

Biotic Control of the Environment

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Abstract—Anthropogenically undisturbed natural communities of species in the global biota represent a unique mechanism for maintaining the environmental conditions appropriate for life on a local and global scale. The stability of the present-day climate may be accounted for by the functioning of the natural biota. Information on functions of the biota that are necessary and sufficient for stabilizing the environment is stored in the genomes of species comprising natural communities. Utilization and transformation of the biota by man leads to the distortion and loss of this information. After the disturbance and exploitation of natural communities cease, the biota restores its ability to form and maintain the optimal environment in several decades.

INTRODUCTION

The existing views on species of the natural biota form two opposite theoretical concepts and practical strategies of man–virgin nature interactions on the local and global scales.

(I) According to the first, traditional, concept, the environment proves to be appropriate for life due only to the unique physical conditions of our planet, which exist owing only to its favorable position on the circum-solar orbit. The biota, i.e., the natural fauna and flora of the biosphere, adapts to any environment. Conversely, significant changes in the latter may occur under the effect of the biota, which adapts to these changes via speciation in the course of evolution. In the past, for instance, the biota caused the transition from the reducing (oxygen-free) to oxidizing (oxygen-containing) atmosphere. This resulted in the emergence of oxygen-breathing organisms and the extinction of many species for which oxygen is toxic or their transition to the oxygen-free local environment.

The ability of life to evolve and continuously adapt to changing environmental conditions is regarded as its main property. There are no exact environmental conditions defined as optimal for life. At the genetic level, adaptation is accounted for by intraspecific variability of the genomes. Any genotypes allowing their carriers to produce the most abundant progeny surviving in the corresponding environment are fixed in the population. Any species capable of adapting to the environment and producing such progeny may compose the Earth's biota. All the evolutionary alterations revealed paleontologically are explained by continuous species adaptation and individual selection (Ayala and Fitch, 1997).

The principal environmental change associated with exploitation of nature and transformation of natural biotic communities in agri-, sylvi- and maricultures, which serve to satisfy the requirements of a growing

human population, is regarded as a stage of the natural evolutionary process. The only ecological problem to be solved by man is to control pollution, which causes unfavorable (for man) transformation of the environment. Gaining mastery over the global biota and transforming the biosphere into the noosphere, a new global biosystem serving exceptionally human needs, is also regarded as a natural process.

Natural biodiversity is regarded as a genetic resource that may be used for the needs of developing biotechnology and gene engineering. It is assumed that biodiversity includes both genetic information carried by different natural species and the intraspecific genetic variability. It is proposed to preserve this biodiversity in the zoos, gene banks, and nature reserves occupying less than one percent of the Earth's territory and not interfering with free development of the civilization.

The continuous economic growth based on the progressive utilization of biosphere resources is regarded as the only way to satisfy demands of the increasing human population.

The traditional concept actually ignores ecological limitations on the size of biological populations and factors underlying the formation of natural species communities and determining the stability of ecosystems, i.e., these communities and their environment.

This traditional concept does not explain two very important empirical facts: (1) notwithstanding rapid environmental changes, particularly those occurring under the effect of the biota proper, environmental conditions never exceed the limits excluding the possibility of existence of life in any form; (2) although adaptation proceeds continuously, all the species remain discrete and do not produce transitional forms, which concerns both the present-day species simultaneously existing in the biosphere and species known from the paleontological data (Jackson, 1994).

(II) The second, opposite concept takes into account the physical instability of the environment existing on the Earth and the possibility of its rapid transition to the stable state resembling that on Mars or Venus, in which life is impossible. The biota is regarded as a unique mechanism for maintaining the local and global environmental conditions suitable for life (Gorshkov, 1995).

According to this concept, the main property of life is the ability of species to perform certain work for maintaining such environmental conditions. Complex interactions with the environment make necessary the formation of communities and ecological systems comprising certain sets of species, which concordantly interact with each other and with the environment. This concordance is similar to that of cells and organs within one multicellular organism. Only the species that perform the work necessary for maintaining the proper environment can form communities and compose the biota. These species maintain their optimal population size and produce the optimal (rather than maximal) number of offsprings. Spontaneous transition to the maximal progeny in any species suggests the distortion of its genetic program. This transition, like tumor formation in an individual organism, disturbs the functioning of the community and causes deterioration of the local environment. As the result, the community loses competitiveness and is supplanted by another community in which the same species retain the normal genetic program and produce the optimal progeny.

The species maintaining certain environmental conditions should apparently keep their genetic program unchanged, rather than continuously adapt it to any environmental fluctuations. They should have mechanisms for stabilizing the genetic program and preventing the accumulation of mutations, which erase genetic information.

