

Chapter 12

Biotic Mechanisms for Supporting Environmental Stability



From the materials of the previous chapter, you can probably already understand the level of organization the biota imposes on its non-living (abiotic) environment, and the role it plays in forming every component of the biosphere. And one must offer tribute to the remarkable balancing ability of this titanic mechanism in bringing the intricate biochemical and hydrological cycles together into a single whole and providing support for the environmental conditions crucial to life. But while we witness such a harmonious concordance on the greatest scale, it's not hard to guess that it begins at the smallest—from the ecosystem and biocenose, the internally correlated cells of the biosphere. In them, each of the species belongs to a biological community, set within a complex trophic chain through which cycle energy and chemical substances necessary for life.

If we take energy as a base, then this cycle begins, as you know, with plants (producers, photoautotrophs). These are the only organisms, with the exception of a few species of bacterial chemoautotrophs¹, capable of synthesizing complex organic molecules from simple mineral compounds using energy from solar radiation (photosynthesis). It is through them that the flow of energy enters a biotic community, along with the organic materials used by consumer organisms of the first, second and following degrees—herbivores, predators and detritivores—and finally the bacteria and fungi that decompose dead tissue (reducers). Each of the species occupies its own particular ecological niche, which is understood to be not only its physical habitat, but also its role in the community—its feeding habits and interrelationship with other species.

Thus, the roots, trunk and canopy of a given tree grant haven to a great multitude of plant-eating insects and their larvae who eat its leaves, bark and adjacent layers of wood. In turn, these too serve as quarry for predatory insects, birds, and other insectivores. Furthermore, flying insects pollinate the tree as it flowers and birds,

¹These bacteria have the ability to gather energy for organic synthesis from the decomposition of several chemical substances—hydrogen sulfide, ammonia, etc. However, in the overall cycle of matter, they play a relatively minor role.

gulping down its ripe fruit, spread its seeds together with their excrement. When the first, second and third complete their life cycles, the forest “garbage men” get to work. These detritivores—insects and other small invertebrates—feed on carrion or store their eggs within it, providing the newborn larvae their first meal. Finally, at the ultimate stage of this transformation, this remaining undecomposed organic material is reprocessed by the true reducers, fungi and bacteria, who decay it to low molecular-weight compounds accessible to the root systems of plants, which thus restore chemical elements necessary for life to the living from the dead.

Of course, the success and efficiency of this cycle would be impossible unless the scale of consumption for each species was balanced by the consumption of all others. Thus, for example, if the activity of birds and other insectivorous animals and insects were on order lower than that of bark-eaters, aphids and other “wreckers” that often reproduce according to a geometric progression (one aphid, by the end of summer, could produce 13 generations of progeny or 1024 individuals), then an entire forest would be stripped bare from top to bottom in a matter of weeks.

But besides the balance of species within a community, no less important to an ecologist is the interaction between this community and its non-living environment. Here a researcher might allow himself to temporarily forget the existence of distinct species (much as a zoologist, researching the behavior of an animal, does not think about the function of its heart or kidneys) and approaches the biological community as an autonomous functional unit, primarily paying attention not to the particular but to the general features independent of concrete conditions or the geography of the habitat. In ecology this is known as the *ecosystemic approach*, and one of its central tasks is to reveal the fundamental rules that equally govern any ecosystem, even those which differ as much from each other as, let’s say, tropical forest, the Eurasian Steppes or the Canadian Arctic tundra.

Let’s start at the basics. Like physics, biology has a concept of *work*. Only this is applied not to a machine, but to a living organism. This concept reflects the quantitative characteristics of consumption and reworking of energy in the process of fulfilling one life function or another. In this sense, work can refer to intracellular synthesis, matter transport from one part of the organism to another and transmission of impulses along the nervous system, not to speak of the mechanics of contracting muscles and the body’s locomotion through space.

As we’ve said, this process of transforming energy begins with plants, capable of directly catching the sun’s rays, while other living things receive it along with food in the form of chemical bonds with complex organic molecules. At the same time, not only the individual organism but the entire biotic community can be like a mechanism that consumes energy and fodder for the mutual execution of work in the interests of the community as a whole. We could mention its support for the water cycle or the processing of dead organic material into low molecular-weight compounds accessible for use by plants. And as a result, the vector of all these interconnected processes, both of the biocenose (ecosystem) level and for the biota as a whole, is directed at preserving environmental parameters beneficial to life, without which it (life) would be simply impossible.

