiversity is quite clear, especially that played by those that, after their death, formed the material of various sedimentary rocks (e.g., limestone) (Huggett). However, it is impossible to

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prove that organisms made these specific changes “on purpose” to make the ambient surrounding more suitable for their offspring or some other species.

The idea of mutual alterations of life and environment is similar to the concept of biologic coevolution articulated by Paul Ehrlich and Peter Raven (1965), who defined coevolution as the process of reciprocal evolutionary change in interacting species. About thirty years ago, these two scientists noted that closely related butterflies feed on closely related plants. The reason for this relationship might be the fact that some plants produce chemicals that are toxic to most insects, and that some insects may have developed a mechanism of breaking through these defenses. Therefore, it is possible that only species of butterflies adjusted to the toxin of a given plant survived.

More recently, ecological economist Richard Norgaard (1981, 1984) extended the concept of coevolution to sociosystem and ecosystem development. According to Norgaard, social practices evolve as economic development changes the quality of the environment, which feeds back to people through economic productivity and might thus change their behavior. In speaking about the low economic productivity of the Amazon tropical rain forest, Norgaard (1981) noticed one principal difference between artificial and natural ecosystems: natural ecosystems are efficient in their recycling of nutrients, while tropical agriculture needs external support in the form of irrigation (during the period when evapotranspiration exceeds precipitation) and introduction of fertilizers to compensate for loss of nutrients from soil by irrigation and crop removal. These problems could be overcome, however, if the sociosystem and ecosystem in the Amazon were developed along the path of coevolution, resulting in changes of human behavior as well as alterations of agricultural ecosystems (Norgaard 1981).

In the latter example, the evident cause of development was human. In a more general case of coevolution of life and the environment, the driving forces are not so obvious. It is equally difficult to determine if the biosphere reached its modern state mainly through response to random variations in external parameters—such as solar luminosity, volcanic

activity, and collisions with asteroids—or if some of the evolutionary paths were actually chosen by organisms.

The questions about the driving force of coevolution, as well as to what extent organisms might govern environmental conditions, are of great importance. If organisms impose only passive control over the environment, then we should keep searching for the governing force of the coevolution in various external factors. On the other hand, if organisms can make “choices” of dominant evolutionary paths, the mechanism of coevolution should be hidden inside a complex web of biogeochemical feedbacks that connects organisms with each other and with their environment. In this latter case, the biosphere as a whole might have significant potential to resist external factors or even completely invert their impacts by maintaining the same evolutionary direction.

In this article, I attempt to address the general question about organism-environment interactions through the historic perspective of some relevant ideas, such as the concept of mutual aid in the biosphere, the nature of organism-environment interactions, and the mechanism of directed evolution. Specifically, I would like to take a closer look on these topics through the works written by a few Russian scientists who lived at the end of the nineteenth and the beginning of the twentieth centuries: Piotr Alekseevich Kropotkin, Rafail Vasil’evich Rizpolozhensky, Vladimir Ivanovich Vernadsky, and Vladimir Alexandrovich Kostitzin. Because political, linguistic, and cultural barriers existed between Russia and the rest of the world through most of the twentieth century, many of their concepts—with the possible exception of ideas by Kropotkin—are not well known in Western science. On the other hand, some of their ideas are considered to be common knowledge and are not associated with the names of these scientists, who first introduced them. In addition, even in Russia, their work was never considered together as a sequence of interrelated studies of directed coevolution of life and environment. Therefore, it is important to organize our discussion on the development of the concept of directed evolution in Russian science in its chronological order to clarify the intellectual connections among these works.

In the discussion section below, I will make

an attempt to synthesize the views of all four scientists to see if their ideas still have more than just historic significance.

Piotr Alekseevich Kropotkin (1842–1921)

Piotr Alexeevich Kropotkin is known as one of the founders of the anarchists' ideology, as a naturalist, and as a geographer. As geographer, Kropotkin pioneered cartographic surveys of Siberia and Manchuria; he explained some morphologic features of the East Siberian highlands and made important contributions to the theory of earth glaciations and physiographic studies of Sweden and Finland (e.g., Kropotkin 1899). At present, it is difficult to find a single book on the history of geographic thought in which the name of Piotr Kropotkin is not mentioned (e.g., Livingstone 1993). In this article, however, I would like to emphasize Kropotkin's contribution to evolution theory: the idea of mutual aid and the concept of evolution directed toward an energetically efficient state.