According to this concept, all the species of the biota should retain their genetic constancy and stability during the geological time periods. All the species should be both viable and capable of concordant interaction with other species of the community, thus providing for environmental control. These limitations explain the discreteness and morphological constancy observed in both existing and paleontological species (Jackson, 1994).

Individual genetic variation in natural species represents random deviations from the normal genetic program, which escape stabilizing selection. The weakening of this selection in conditions differing from those in the natural ecological niche leads to increased genetic variation and the accumulation of individuals with different genetic abnormalities in the population. When natural conditions and the normal strength of the stabilizing selection are restored, all the individuals with genetic deviations from the norm are immediately eliminated from the population.

Man uses such genetic deviations in natural species for creating and cultivating animal breeds and plant varieties satisfying his own needs. Not all of the natural species produce viable individuals with genetic deviations that can be utilized by man.

Evolutionary transitions to new species are limited and occur only when the ability to stabilize the environment in the ecological community is retained. On a large time scale (billions of years), evolution may proceed with the change of the environment into different states (e.g., change from the reducing to oxidizing atmosphere), accompanied by significant reorganization of the biota. The latter, however, retains the ability to prevent the transition of the environment to a state unsuitable for living organisms. This is associated with the existence of so-called "degenerate levels" of environmental conditions, and evolutionary changes of the biota may result in its transition through the entire set of degenerate levels suitable for life.

Let us consider the main factors forming the basis of the second concept.

CLIMATE STABILITY

The Earth surface temperature is the most important characteristic of the climate. The biota as a whole can exist in a relatively narrow temperature interval in which water remains in the liquid state. At temperatures below the freezing point, only poikilotherms—mammals and birds—can survive, and temperatures approaching boiling point are tolerable only for some bacteria of hot springs. The optimal interval of environmental temperatures for the biota is between 10 and 20°C, and the average global surface temperature of the Earth has been maintained in this range over the past hundreds of millions of years, decreasing to 10°C in the glacial epochs and rising to 20°C in the warmest periods. Currently, this temperature is 15°C, and deviations from it during the last centuries did not exceed several tenths of a degree (Gorshkov, 1995).

The constant temperature of Earth surface is maintained owing to solar radiation. The magnitude of solar radiation flow depends on the position of the Earth on the circumsolar orbit. The planet reflects part of solar radiation, and this makes other planets and their satellites visible in the sky like stars. This reflected part of solar radiation is called albedo.

Absorbed solar radiation heats the Earth surface, and this heat is released again in the form of thermal radiation. The latter is absorbed in the atmosphere by the so-called greenhouse gases and partially returns to the planet surface, which results in the further increase of its temperature. This phenomenon is called the greenhouse effect. The proportion of greenhouse gases in the atmosphere is very small, and the main atmospheric gases, nitrogen (N₂) and oxygen (O₂), do not produce a greenhouse effect.

Water vapor, which accounts for less than 0.3% of the atmosphere, is the main greenhouse gas, and carbon dioxide (CO₂, 0.03%) is the second most important. The relative content of the remaining greenhouse gases does not exceed $3 \times 10^{-4}\%$.

There are two physically determined stable states of the climate, i.e., complete surface glaciation with temperature close to -100°C or complete evaporation of the oceans with temperature reaching 400°C , i.e., the states resembling the stable climates of Mars and Venus (see table) and unsuitable for life. No physical barriers capable of preventing the transition of the existing climate into these stable states have been discovered to date (see figure). The period required for such a transition is less than ten thousand years.

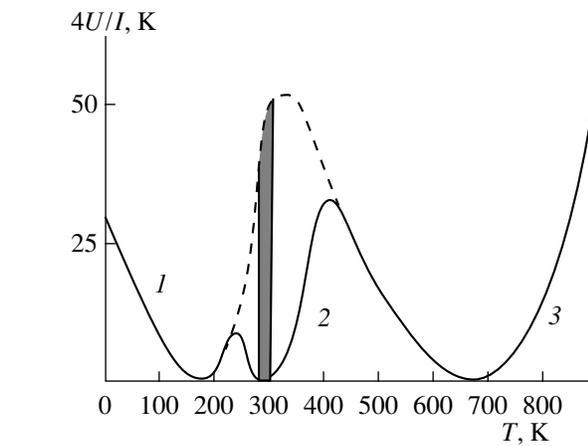
Life on the Earth has existed for 3.85 billion years (Hayes, 1996). During this period, the average surface temperature was within the range of $5\text{--}50^\circ\text{C}$, and in the last 600 million years it varied from 10 to 20°C (Gorshkov, 1995). This state of the climate is not determined physically and can only be explained on the basis of the assumption concerning biotic control of the environment. According to this assumption, the Earth's albedo, the greenhouse effect, and other parameters of the climate that are significant for life and may be affected by it are controlled by the global biota (see figure and Appendix).