Supporting conditions beneficial to life, however, primarily means effectively opposing those forces which are ever ready to stamp that life out, or at the very least to expel it from some territory or another. In the language of non-equilibrium systems theory, this effect means one thing: *perturbation*. Perturbation for the biosphere includes sharp cooling of the climate (glaciation), shifts in the concentration of chemical substances necessary for life, hurricanes, forest fires, and so on.

It stands to reason that the biota is incapable of influencing such natural events as volcanic activity, tides or tectonic shifts. However, it can adapt to them, forming corresponding mechanisms able to compensate or tamp down on detrimental consequences of these and other natural events, shifting the balance of nutrient consumption toward neutralizing perturbations as they occur and thus easing a return of the environment to an unperturbed state (analogous to Le Chatelier's principle of thermodynamic equilibrium in physio-chemical systems). And since the biota's basic instrument to affect the environment is the synthesis of organic substances and their destruction, then we might speak of changes in the relative intensity of these two processes in the biosphere (Gorshkov et al. 2000a: p. 110–111).

So, excess carbon dioxide gas in the atmosphere can be absorbed by way of intensifying organic synthesis and transformed into the form of organic carbon. By the same token, a shortage of CO₂ in the atmospheric air could be supplemented by the decomposition of organic stores created earlier and stored in soil humus, peat or organic substances dissolved in the ocean (oceanic humus), where 95% of these substances in the biosphere are concentrated. At the same time, the biota's ability to create raised localized concentrations of nutrients bears unquestionable witness to the fact that synthesis flows and the decomposition of organic material significantly exceeds physical transfer flows of nutrients.

For example, the level to which soil is enriched with the organic and inorganic compounds plants need significantly increases their concentration in lower soil layers where organisms do not live. From this, it follows that nutrient concentrations in the soil are regulated biotically. The same relates to phytoplankton absorbing excess carbon dioxide arising from the ocean depths (a biotic pump). Therefore, and here we observe the same productive role of the biota, the supporting gradient of CO₂ concentrations is an order larger than if it were conditioned only by physical factors—the stirring of the deep water and surface layers of the ocean. In this way, by absorbing carbon dioxide gas dissolved in the ocean, it erects a roadblock to its unencumbered diffusion into the atmosphere, helping to maintain CO₂ concentrations in the air at the level necessary for life.

Another, even more massive reservoir of inorganic carbon, and a source of its entry to the atmosphere, is volcanic activity. Scientists estimate that the power of this geophysical flow is roughly equal to 0.01 gigatons per year. At the same time, global reserves of biospheric carbon make up within an order of magnitude of 10³ gigatons (Degens et al. 1984; Holmen 1992), and, therefore, this quantity could accumulate through emissions from the inner Earth over the course of about one hundred thousand years. Life on Earth, however, has existed for about four billion years. Thus, over only the Phanerozoic Eon (the last 800 million years), the overall quantity of inorganic carbon in the biosphere should have, theoretically, grown by

ten thousand times. As you can see, this did not occur. The reason for this is the depositing of organic carbon in sediments formed in the process of rock erosion. And, as has recently been established, a crucial role in this is played by plants and micro-organisms (Schwartzman and Volk 1989).

As noted above, carbon dioxide, in the process of erosion, dissolving into rain and groundwater to produce carbonic acid, reacts with silicate minerals in rock and is carried out to the World Ocean in the form of bicarbonate ions. Here, after a number of transformations through the sea biota and after it dies away, carbon, now in the form of organic compounds, is removed from circulation and forms seabed sediment deposits. The depth of these deposits reaches dozens of meters in some places, and, as researchers of recent decades have shown, concentrations of these dispersed granules in them are on the order of 10^7 gigatons of carbon (GtC), accumulated over the period of roughly a billion years (Budyko et al. 1987). In this way, the flow of deposited organic carbon in sedimentary rock coincides with the geophysical flow with relative exactitude on the order of 0.01 gigatons per year (Fig. 12.1).