The culmination of Kropotkin's writings on biologic evolution came after 1888, when Thomas H. Huxley published his influential essay on "The Struggle for Existence in Human Society" (Huxley 1888). From Kropotkin's point of view, Huxley and other social Darwinists overlooked the mechanism of possible survival through mutual aid and coexistence. In his critiques of Huxley, Kropotkin demonstrated how survival in the biosphere was often enhanced either by one individual helping another or by one species aiding another for mutual benefit. The major conclusion Kropotkin reached in his 1902 book *Mutual Aid as a Factor of Evolution* was that "Sociability is as much a law of nature as mutual struggle" (Kropotkin [1902] 1972, 30). Here, the words "law of nature" should be interpreted in light of the method of scientific deduction, which Kropotkin followed in naturalistic as well as social research. According to Kropotkin, scientific deduction has three steps: (a) observation and accumulation of facts, (b) formulation of hypothesis, and (c) verification of this hypothesis on other facts and observation (Udarcev 1989). The last step in this sequence should transform a hypothesis into a law of nature (Kropotkin 1920). However, this interpretation of natural

laws does not explain at what level of accumulation of facts hypothesis might be considered law.

In *Mutual Aid* ([1902] 1972), for example, Kropotkin elevated cases of social behavior to the level of the law of nature, considering local and regional examples of mutual aid among different animals and groups of animals. In this book, Kropotkin described spatial patterns among wolves in the Russian steppe, where they hunt in tight packs, or among horses, that self-organize in a closed circle under danger of wolves' attack. Other examples included behavior of insects (e.g., communities of ants and bees, mutual aid among some species of beetles) and cases of social behavior among birds. Overall, Kropotkin believed that social behavior helps organisms to better adjust to their environment. Once acquired, this adaptation might be simply passed from one generation of organisms to another (Kropotkin [1902] 1972).

Mutual Aid ([1902] 1972) is not the only text Kropotkin wrote on this subject. Later in life, he amassed further evidence in support of the theory of mutual aid and inherited adaptations. In the periodical *The Nineteenth Century*, he published a series of works on subjects including the interaction of the environment with plants and animals, inheritance of acquired characteristics, inherited variations in plants and animals, and others (Campbell and Livingstone 1983). In the opinion of Campbell and Livingstone, these works represent a convincing argument that the geographic and anarchistic humanism in Kropotkin's work has deep roots in his naturalistic endeavors and especially in his neo-Lamarckian views. The latter is visible, for example, in his belief that plants and animals were directly modified by their environments and that any such modifications were simply inherited by their offspring (Campbell and Livingstone 1983).

Interestingly enough, Kropotkin's neo-Lamarckism was closely tied to the concept of Darwinian natural selection. The reason for this evolutionary dualism was Kropotkin's belief that mutual aid is the most energetically efficient adjustment to environment. Therefore, from his point of view, organisms that acquired or inherited social behavior at the same time obtained the evolutionary advantage over other organisms. Another interesting feature of Kropotkin's theory is its view of evolution as a

product of “micro-forces” that work independently yet coherently with each other (Kropotkin 1920).

Kropotkin ([1902] 1972) used the term “micro-forces” to describe interactions among individual species at a local scale. An example of such an interaction driven by the same principle of mutual aid might be found amidst burying beetles, *Necrophorus*, which use the decaying corpses of small animals as incubators for their eggs. To provide safe conditions for the eggs, *Necrophorus* beetles search for mice or bird corpses that can be buried underground. However, no single bug can do this work alone. Therefore, the first beetle to find a corpse would usually bring two, three or more beetles to the scene and use their help to bury the corpse or move it to softer ground where burial would be possible with a minimum expenditure of energy.

These and other observations led Kropotkin ([1902] 1972, 81) to a simple formula of directed evolution: “In the great struggle for life—for the greatest possible fullness and intensity of life with the least waste of energy—natural selection continually seeks out ways precisely for avoiding competition as much as possible.” In this phrase, Kropotkin made an important generalization about the direction of evolution, which is “the greatest possible fullness and intensity of life with the least waste of energy.” Speaking about the natural tendency of organisms and groups of organisms toward a state with the least waste of energy, Kropotkin meant, first of all, energetic advantages of mutualism over competition.

In Russia Kropotkin had many followers who tried to apply his theory of mutual aid in natural sciences. Rafail Rizpolozhensky was among those who attempted to answer the question about the ultimate moving force of social behavior. According to Rizpolozhensky, this force is powered by the benefits of joint preparation of food.

Rafail Vasil'evich Rizpolozhensky (1847–1918)

Rizpolozhensky had an unusual combination of three degrees: a theological degree from Kostroma Seminary and degrees in biology and mathematics from Kazan University (Koloskova 1981). During most of his career (1892–

1918), Rizpolozhensky worked as a custodian of the Museum of Natural History in Kazan and had a reputation as an innovative soil geographer and an excellent soil collector—he was the author of a famous collection of Russian soils that was on display at the 1900 World's Fair in Paris (Otocky 1961).