Let us consider the mechanisms of this phenomenon.

MECHANISMS OF BIOTIC ENVIRONMENTAL CONTROL

Many facts confirm the existence of biotic control of the environment, and the most important of them are as follows.

1. (a) According to the analysis of Antarctic ice cores, concentrations of inorganic (CO₂) and organic (biotic) carbon in the biosphere changed by less than an



Potential function of the Earth's climates. Ordinate shows values of the potential function $4U/I$ plotted against the absolute temperature T (see Appendix). The broken line corresponds to the physical states of complete glaciation (1) and complete ocean evaporation (3), which are separated by a physical barrier with a maximum in the region $T \approx 300$ K (27°C). The solid line includes the region corresponding to the current state of the climate (2), which is determined by the stable minimum separated from states (1) and (3) by potential barriers maintained by the biota. These barriers have maxima near the points where the potential curve 2 (see the table) intersects potential curves 1 and 3. The region of temperatures observed on the Earth is hatched.

order of magnitude: $m \approx 10^3$ Gt C during $\tau \approx 10^4$ years (Lorius and Oeschger, 1994). The rates of organic carbon synthesis P^+ and decomposition P^- were about 100 Gt C/year (Degens *et al.*, 1984). These figures indicate that the global fluxes of synthesis and decomposition coincide with an accuracy of up to four significant digits: $(P^+ - P^-) \tau \leq m$.

(b) The flux of inorganic carbon from depths of the Earth to the biosphere (F^-) is about 10^{-2} Gt C per year (Degens *et al.*, 1984). During $T = 10^9$ years, the biosphere

Thermal characteristics of planets (according to Mitchell, 1989)

Planet	Solar constant	$A = \alpha = 0$ (orbital temperature)	$A > 0, \alpha = 0$ (thermal radiation into cosmos)		$A > 0, \alpha > 0$ (average values on planet surface)	
	$I, \text{W/m}^2$	$t, ^\circ\text{C}$	$A, \%$	$t, ^\circ\text{C}$	$\alpha, \%$	$t, ^\circ\text{C}$
Mars	589	-48	15	-56	7	-53
Venus	2613	+58	75	-41	99	+460
Earth	1367	+5	30	-18	40	+15
Earth upon complete glaciation			80		7	-90
Earth upon complete evaporation of oceans			75		99	+400

Note: I (solar constant) shows the power of solar radiation per unit area of perpendicular surface on the planet orbit; A (albedo) shows the ratio of reflected flux to the total flux of solar radiation; α is a coefficient of the greenhouse effect, i.e., the ratio of the thermal radiation flux reflected back by the atmosphere to the total amount of thermal radiation from the planet surface. Upon complete glaciation, the Earth's albedo is taken as equal to that of the glacial and snow covers, and the coefficient of the greenhouse effect as equal to that of Mars. Upon complete evaporation of oceans, the greenhouse effect and albedo are taken as equal to those of Venus.

should have accumulated $M \approx 10^7$ Gt C, which is 10^4 times as great as the observed amount $m \approx 10^3$ Gt C. This difference is explained by the fact that the rate of organic carbon deposition in sedimentary rocks is similar: $F^+ \approx 10^{-2}$ Gt C/year (Budyko *et al.*, 1985). Accordingly (see above), the fluxes of inorganic carbon emission and deposition coincide with an accuracy of up to four significant digits: $(F^+ - F^-) T \leq m$.

The maintenance of the climate suitable for life indicates that the concentration of CO₂, a greenhouse gas, had the same order of magnitude during the last billion years. This means that the biota controls the magnitude of synthesis and decomposition with an accuracy of up to eight significant digits. In the absence of the biota and organic carbon deposition, CO₂ emissions from the depths of the Earth would have resulted in severalfold changes in the amount of atmospheric CO₂ over the period of several hundreds of millennia.

2. The ratio of biogenic elements C/N/P/O₂ in the ocean (Redfield ratio) coincides with that during organic matter synthesis. This indicates that concentrations of these biogenic elements (BEs) in the ocean have been created and maintained by the biota (Gorshkov, 1995; Redfield, 1958; Chen *et al.*, 1996).

3. The hydrologic cycle on land is also governed by the terrestrial biota. River runoff into the ocean is equal to precipitation delivered from the ocean and is three times as small as the amount of precipitation on land. Hence, two-thirds of precipitation is accounted for by water evaporation on land, which would not occur in the absence of biota (L'vovich, 1974; Gorshkov, 1995).