On the other hand, we cannot fail to notice the correlation in order of magnitude between global reserves of organic and inorganic carbon, which speaks of an equality between flows of organic synthesis and organic destruction maintained by the biota to a highly exact degree. Granted, it is not yet possible to measure these reserves directly with sufficient reliability. Thus we can only judge them within the order of magnitude $\sim 10^2$ GtC (Whittaker & Likens 1975; Holmen 1992; Gorshkov et al. 2000b), and by their tendency to change in the past—through indirect evidence. So, for example, research into the CO_2 content in air bubbles from ice cores in Antarctica and Greenland, taken at various depths and, therefore, at different ages, have shown that its atmospheric concentration has stayed more or less constant for the past ten thousand years (Neftel et al. 1982). For times measured in hundreds of thousands of years, atmospheric CO_2 concentrations maintained an order of magnitude (Barnola et al. 1991). Such a correlation, of course, cannot be a coincidence. It bears witness to the enormous potential of the natural biota, providing compensation for environmental perturbations in the interest of maintaining its own stability.

Along with this, on the basis of relative values shown in the diagram, you can calculate the rate at which the biota runs through all the organic and inorganic carbon in the biosphere through the processes of synthesis and decomposition. The relative value for reserves of both one and the other ($\sim 10^3$ GtC) to the global biota's productivity ($\sim 10^2$ GtC/year) characterizes the turnover time for nutrient reserves in the biosphere on the order of less than one hundred years. That is, using only the synthesis of organic substances, all of the inorganic carbon in the biosphere could be expended and converted to organic compounds in the space of mere decades. The inverse also holds true: using only decomposition, all the organic carbon in the biosphere could also be expended in a matter of decades.

Due to this, the question must arise: Why does the biota “need” this enormous and even seemingly excessive biological productivity? After all, to compensate for perturbations such as inorganic carbon emissions from volcanic activity, it would theoretically require a productivity level lower by four orders of magnitude.

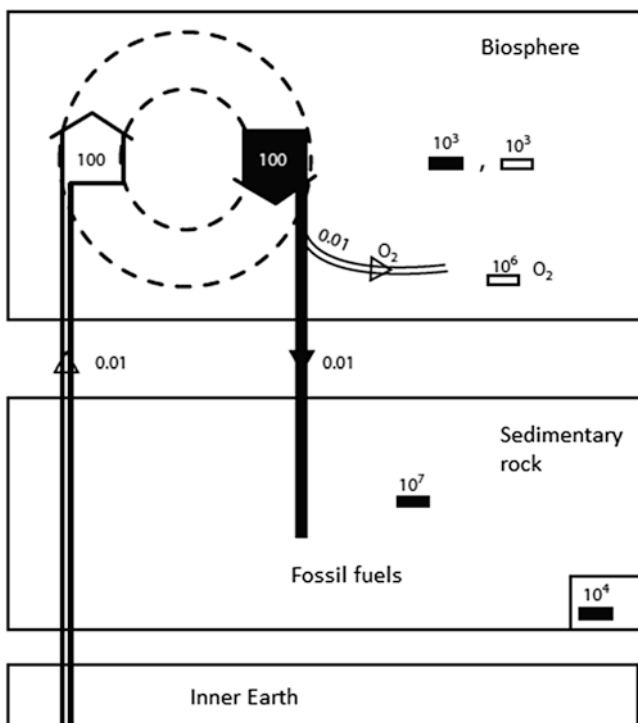


Fig. 12.1 Yearly flows and reserves of carbon in the biosphere, according to Viktor Gorshkov (1995). Carbon reserves are the numbers above small rectangles in units of gigatons of carbon (GtC). Carbon flows are numbers on arrows GtC/year. Flows and reserves of organic carbon are in black or above black rectangles, respectively. Flows and reserves of inorganic carbon are depicted in the white arrow or above empty rectangles. The flow of organic carbon deposits in sedimentary rocks is equal to the difference between its synthesis and decomposition in the biosphere. This flow coincides with a pure flow of inorganic carbon into the biosphere, with relative exactitude on the order of 10^{-4} . The flows of synthesis and decomposition coincide so exactly that they have provided a consistent reserve of organic and inorganic carbon for the whole Phanerozoic Eon (6×10^8 years). At the same time, all oxygen liberated through photosynthesis has accumulated in the environment (underlined by the hollow line and rectangle, number in GtO₂) and is not deposited in sedimentary rock (Gorshkov et al. 2000 p. 117)

However, inconsistency defines geophysical processes on Earth, and, along with more or less regular environmental perturbations, the geological record also contains instances of significantly more serious cataclysms like the great glaciations, sudden outbreaks of volcanic activity or the crash of major asteroids. Therefore, the surplus power of the biota in terms of organic synthesis and decomposition cannot be treated as anything other than an adaptation, kept in reserve, you might say. This allows it, in a relatively short period of time, to also compensate for extreme environmental perturbations and thus provide for the survival of most biological species—as it was, for example, during the last ice age.