In 1892, Rizpolozhensky formulated his original concept of “soil” as “a border between the chaotic environment and the world of order” (Rizpolozhensky 1892, 6).¹ The world of order is represented by living organisms, and chaos is the abiotic environment that includes the atmosphere, hydrosphere, and lithosphere. According to Rizpolozhensky, interaction between chaos and order can produce three major formations of soil: (1) soils at the border of living organism and lithosphere—solid soils; (2) soils at the border of living organism and hydrosphere—liquid soils; and (3) soils at the border of living organism and atmosphere—gaseous soils.

In Rizpolozhensky's (1892, 20) world of soil, living organisms change the soil's properties during their “search for necessary resources inside the atmosphere, water, and solid geologic rocks” by mixing the environment and producing various wastes, which in turn can be used as food for other communities or organisms. . . . The utilization of these resources by any single plant or animal would unintentionally help in the preparation of food for another living organism.” According to Rizpolozhensky, this mutual aid in the “preparation of food” for each other is never interrupted. Living organisms “work together by uniting into more or less friendly groups, associations, and one association would immediately replace another if the first association exhausted all necessary resources it could reach, the second, better adjusted for a given soil and climate, could continue its work” (Rizpolozhensky 1897, 34). Permanent work on the preparation of food gradually transforms the border between organisms and chaotic environment (e.g., geologic rock) “to an environment more favorable for elaboration of life in general” (Rizpolozhensky 1897, 34). Keeping in mind Rizpolozhensky's understanding of soil as a place of contact between living organisms and the hydrosphere, atmosphere, or lithosphere, one concludes that the citation above defines a concept of directed evolution of the earth's

biosphere, a concept similar to the strong version of the Gaia hypothesis.

The evolution of soil through the development of waste-food relations is consistent with Kropotkin's view of mutualism as a factor of evolution. Indeed, we should agree with Kropotkin that the ability of an organism to take a stand at the end of the waste-food chain provides energetic benefits for this specific organism. No energy would be wasted, for example, in a fight for resources by the species, and such a species could peacefully coexist with the rest of the community. Therefore, with the evolution of new species on the geologic time scale, the whole system might have a tendency toward greater complexity because of extension of the food web and better adjustment for all through satisfaction of needs for each individual.

At the same time, Rizpolozhensky (1897) claimed that over short time scales, changes of soil properties could follow a direction favorable for organisms as easily as a direction that would lead to reduction or even destruction of their population. To demonstrate this thesis Rizpolozhensky suggested an example of forest soil, where leaching of organic matter and washing of minerals from the upper horizon could lead to the formation of a nonpermeable layer in lower horizons. The formation of such a layer would turn a fertile soil to a swamp or useless solonetz (saline and usually calcareous soil), leading to the death of deep-root forest vegetation. However, with time, an open and deforested land would be occupied by grasses, shrubs, and new types of soil-burrowing animals, and—with the help of denudation—could eventually be returned to fertility. This example represents a clear case of secondary succession in forest community where bioturbation played a central role in restoring the fertility of the soil. Rizpolozhensky described this example independently from Eugenius Warming, who introduced the concept of succession to Western science at about the same time (Odum 1996).

Rizpolozhensky's views were not well understood by his colleagues. He was criticized sharply for the controversial character of his theories, his overwhelming emphasis of bioturbation in soil formation processes, and the alleged uselessness of his soil classification in practice (Sibirtsev 1892). However, from my point of view, the apparent controversy be-

tween Rizpolozhensky's views on soil evolution at short versus long time scales can be resolved: the solution of this problem can be found in the theory of internal instability of biogeochemical cycles proposed by Vladimir Kostitzin about twenty years after Rizpolozhensky's death. First, though, we should move to the scientific heritage of the next in this chronological sequence of scientists: Vladimir Vernadsky, who developed ideas by Kropotkin, Rizpolozhensky, and others into the theory of biosphere.

Vladimir Ivanovich Vernadsky (1863–1945)

Some researchers—including Lovelock (1988) and Lynn Margulis (and Sagan 1997), the authors of the Gaia hypothesis—credit Vernadsky with being the first scientist to demonstrate many important functions of the Earth's biosphere, proving that the modern atmosphere and hydrosphere both result from past activities of living organisms. Others—for example, Mark and Dianna McMenamin (1994)—go further and cite Vernadsky as a Russian source for the Gaia hypothesis.