4. The recent data on the distribution of radioactive carbon in the ocean and changes of oxygen content in the atmosphere indicate that the undisturbed oceanic biota absorbs excess CO₂ discharged into the atmosphere in the course of human activities. In other words, this biota functions on the basis of negative feedback, whereas the anthropogenically disturbed terrestrial biota lost this ability (Gorshkov, 1995).

5. The concentration of CO₂ in the atmosphere coincides with the concentration of dissolved CO₂ in surface waters of the ocean and is three times as low as that in its depths. This situation is maintained by the biotic pump: inorganic carbon diffusion from deep ocean waters to the surface is counterbalanced by organic carbon synthesis in the surface layer. Synthesized carbon descends to the ocean depths and is decomposed there. As a result, CO₂ concentration in the atmosphere is three times as low as it would have been in the absence of the oceanic biota (Gorshkov, 1995).

In natural communities forming local ecosystems, the relations between the physical outflow of BEs F^- and biological productivity P^+ may be different. For the soil elements, $F^- \leq P^+$. Concentrations of these BEs (for instance, nitrogen and phosphorus) may differ several times or even by several orders of magnitude from those in territories beyond the zone of activity of living organisms (Gorshkov, 1995). Changes in BEs their

concentrations in local ecosystems occur because synthesis prevails over decomposition or vice versa.

For all atmospheric gases, $F^- \gg P^+$. In this case, BEs their concentrations in a local ecosystem may differ from their concentrations in the external environment by a small value of the same order as P^+/F^- . However, if the magnitude of P^+/F^- exceeds sensitivity of the biota, the communities changing BEs their concentrations in the favorable direction gain an advantage and improve their competitiveness. The remaining communities are affected by natural selection. Therefore, all homogeneous communities occupying vast territories provide for the decrease or increase of BEs their concentrations (with respect to those in the environment) in the direction favorable for the biota. This results in the flows of inorganic elements between the environment and local ecosystems in which the mass of organic matter increases or decreases. These processes will apparently continue until the environmental concentration of inorganic element reaches the level favorable for the biota. This is how the biotic control of global BEs reserves occurs in the biosphere.

All the physicochemical systems occurring in nature are stable; i.e., they return to their initial state after the cessation of external disturbances. If the latter persist, the point of physicochemical balance is displaced. In buffer systems, this displacement is small even upon strong and permanent disturbances. The systems regulated by the biota do not change the point of stable equilibrium under the effect of any permanent disturbances that do not exceed the threshold of system destruction. In this sense, they are equivalent to physicochemical systems with an infinite buffer capacity.

BIOTIC ENVIRONMENTAL REGULATION OR ADAPTATION TO THE CHANGING ENVIRONMENT?

Two opposite responses of living organisms to environmental changes are possible.

In the first case, deviation from the optimal (for life) environmental state evokes a concerted response aimed at returning the environment to its previous state in all the species organized into natural communities. In other words, the biota responds to any accidental fluctuations of the environment by bringing it back to the optimum, preventing significant deviations from this state. This is biotic regulation of the environment.

In the second case, individuals of each species adapt themselves to changing environmental conditions so that these new conditions become optimal for them. Representatives of different species also adapt themselves to the presence of each other, which leads to their concerted existence or, in other words, to the formation of a community. This is an example of adaptation to the changing environment.

These two responses cannot be compatible. Organisms can either bring the environment back to the opti-

mum, or adapt themselves to altered conditions. If biotic control exists, species of the biota generally cannot develop adaptations to accidentally changing environmental conditions. If the biota as a whole is characterized by the adaptation strategy, biotic environmental control is excluded. Which of the strategies actually takes place can only be ascertained on the basis of unequivocally interpretable empirical data. As shown above, many observations on the stability of climate and the global cycle of matter provide evidence that biotic environmental control actually exists.

Biotic control is a very complex program, and information about it should be encoded in the genomes of species comprising natural communities. This program is aimed at supporting the concrete optimal environment. Information about characteristics of this environment should also be recorded in the genomes. If species alter their genetic program under the effect of accidental environmental changes, the new environment may become optimal for them, and this is the essence of adaptation. However, random changes of the genome in the course of adaptation cannot lead to the emergence of a new consistent program that would maintain the new environment in a stable state. If the biota regulates the environment, no uncontrolled changes can occur in the latter, and adaptation is not required. Thus, adaptation excludes biotic regulation, and vice versa.