The enormous power acquired by the biota, however, presents a certain danger to the environment. When the parity of synthesis and decomposition is violated, the environment can undergo dramatic changes in the space of a few decades. This may occur, for example, in cases of deep change to the internal structure of the biosphere which we will explore later. For now, we will only mention that attempts to artificially reconstitute nature, like the drive to maximize productivity levels in man-made agrocenoses, threaten much greater perturbation and accelerated degradation of the environment than even complete local extirpation of a biota, as in cases of desertification.

The rapid increase in atmospheric carbon dioxide concentrations over the past century stands as indirect witness to this. Until recently this was linked only to combustion of fossil fuels. In answer to such an environmental perturbation, it would seem the biota, reacting in accordance with Le Chatelier's Principle, should swallow up the excess carbon dioxide gas accumulated in the atmosphere. A global analysis of land usage shows, however, that on land under human cultivation, the quantity of organic carbon accumulated by disrupted ecosystems is not increasing but decreasing (Houghton et al. 1983, 1987). Meanwhile, the rate of carbon emissions into the atmosphere from the perturbed continental biota corresponds within an order of magnitude to the rate of fossil carbon emissions from combusting coal, oil and gas (Watts 1982; Rotty 1983). How this threatens the biosphere and what practical conclusions we should draw from this will be discussed in detail in Chap. 15.

But how can the biota maintain so exactly the parity of synthesis and decomposition of organic matter over the course of millennia and even geological epochs? After all, the unusual complexity of life expressed at the biomolecular, cellular and organism level is at once its Achilles heel. For the more complex the organization of a given system, the more vulnerable it is to gradually mounting disorder (entropy) and the more inevitable its chances of degradation and collapse. This rule proves true even for the genetic program of an organism, that guarantee of reproducing life over generations, which is also vulnerable to mounting destructive changes appearing among the progeny of each individual. At the same time, the number of defective individuals could be viewed as a specific characteristic of a species. Thus among humans, for example, one of 700 newborns suffers from Down's Syndrome, and of a hundred people living to age 55, one will come down with Schizophrenia, the predisposition for which, as you know, is genetic.

Among the above-mentioned types and levels of correlated life systems, we do not see great distinctions in biocenoses, the elementary cells of the biosphere where each species occupies its own ecological niche without overlap from other species and fulfills its own specific share of work to stabilize the environment. Correlations within a single given community, however, can be rather strict. Each of the ten-thousand-plus species of lichen, for example, is not an organism at all, but a symbiosis of organisms: a very particular sort seaweed and a particular type of fungus (Farrar 1976). Some insects can feed on only single, lone species of plants (Raven and Johnson 1998), while the flowers of some of those plants can be pollinated only by a particular species of butterfly, etc. So in a normal, unperturbed community, there is no interspecies competition, and, thanks to almost total impermeability of

the cycle of matter, practically no waste. Specifically, it is the need to maintain a high degree of isolation in the matter cycle that dictates the need for the existence of sustainable biological communities.

But while the correlation of a biogeocenose community is brought about by the necessity of maintaining parity between organic synthesis and decomposition, that very correlation also serves as the cause of its relative short-livedness and inevitable collapse with the passing of time. Collapse of a community owes itself to the accumulation of mutant individuals diverging further and further from the species standard and the gradual weakening of the correlation of species, which, in the struggle for food resources, begin to occupy overlapping ecological niches. Such a community, being already in no condition to maintain the stability of the local environment, loses its ability to compete and ultimately disappears from the face of the Earth.

This contradiction between the finiteness of both individual and “collective” organisms (biocenose) and the infiniteness of life in the whole of nature is resolved along a path both prodigal and the only possible: on the basis of competition and selection of autonomous individuals (within a single species) or independent biological communities (within an ecosystem). Thus, among the population are preserved only individuals with an undistorted genetic program and only communities with a species structure that preserves the ability to successfully compensate for chance fluctuations and perturbations in the environment.

Interestingly, humanity came to this very principle of competitive interaction as a result of its many-thousand-year social evolution. This is how the free market functions, crowding out inefficient producers. Extending this principle to such natural structures as biogeocenoses and ecosystems, Gorshkov came to a conception of its universality for nature and society. And it’s no coincidence that he named one chapter of the monograph, *Physical and Biological Bases of Life Sustainability* (1995), “The Biosphere as Free Market.”