The similarity between Vernadsky's concept of the biosphere and the Gaia hypothesis is evident in, for example, Vernadsky's holistic view of nature, specifically in his concept of *living matter*, which represents the totality of all organisms. This vision extends to the inorganic environment, in which Vernadsky ([1926] 1998) viewed igneous rocks, juvenile water, or volatile products of volcanic eruptions as another integrated property: the *inert matter*. In his later works, Vernadsky introduced a new part of the biosphere in addition to living and inert matter: *bio-inert matter* (e.g., Vernadsky [1931a] 1993). Although Vernadsky never referred to Rizpolozhensky, his concept of bio-inert matter is very similar to Rizpolozhensky's "soil," representing a medium formed from inert matter by activities of living organisms. Thus, bio-inert matter is represented, for example, by terrestrial soil, a bioturbated layer of oceanic sediments, the surface layer of the world ocean, forest canopy, and any other environment with properties substantially changed or still under the influence of living organisms. The numerous fluxes of matter and energy between living, inert, and bio-inert matter integrate these pieces into a single, complex system

or “mechanism” of biosphere (Vernadsky [1926] 1998).

Another feature common to both Vernadsky’s concept of the biosphere and the Gaia hypothesis is the concept of directed evolution. In Vernadsky’s biosphere, however, evolution is driven by groups of individual organisms, each subjected to the same single criterion of biogeochemical selection. Therefore, the direction of global changes results from the sum of collinear vectors of individual developments, rather than from consciousness or the altruism of a single entity.

Perhaps Vernadsky’s most important work on the scientific basis of directed evolution was the lecture entitled “Study of Phenomenon of Life and New Physics” ([1931a] 1993) that he delivered to the Leningrad Society of Nature Explorers in 1931, in which he introduced his two main principles of biogeochemistry.

The First Principle

“The biogeochemical energy in the biosphere has a tendency toward its maximum manifestation (the first principle of biogeochemistry)” (Vernadsky [1931a] 1993, 348). This first principle of biogeochemistry followed from the earlier concept of the “pressure of life” (Vernadsky [1926] 1998). The concept of life’s pressure is based on the observations of different species and communities in the modern biosphere, in which multiplication of living organisms is limited by only a few external “forces.” The multiplication of living organisms slows down “at low temperatures, and weakens or ceases in the absence of food, of gas to breathe, or space for the new born” (Vernadsky [1926] 1998, 66). In all other cases, life has a tendency to maximum possible expansion, which is similar to adiabatic expansion of gases. “The tension of water vapor and the pressure of life are analogous” (Vernadsky [1926] 1998, 67). The concept of the pressure of life sounds similar to Kropotkin’s principle, outlined above, of the greatest possible fullness and intensity of life. However, Vernadsky ([1931b] 1993, 348) developed this principle further by introducing the concept of the “biological factor of time.”

Vernadsky ([1931b] 1993) showed that biologic productivity cannot increase indefinitely and is limited by the biological factor of time, or the finite maximum speed of cell division. Some living organisms (e.g., bacteria) undergo

regular cell division, which can be used as a measure of “biologic time” and which Vernadsky introduced in addition to the concept of geologic and conventional time. Wherever the biological factor of time is not a limit, life always increases its biochemical energy within the thresholds of other limiting factors.

The Second Principle

“In the process of evolution of the species, survival belongs to the species capable of increasing the total biogeochemical energy of the biosphere (the second principle of biogeochemistry)” (Vernadsky [1931a] 1993). In this statement, Vernadsky again follows Kropotkin’s energetic perspective of the Darwinian principle of the survival of the fittest. He did not specify, however, which mechanism of survival is more energetically beneficial—competition or mutual aid. Instead, Vernadsky compared organisms from the point of view of their ability to contribute to the total biochemical energy of the biosphere. Without the context of his other works, Vernadsky’s formulation of the second principle might sound vague. In which way, for example, could living organisms contribute to the increase of the total biogeochemical energy of the biosphere in order to receive an evolutionary advantage over organisms that do not contribute the same amount of energy?

Later, in 1940, Vernadsky proposed a new principle of biogeochemistry: “[E]volution of species during geological time goes in the direction of increasing biogenic migration of atoms in the biosphere” (Vernadsky [1940] 1987, 40). By the phrase “biogenic migration of atoms” Vernadsky meant involvement of different elements in biogeochemical cycles. Therefore, according to Vernadsky, the evolution of species should go in the direction of faster biogeochemical cycling of elements. The increase in biogenic cycling can be achieved through an increase in biologic productivity. Thus, this latter concept represents just another formulation of the same second principle of biogeochemistry Vernadsky had formulated in 1931 (see above). Unfortunately, Vernadsky’s book *Chemical Composition of Earth’s Biosphere and Its Surrounding* ([1940] 1987) was never completed and was only published in draft form twenty years after his death.

One of the most unusual features of Vernad-

sky's writing in *Chemical Composition* is that he states the second principle of biogeochemistry without providing the detailed arguments and discussion typical of his work. Perhaps Vernadsky thought the second principle was a self-evident summary of his previous publications and therefore needed no proof.