Adaptation is associated with the ability to survive under certain conditions. The degree of adaptation is reflected in the ability to produce the most numerous progeny under given conditions. There are examples showing that two populations of the same species turn out to be adapted to two different sets of conditions so that individuals of the first population do not survive (or produce smaller progeny than members of the second population) under conditions favorable for the second population, and vice versa. This is regarded as evidence for genetic adaptation.

All such examples have a simple explanation that is not related to genetic adaptation. The genetic program of individuals is unstable and can be erased or destroyed by mutations, and this is prevented by the competitive interaction of individuals. The individuals with a strongly damaged genetic program develop obvious abnormalities and are eliminated from the population by stabilizing selection. However, competitive interaction is the process of measuring the quality of individuals, and, as any measurement, it has a certain resolving power. Until the extent of damage to the genome remains below a certain threshold, obvious malformations do not appear, and such individuals are not eliminated by selection. All subthreshold deviations from the normal genetic program are retained in the population and account for the genetic diversity of its members. This diversity is random and inadaptive. The existence of a certain threshold in the accumulation of genetic deviations is confirmed by the fact that genetic

diversity in all species is limited (Gorshkov and Makar'eva, 1997).

Stabilizing selection operates efficiently only under conditions of the natural ecological niche of the species, where normal individuals (with subthreshold levels of genetic alterations) have the highest competitiveness. Upon strong deviations from normal conditions, their competitiveness decreases, stabilizing selection ceases, and the population begins to accumulate individuals that have distinct abnormalities but remain reproductive. Their distorted genotypes lose information as to which conditions are normal and what actions are necessary for returning to them. Some of these genotypes may account for very high fecundity of their carriers, which is interpreted as adaptation to new conditions. Such phenomena may occur only in a very small part of the biota. If significant deviations from normal genotypes occurred in all species of the global biota, biotic regulation would be lost entirely, giving rise to the process of uncontrolled environmental change with climate transition into the states unsuitable for life (see the figure and the table).

Obviously, although the carriers of such altered genotypes survive and produce numerous progeny under certain abnormal conditions, this will not happen under other abnormal conditions. Domestic animals and agricultural plant varieties are illustrative examples. Indeed, domestic animals perish in wild nature, whereas closely related wild animals cannot live in captivity because they do not satisfy human requirements. Agricultural plants do not survive in the wild nature, and closely related weeds are exterminated in cultivated fields.

Thus, differences in survival and fecundity between organisms with different genotypes under different abnormal environmental conditions, provided these genotypes are eliminated by stabilizing selection under normal conditions, provide evidence for the processes of genome deterioration that erase information related to the program of biotic environmental control, rather than for adaptation of these organisms.

There is another prerequisite for the existence of biotic environmental control. The biota cannot be a globally correlated system, such as Gaia proposed by Lovelock (Lovelock, 1982). Any processes in an ordered and internally correlated system should disturb its orderliness. This process is equivalent to the accumulation of disorder (entropy) in closed physically organized systems. The only mechanism maintaining orderliness is stabilizing selection, which can operate only through competitive interactions of similarly organized individuals in a relatively large population. As the community of organisms is the basic ordered unit performing the biotic control, the biota should consist of a set of competing homogeneous communities. In this case, a community that controls the local environment in the most efficient way and provides the most favorable living conditions for its constituent species is regarded as normal (see above).

When biotic adaptation to disturbed environmental conditions is lacking, the impairment of biotic control in anthropogenically affected is reversible. The cessation of anthropogenic impact is followed by restoration of aboriginal natural communities, which carry correct information concerning normal environmental conditions and methods of their regulation.

REGENERATION OF NATURAL COMMUNITIES AFTER DAMAGE

Any disturbances of the biota or its local extermination are followed by the process of plant regrowth and restoration of natural species communities. This process, named succession, is characterized by several important properties and resembles embryonic development and regeneration of organs after damage.

In the course of succession, dominant species replace one another in a series of consecutive stages until a certain community is formed, which retains the constancy of species distribution for an infinitely long period of time in the absence of disturbances from outside. Such a system is called a climax community. Thus, climax communities in boreal forests of northern Europe are represented by spruce forests on loams and pine forests on sandy soils. Both spruce and pine forests determine the presence of corresponding communities of other species, each having a fixed population density. The climax community contains all the species determining the course of succession. In this course, the density and age distributions of species change drastically. As the process of embryonic development, succession is characterized by a definite duration: in boreal forests, the period of time required for the complete restoration of the climax community is about 150 years (Gorshkov, 1993). The similarity of these processes is also manifested in the coincidence of parameters characterizing restoration of specific climax communities in different geographic regions.

The reestablishment of plant cover after damage is accompanied by significant changes in chemical composition of the local environment, with concentrations of many biogenic elements changing by two or even three orders of magnitude (Bergeron and Frisque, 1996). The species determining successional modifications in the environment change this environment favorably for the climax species and unfavorably for themselves. These species may be called repair species. The repair species of the coniferous climax forests include birch, aspen, alder, berry-bearing plants (raspberry, cowberry), edible mushrooms, and most animals that move and feed on these repair plant species. The man, a typical repair species in the past, feels himself most comfortably among repair species in a disturbed and recovering climax community. The climax community proper appears wild and inhospitable to man.

Climax communities can maintain the most favorable local environmental conditions in a steady state,

compensating any accidental perturbations. This behavior of the natural biota accounts for biotic environmental control.

The repair species of a succession are programed to change the local environment unfavorably for themselves. Therefore, they cannot principally maintain the environment in a favorable (for them) state. This fact may be erroneously interpreted as a lack of biotic control. In the course of succession, the local environment passes through several stages, each characterized by a certain range of changes in concentrations of nutrients in organic and inorganic forms, the distribution of energy fluxes in different species of biota, and the pattern of biochemical reactions. These parameters are favorable for certain repair species, and the latter become more competitive, displacing all the repair species of other succession stages, including the climax species. The activity of the repair species at the corresponding stage leads to directed changes in the concentration of nutrients, which eventually goes out of the range favorable for these organisms; hence, they lose competitiveness and are replaced by the repair species of the next stage. This process is the essence of succession. It continues until all environmental concentrations reach the values favorable for the climax species at which these species acquire the highest competitiveness and the ability to maintain the environment in this state until the next serious disturbance.

It is impossible to halt succession in the steady state at any of its stages, as it is impossible to interrupt embryonic development. External disturbances can either hinder the succession process or, if their magnitude exceeds a certain threshold, destroy it. After the cessation of such a strong disturbance, succession begins from the initial stage.

The climax species can maintain genetic stability of the repair species by removing from the population degraded individuals with a distorted genetic program, which have lost the required level of competitiveness. This is equivalent to "artificial" selection among representatives of the repair species performed by the species of the climax community. This selection makes it possible to "switch off" competitive interactions between individuals of the repair species and to maintain its existence in the form of isolated individuals that interact only with the climax species and do not form their own population in a climax state. The repair species, however, necessarily forms a population at the corresponding stage of the succession process. In this case, direct competitive interactions between representatives of the repair species additionally support its genetic stability due to stabilizing selection in its population.

When communities do not return periodically to the climax state, they lose information about the environmental conditions optimal for and maintained by the climax species and about the consecutive stages of succession leading to the restoration of these conditions.

The loss of this information and the exclusive preservation of forms necessary for man—repair species of a certain stage or their genetic modifications—results in irreversible damage of biotic environmental control, and the environment loses its stability on a global scale.

CONCLUSIONS

Thus, when biotic environmental control is in effect, the biota is not simply a random aggregation of species adapting themselves to existing environmental conditions, but rather the mechanism of environmental management based on the species selected in the course of evolution and carrying genetic information necessary for this purpose.

The total number of organisms in the biosphere is in the order of 10^{28} , and most of them are unicellular. The biotic control of the environment is based on the functioning of dozens of living organisms per square micron of the Earth surface. Each cell of these organisms processes the amount of information on the environment comparable to information flows in modern personal computers (Gorshkov, 1995). Hence, there is no technological means to substitute 10^{28} organisms of the biota in their work or to improve biotic control.

The magnitude of biotic control is sufficient for counterbalancing current anthropogenic disturbances, provided that the natural biota is restored in vast areas. The prospects of mankind's survival depend on the restoration of the natural biota on the greater part of the planet to the extent sufficient for maintaining its ability to regulate the environment on a global scale. The main ecological task of mankind is to preserve the natural biota, rather than to reduce anthropogenic pollution. To do this, it is necessary to prevent the advancement of exploitation of the biota (in particular, in the open ocean) and to restore the natural biota on the major part of the developed land.

Appendix

PHYSICALLY AND BIOTICALLY STABLE CLIMATES ON THE EARTH

The thermal balance of the Earth surface is determined from the equation

$$\begin{aligned} c \frac{\partial T}{\partial t} &= \frac{I}{4}(1-A) - \sigma T^4(1-\alpha) \\ &= \frac{I}{4}a - \sigma T^4 b \equiv -\frac{\partial U}{\partial T}, \quad a = 1-A, \quad b = 1-\alpha, \end{aligned} \quad (1)$$

where $T = \tau + 273^\circ\text{C}$ is absolute temperature on the Kelvin scale, τ is temperature on the Celsius scale, I , is solar constant, A is albedo, α is coefficient of the greenhouse effect, σ is Stefan-Boltzmann constant, c is global average heat capacity per unit surface area, cT is thermal energy of unit of surface area, and t is time; it

is assumed that $\partial c/\partial t \approx 0$; coefficients a and b in general case depend on temperature T (see the table). The right side of (1) may be regarded as force equal, by definition, to the negative gradient of the potential function U (the Lyapunov function) with respect to temperature T .