In their summary of Vernadsky's views on the mechanism of global biogeochemical cycles, Margulis and Sagan (1997) stated that his global thinking was always based on the integration of very specific, local processes. In Vernadsky's mind, the global flux of phosphorus, for example, consists of many components, including a single sea gull flying over water and bringing phosphorus from ocean to land (Margulis and Sagan). A gopher digging its burrow might represent a flux of organic carbon in soil, a fox running from the steppe back to its hole in the forest exchanges nutrients between different geographic zones, and so on. In other words, behind global cycles of elements, Vernadsky always saw very specific biogeochemical processes. Different organisms in Vernadsky's biosphere contribute different amounts to the pool of total biochemical energy and cycle unequal amounts of different elements. Therefore, Vernadsky's second principle should propose a very specific mechanism through which the single organism or groups of organisms first initiating the process of change in the environment would benefit the most. However, he did not provide a clear answer to the question of why the faster biogeochemical cycling of elements might always provide a species or groups of species with an evolutionary advantage.

Vladimir Alexandrovich Kostitzin (1886–1963)

The major direction in Kostitzin's works, in his own words, was the "attack" on the problem of biological evolution. According to Kostitzin (1939, 414), the concept of evolution can be given the quantitative definition of the "processes that lead from a more probable state to a different, less probable one, or that are directed against an increase in entropy." He considered the increase in entropy to be a universal tendency and the decrease to be a local phenomenon of very low probability. "Universal tendencies would undoubtedly be directed toward a more probable state if this state had not already

been attained. . . . Local tendencies can be ascendant or descendent, and undoubtedly the former is far less probable than the latter. Still, their probability is not zero . . . Evolution must then be a very rare phenomenon, highly localized in space and time" (Kostitzin 1939, 414).

In other words, according to Kostitzin, in the complex system described in terms of nonlinear differential equations—including global biogeochemical cycles (Kostitzin [1935] 1978)—the probability always exists of the parameters of such a system shifting in a direction opposite to equilibrium. In the first known publication on the application of mathematical methods to problems of biogeochemistry, "Evolution of the Atmosphere: Organic Circulation, Glacial Periods" ([1935] 1978), Kostitzin demonstrates that the relationship between organisms and bio-inert matter can be described by the same types of nonlinear differential equations Lotka used to describe interactions among different species. Kostitzin proposed a clever analysis of the stability of biogeochemical cycles of oxygen, carbon, and nitrogen. His results defined the conditions necessary for the appearance of periodic oscillations in the chemical composition of the atmosphere, ocean, and soil. The range of these conditions was found to be very wide, and Kostitzin concluded that periodic changes in biogeochemical cycles are natural and are important for an understanding of governing principles in the evolution of the atmosphere and ocean (Kostitzin [1935] 1978).

This vision differs from the deterministic views on evolution held by Kropotkin and Vernadsky. Indeed, they believed that organisms survive because they behaved in a certain manner, while Kostitzin demonstrated that organism and environment—at least for some period of time—might undergo a number of interrelated changes by simple chance, often directed from the equilibrium. Kostitzin's opinion, however, fits well with Rizpolozhensky's view that on a short time-scale, organisms might transform the environment towards conditions favorable to as well as hostile for life.

Kostitzin ([1935] 1978) demonstrated that the introduction of new species with any evolutionary advantage is not necessarily beneficial for the whole community and could cause the decline or death of other organisms and groups. With an increase in the total number of

species, however, the introduction of new species is more likely to result in their coexistence (Kostitzin [1939] 1978). This result can be explained by an increased chance that the new organism will find its best fit inside a system with a complex web of food chains. Therefore, from the mathematical point of view, Kropotkin's idea of mutual aid is not a strict rule, but rather an attractor to which the system has a tendency to evolve as its biocomplexity increases.

At the end of the 1930s, Kostitzin published a few works in which he investigated how life could follow this chain of unlikely events against an increase in entropy. In his view, the mechanism of this motion is selective accumulation of small, randomly produced genetic mutations inside the "germ plasma" (Kostitzin [1939] 1978, 435). A similar approach can be found in works published by Volterra ([1938] 1978) at about the same time. At this time in history, these two scientists came close to the theoretical discovery of the DNA code. Unfortunately, Volterra died at the beginning of the war, and Kostitzin was arrested after the occupation of France by the Nazis and was placed in a concentration camp. After the end of the war Kostitzin lost interest in mathematical ecology and directed all his attention to astrophysics (Moiseev 1984).