The function U is derived by integrating the equation (1). The integration constant is fixed by the condition of minimal U value reduction to zero. In the interval where coefficients a and b are constant,

$$\begin{aligned} U &= \frac{I}{4}aT \left[x \left(\frac{x^4}{5} - 1 \right) + \frac{4}{5} \right], \quad x \equiv \frac{T}{T_0}; \\ T_0 &= \left(\frac{aI}{4\sigma b} \right)^{1/4}, \quad \sigma = 5.75 \times 10^{-8} \text{ BT}/(\text{M}^2 \text{ K}^4), \end{aligned} \quad (2)$$

where T_0 is stationary equilibrium temperature appearing at $\partial T/\partial t = \partial U/\partial T = 0$. The inequality $\partial^2 U/\partial T^2 > 0$ corresponds to steady stationary states. In the domain where coefficients a and b are constant and independent of temperature, all states are stable.

The states of complete glaciation (1) and complete ocean evaporation (3) (see the figure) correspond to the solid and gaseous states of water (see the table), in which albedo and the greenhouse effect change insignificantly with temperature, and coefficients a and b in (1) and (2) may be considered constant. The current state of the climate (water in the liquid phase) corresponds to coefficients a and b physically changing with temperature and, within the accuracy of recent data (North *et al.*, 1981; Gorshkov, 1995), is not physically stable with respect to the transition into states 1 or 3 (figure, broken line). The stability of the existing climate may result from biotic environmental control, which apparently maintains average global values of coefficients a and b on a more or less constant level, notwithstanding the observed latitudinal changes of this coefficients with temperature (North *et al.*, 1981); hence, a stable potential well appears, which is separated from states 1 and 3 by potential barriers (figure, solid line). Transitions between the states are possible near intersections of the respective potential curves, which approximately indicate the maxima of these barriers.

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The problem elucidated by the authors of aforepublished paper is of obvious interest both for specialists in the sphere of environmental protection, in geosciences and for biologists. Editorial Board considers it necessary to publish, in connection with the significance of given problem, the biologist's (who reviewed the manuscript) viewpoint as well.

Editorial Board

Fitness or Biotic Regulation?

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The paper presented by V.V. Gorshkov, V.G. Gorshkov, V.I. Danilov-Danil'yan, K.S. Losev, and A.M. Makar'eva deals with an important problem which has arisen at the current stage of development of biology and, in particular, ecology. The question is posed as to *the compatibility of concepts of the biota as a complex system that provides the local and global conditions of its own existence (i.e., a self-organizing and self-regulating system) with the evolution paradigm*, which is the cornerstone of the modern biology. This question is indeed extremely important and calls for further discussion. The authors state that the fitness concept, which is generally accepted in the modern evolutionary biology, contradicts the decisive evidence indicating that living organisms and their ensembles are involved in sustaining the constant environmental conditions that ensure the very existence of life on the earth.

Before we consider this question, some remarks are in order. First, the generally accepted criterion of fitness is not merely the number of offspring (as might appear from the article). It is actually *the average number of offspring produced by an individual throughout life and surviving until reproductive age*. These definitions substantially differ from each other. In the latter case, not only reproduction rate per se, but also other demographic characteristics (period of maturation,

lifespan, and mortality at different stages of the life cycle) are taken into account. These characteristics are integrated in the form of the so-called instantaneous rate of population growth (Gaughley, 1979). In the modern evolutionary ecological studies, this value is assumed to be the measure of fitness (Stearns, 1992). In these studies, it was theoretically demonstrated that different types of life cycles will be optimum (in terms of providing the maximum possible instantaneous rate of population growth) under different conditions. For example, a certain set of environmental conditions may favor a high fecundity accompanied by a rapid maturation and a short lifespan, whereas some other conditions will favor a low fecundity, a slow maturation, and a long lifespan. Empirical data agree with this suggestion and fit the concept of the *r*- and *K*-selection (MacArthur and Wilson, 1967).

Second, it is incorrect to draw an analogy with a closed system when speaking of the biosphere, as the authors do albeit in an implicit form. Indeed, all the work in the biosphere is performed due to solar energy; hence, the biosphere is undoubtedly an open system. Disorder (an increase in entropy and a loss of free energy) is not necessary for open systems, although the second law of thermodynamics (i.e., the necessity of irreversible processes) still holds true for them. Disorder is not inevitable because the difference between

the influx of free energy from outside and its loss due to irreversible processes may be both negative and positive (Popper, 1965; Prigogine and Nikolis, 1973).