Discussion

Figure 1 shows the possible links between the intellectual contributions made by these four Russian scientists. This diagram should not be considered an ambitious attempt to summarize the scientific heritage of Kropotkin, Rizpolozhensky, Vernadsky, and Kostitzin in a few columns of a single table. Instead, it is designed to demonstrate only the transformations of their views on three key topics:

1. Mutual aid.
2. Relationship between organisms and environment.
3. Mechanism of directed evolution.

The evolution of the idea of mutual aid in works by Kropotkin, Rizpolozhensky, and Kostitzin is shown with help of the link 1a→1b→1d. Vernadsky's contribution to this idea was not direct. In his works, the biosphere represents not only biota or the space occupied by living organisms, but also the system of bio-

geochemical cycles that connect life and the environment into a single mechanism. In other words, Vernadsky connected Kropotkin's view on the environment as a factor that can change organisms with Rizpolozhensky's view that organisms change the environment into the concept of a single biogeochemical feedback mechanism, which links organisms and their environment (link 2a→2b→1c).

The same diagram demonstrates Kostitzin's formalization of Vernadsky's concept of the biosphere to the system of the nonlinear differential equations similar to those used by Lotka and Volterra to describe regional population dynamics (1c→2d).

Finally, at the bottom of the diagram we see the transformation of views on directed evolution by Kropotkin, Rizpolozhensky, and Vernadsky (link 3a→3b→3c). Kostitzin, who participated in the discussion of possible direction in evolution of species (e.g., Kostitzyn [1936] 1978), never formulated any specific law or principle of directed evolution. At the same time, his ideas about the ultimate tendency toward mutualism in the evolution of complex systems, as well as the concept of internal instability of biogeochemical cycles, the random nature of genetic mutations, and the transfer of information on inherited or acquired characteristics from one generation to another through the germ plasma (item 3d) might be of great importance to our search for a possible governing force of directed evolution.

Indeed, if the biogeochemical cycles are internally unstable, they should impose a regular environmental stress on organisms. This stress might manifest itself through changes in the concentrations of nutrients, chemical composition of the atmosphere, chemical composition of oceanic waters, or related changes in the atmospheric greenhouse effect and climate. However, at present we know that during times of stress, genes that are normally suppressed can become part of a species' phenotype (see, e.g., Rutherford and Lindquist 1998). Therefore, as long as environmental stress is in place, the biota constantly produces species incorporating a wide range of features.

External factors, such as volcanic eruptions or Earth's collisions with asteroids, undoubtedly imposed stress on organisms similar to or even greater than biogeochemical stress. However, the biogeochemical factors never stop

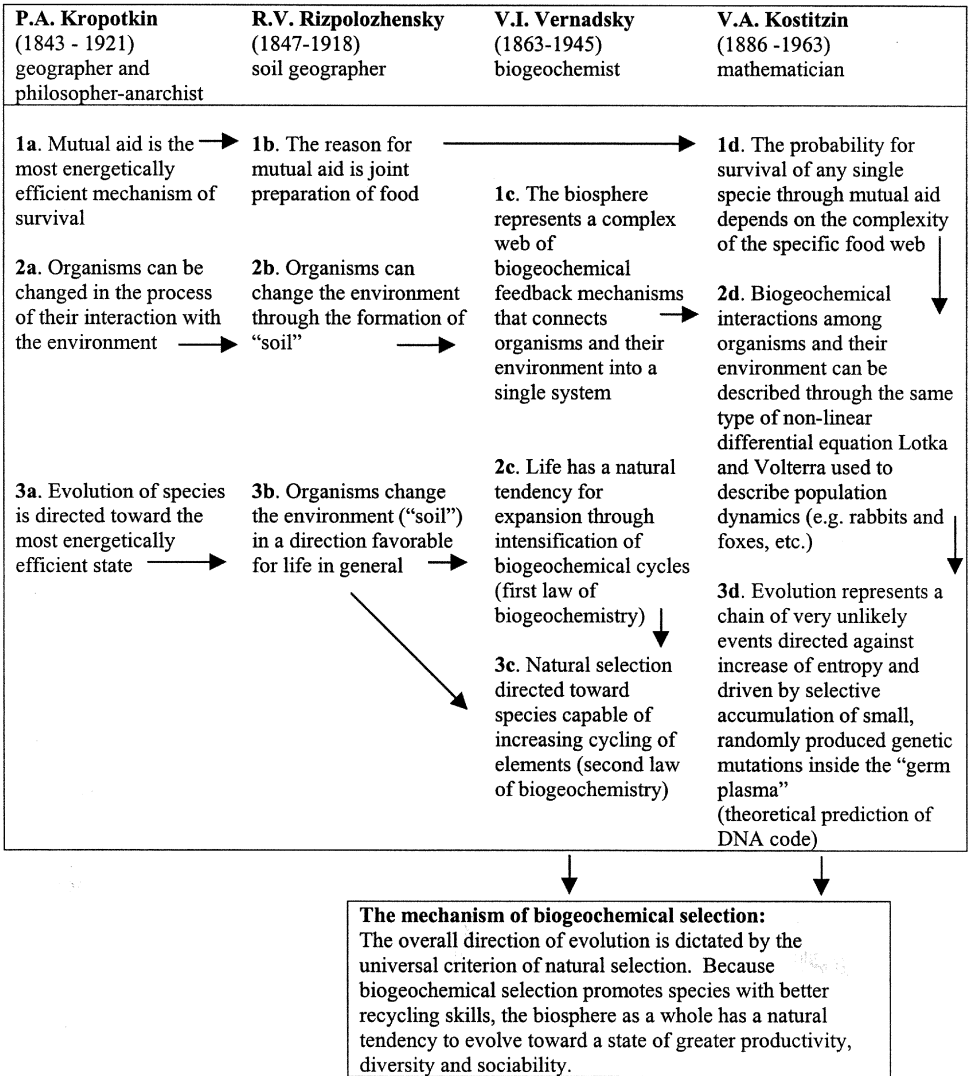


Figure 1 Intellectual Connections between Four Russian Scientists Who Worked on the Idea of Directed Evolution of the Biosphere

their work, while an external disturbance of large magnitude represents a rather rare event. It is also important to mention that some large impacts during the last half billion years caused extinction of up to 80 percent of Earth's species (Rampino and Haggerty 1995). Despite these dramatic changes in the structure of biosphere, after each of these impacts, life managed to recover to the level of biologic productivity and

complexity it had reached before the impact, or even to overgrow that level (Rampino and Haggerty).

The random nature of genetic mutations in organisms dictates, however, that some of these alterations might increase, while other have no effect or might slow down biogeochemical cycling of nutrients. Therefore, genetic mutations caused by internal or external factors

cannot explain the persistent motion of the biosphere towards a state of greater productivity and complexity.

A possible answer to the question of how the biosphere managed to keep a constant course despite the random nature of genetic mutations might be found with the help of Vernadsky's idea of biogeochemical selection. From Vernadsky's point of view, persistence in biospheric development occurs through the biogeochemical selection of organisms that accelerate the exchange in mass and energy between the biota and the environment. It is not important how organisms achieved this intensification of biogeochemical cycles. The anatomy of the sea gull, for example, might be modified through genetic mutations to allow it to dive deeper. This alteration would allow the bird to bring more food to land and make its offspring healthier. The bottom line of all these adaptations, according to Vernadsky, is that the biogeochemical cycling of elements might go faster through some organisms and groups of organisms than through their competitors, and because of that, these specific organisms would win the competition.

Of course, natural selection based on any criterion might work only if it provides organisms with a specific advantage over other species. Therefore, the question of evolutionary advantage must be addressed before we can say that this specific biogeochemical criterion can be of any importance for the evolution of species. Unfortunately, as has been mentioned previously, Vernadsky himself never attempted to explain why the ability of species to accelerate biogeochemical cycling of elements might be considered an evolutionary advantage.

From my point of view, it is possible to prove that the second principle suggests at least two very specific evolutionary advantages:

1. Faster cycling of elements diminishes the dependence of organisms on external sources of nutrients.
2. Intensification of biogeochemical cycles usually leads to the accumulation of available nutrients in proportions congenial for organisms.

By using Vernadsky's terminology, we may say that the first effect follows from the fact that the delivery of nutrients from inert to living matter usually occurs through the medium of

bio-inert matter. If contact between organism and inert matter is unavoidable (e.g., contact between vegetation and products of a fresh volcanic eruption) over a short period of time, organisms would produce a layer of waste that with time and the help of climate and other factors could be transformed to soil or food for other organisms. The layer of soil or bio-inert matter would dynamically decouple living and inert matter. This separation is energetically beneficial for organisms. Indeed, the soil organic matter can be decomposed to a mineral state with less energetic cost than required by the production of the same nutrients (e.g., carbonate ion, calcium, etc.) through the process of chemical weathering of geologic rocks (Ross 1987).

Therefore, groups of organisms capable of increasing cycling of bio-inert matter should be less dependent on external source of nutrients. In the case of a decline in the rate of chemical weathering of geologic rock due to a decline in atmospheric carbon dioxide concentrations (or cooling of global climate), for example, the communities that can intensify cycling of limited nutrients could stabilize their productivity, but the productivity in communities where intensification of biogenic cycling of elements was impossible must decrease.