However, these notes do not eliminate the problem posed by the authors, who essentially propose an alternative to the generally accepted criterion. This alternative is *the evolutionary criterion, i.e., the ability to sustain a certain constant state of the environment*. In this case, the term “environment” refers primarily to the abiotic component of the biosphere. To estimate the validity of the authors’ statements, it is necessary to understand whether the requirement of constancy actually contradicts the possibility of selection for the maximum growth rate.

In this connection, the mathematical model suggested by Eigen (1973) appears to be relevant. This model describes the system of carriers, which are interconnected by flows of matter and energy and are capable of replication, as a set of nonlinear differential equations. Eigen developed this model as a part of the theory of biological hypercycle (which won him the Nobel Prize) and considered it a model of prebiological evolution; however, this is also an appropriate model of interacting population in an ecosystem. In this case, the conditions postulated by Eigen result in self-regulation, competition, and interactions of the predator–prey type, and Eigen’s model becomes a generalization of Lotka–Volterra equations, in which these relationships are postulated a priori (Hofbauer and Sigmund, 1988). The main conclusion drawn from the analysis of the model is that, in such systems, the proportion of elements with the maximum replication rate increases. The system approximates a certain metastable state characterized by a definite distribution of elements of different type. Eigen theoretically proved (which is his generally recognized merit) that selection for reproduction rate inevitably appears in the system that has certain properties and consists of elements exchanging the substance and energy flows with one another. In terms of the problem in question, the main property postulated by Eigen is the constancy of the total number of elements. Eigen interpreted this as a constant total concentration of macromolecules of different type; if we simulate an ecosystem, this should be interpreted as a constant total mass of living organisms.

Ecologists know that the density of biomass of different species at the same trophic level is almost constant, notwithstanding individual differences in body weight and abundance of each species. Apparently, the concept that the density of living matter in the biosphere is relatively constant (Vernadskii, 1978) holds true.

However, the suggestion concerning the constancy of the mass of biota as a principle of its existence is not convincing. In any case, we may assume that the constant conditions of the environment in which life is possible at all (the principle postulated by the authors) are

indeed necessary for the biota to exist. If a self-reproducing system expends energy on maintaining the constant environment, counteracting irreversible processes that destroy it, then the dynamics of this system may be described in a simplified form as

$$x'(t) = x(A - R) - Re,$$

where A is the specific rate of energy influx to the system, R is the specific energy expenditure on maintenance, and e is a constant reflecting the constancy of environment. Since the work on maintaining the environment is performed at the expense of the system x , the total expenditure on maintaining the environment must be proportional to x : $Re = Fx$. Then, the system dynamics is described by the classical Verhulst–Pearl equation:

$$x'(t) = rx(1 - x/K),$$

where $r = A - F$ and $K = re/F$.

The logistic equation is interpreted in terms of the necessity to maintain environmental conditions. In this case, K (the environment capacity) reflects the sufficiency of energy resources (A), expenditures for maintenance (F), and (which is important) the state of the abiotic environment (e). If the system consists of a multiplicity of “populations” exchanging the flows, and the contribution of each “population” to the maintenance of the common environment directly depends on its proportion in the total mass, then the behavior of each “population” in a constant environment can be described as follows:

$$x_i(t) = (A_i - \sum F_{ij}x_j/e + \sum k_{ij}x_j)x_i,$$

where k_{ij} is the intensity of the flow from the j th to the i th population. This value may be either positive (“predators”) or negative (“prey”). The value A_i may be either positive or zero (“autotrophs” and “heterotrophs,” respectively). It is important that the coefficients of self-regulation, competition, and predation are determined by the conditions of the environment constancy. In general, the behavior of the system follows the same pattern as Eigen’s canonical model; namely, selection for the maximum reproduction rate arises.

Thus, the above considerations demonstrate that, in theory, *selection for reproduction rate* (which serves as a criterion of fitness) *does not contradict the concepts of the environment-maintaining function of biota*. However, the question remains as to whether “malignant tumors” deteriorating the environment can emerge and temporarily flourish; and this appears to be the most important question today.

An undeniable merit of the authors is the fact that *the principle of the maintenance of environmental conditions*, which they propose as the necessary condition of existence (and, apparently, evolution) of the biosphere, may revolutionize evolutionary ecological con-

cepts and have impact on other related sciences. If this principle is generally accepted, its scientific and practical importance will be difficult to overestimate.

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