Under constant environmental conditions, the evolution of new species capable of increasing cycling of limited nutrients would lead to a greater rate of decoupling between living and inert matter, and, thus, to a lesser dependence of biota on possible changes in external conditions.

A second possible advantage of organisms that can increase biogeochemical cycling of elements can be found in a recent book by Tyler Volk, *Gaia's Body* (1998). In this book, Volk demonstrated that faster cycling of limited nutrients by soil organisms usually results in better conservation of these elements in proportions congenial for living matter. The soil organisms do not know, of course, that the cycling and accumulation of soil organic matter is beneficial for plants. As they recycle organic matter for their own needs, they are at the same time keeping in circulation material with a proportion of elements required for plants to spin another round of nutrient control (Volk).

The biogeochemical cycling of elements is faster in large detritus-based food chains,

where organisms might effectively share the most needed nutrients (Volk 1998). The cycling of these nutrients in the whole system increases “as life forms evolve to fill the ecological niches available upon the various types of detritus in different degrees of degradation” (Volk, 187). Therefore, the evolution of new species that can coexist with the rest of community should be related to the intensification of biogeochemical cycles of needed nutrients.

Summarizing these two types of evolutionary advantages, we can conclude that faster biogeochemical cycling of elements helps organisms (a) reduce their sensitivity to external factors and (b) make their environment closer to their chemical composition, and thus, in most cases, “friendlier” for the majority of species.

Conclusions

At the end of the nineteenth and beginning of the twentieth centuries, a few Russian scientists proposed an interrelated hypothesis on the nature and direction of coevolution of life and the environment.

Piotr Kropotkin viewed mutual aid among animals as a factor of their evolution where survival usually belongs to species and individuals with better social skills. According to Kropotkin, the victory of mutual aid over struggle directs evolution towards an energetically efficient state in which organisms might coexist with each other, avoiding competition as much as possible.

Rafail Rizpolozhensky attempted to explain Kropotkin’s idea of mutualism through the joint preparation of food by various organisms. The development of this idea led Rizpolozhensky to the concept of evolving soil, a concept similar to the Gaia hypothesis. Rizpolozhensky’s “soil,” however, is hardly a superorganism, where one part can sacrifice itself for the benefit of other parts. Instead, Rizpolozhensky believed that mutual preparation of food is beneficial for all participants—the waste of one organism represents food for another, and so on.

The ideas of Kropotkin, Rizpolozhensky, and others were brought together into the theory of biogeochemical cycles by Vladimir Vernadsky, who formulated the principle of natural selection of species capable of increasing the cycling of nutrients. Therefore, Vernadsky’s

biosphere has a natural tendency to evolve towards the state of higher total productivity. This development, however, is limited by the biologic factor of time and a number of other physical and chemical factors.

Vladimir Kostitzin developed Vernadsky’s theory further by introducing random variations in the biosphere due to internal instability of biogeochemical cycles and accumulation of genetic mutations inside the “germ plasma.”

The combination of Vernadsky’s second principle, Kostitzin’s internal instability of biogeochemical cycles, and some modern ideas on the relationship between environmental stress and genetic mutations leads to the formulation of the mechanism of biogeochemical selection, which can be broken down to three principal elements:

1. The internal instability of biogeochemical cycles that impose stress on organisms through permanent variations in the composition of atmosphere, ocean, or soil.
2. The biogeochemical stress that triggers genetic mutations of organisms. Some mutations might increase the biogeochemical cycling of nutrients, while others have no effect on the process or might slow it down. Species with the ability to increase biogeochemical cycling of elements, however, have an evolutionary advantage over other species (see Discussion section above). Therefore, the chances of their survival are higher than the chances of other species.
3. The occupation of available niches in the detritus-based food chains by species with advanced recycling skills that increase biogeochemical cycling of needed nutrients and boosts productivity in the whole ecosystem. The increased complexity of the food web promotes mutual aid as a factor of survival (see Figure 1). Therefore, the biosphere as a whole has a natural tendency to evolve towards the state of greater productivity, complexity, and sociability.

Bearing in mind that the natural tendency of the biosphere towards greater productivity, complexity, and sociability can be interpreted as a tendency towards more favorable conditions for the totality of living organisms, we can conclude that the principle of biogeochemical

selection expresses a concept similar to the strong version of the Gaia hypothesis. This similarity, however, is only apparent, and we cannot extend it to the reasoning in these two approaches. The mechanism of biogeochemical selection is based on verifiable scientific principles, while the hypothesis of Gaia reflects a spiritually charged but not strictly scientific vision of nature. Besides, the actual explanation of directed evolution might not be less inspiring than Gaia. One might find wisdom, for example, in mutual aid, joint preparation of food, or an understanding that effective recycling is an important criterion of evolution. ■

Note

¹All translations from Russian are by the author.

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