If the reader has not forgotten the barrage of criticism that evolutionary biologists once unleashed on the “Gaia Hypothesis,” then now would be a good time to recall the main points emphasizing a distinction between Lovelock’s concepts and Gorshkov’s. Lovelock imagined a grandiose global mechanism uniting living and nonliving components into an indivisible whole in the interests of preserving the planetary environmental parameters necessary for life. Gorshkov conceives of a “biotechnology marketplace” formed of a great multitude of biological “players”—communities and individuals. Lovelock—the colossal complexity of energy and matter flows penetrating the biosphere, maintained over the course of tens or hundreds of millions of years, but at the same time initially unsustainable and doomed to inevitable collapse and death. Gorshkov—the necessity of permanently maintaining “ecological solvency” and of the right to a place in the sun for each separate individual and each local community as they are run through the sieve of competitive selection, thus attaching to progeny their own species and genetic makeup. In this way, according to Gorshkov, nature “imposes order,” working upon an uncounted multitude of independent operating units on the basis of the statistical law of averages, thus minimizing chance fluctuations that threaten the existence of any complexly organized system.

And if we descend one or two steps lower, from the biological community to the separate individual, then we can give examples of how the biota resolves problems analogously at the organism level. For example, the “distributive” circulatory system in animals, using many mutually uncorrelated blood vessels with the aim of dependably providing cells with oxygen (erythrocytes) and disarming elements alien to the body (leukocytes). Or the chaotic mass of randomly oriented leaves on trees and bushes, allowing for maximal catching of the sun’s solar rays, and so on.

The idea of the biota’s sensitivity to environmental perturbation occupies a special place in the concept of biotic regulation so we will look into it at some depth. The thing is, like the “Gaia hypothesis,” Gorshkov’s theory also has its thorny spots from the evolutionary biologist’s point of view, though of a different order. As we have noted, classical evolutionary theory focuses its attention upon the fate of the individual, the isolated exemplar jokingly dubbed an individualist. But, as we say in Russia, in every joke there is a bit of truth, and this is no exception. Natural selection in the Darwinian understanding has to do with manifold variations within a single population (the species) and the differing degrees of success in adapting to the changing conditions of the environment which provide a greater chance of survival (and preservation of a genotype in offspring) to some and deny such chances to others. At the same time, that which is adequate for a changing habitat has nothing to do with what kind of changes occur, or if they ultimately threaten the well-being of the population or the community as a whole. It is enough for them to survive for the moment and adapt to the concrete conditions that arise.

Things stand entirely differently when the criteria for selection is the capacity to perform work to stabilize the environment. It would seem that selection should make no distinction between communities or individuals forming them, dependent on how well or poorly they execute this mission of theirs. After all, if environmental conditions get worse, both one and the other would find themselves in the same disadvantageous position. And, furthermore, communities that successfully work “for the common good” are also using a portion of their energy resources, and should lose out in competition with those communities that economize them. How then can they survive in the struggle for a place in the sun, and why, in the billions of years that life has existed, has its capability for biotic regulation not disappeared in the endless chain of mutations passed from generation to generation?

To find a way out of this theoretical dead end, Gorshkov proposed adding the concept of *biotic sensitivity* – ϵ to external perturbation. According to this idea, the biota reacts only to those changes in the environment that surpass a certain particular ϵ point (understanding that as the level at which an environmental parameter diverges from its average value).

Probably some of our attentive readers, having visited the forest in summer, managed to notice that breathing feels different under the dense cover than it does in an open, freely circulating field. Even temperature and moisture there distinguishes itself from that of neighboring tracts. Within their canopy cover, trees are able to support their own microclimate and maintain soil conditions on the area of their root systems (Gorshkov and Makarieva 2007). Soil scientists have cast their gaze elsewhere: when moving from tree to tree, cross-sections of soil even from a single

source rock have boundaries clear to the naked eye in color, structure and texture. But as we've already established, soil forms through the collective work of all components of a biological community, including bacteria and fungi. If the results of this work can vary even between the territories of neighboring trees, that confirms the fact that each such community acts as an autonomous cell of the biological cycle.

Of course, a local environment on the scale of a single tree and its correlated soil biota is incomparable with the internal environment of an animal's body maintained in a homeostatic regime. The former is blown by winds and washed by storms, and so various fluctuations are practically inevitable. And furthermore, the processes of nutrients, dissolving in the atmosphere and physically mixing with the soil, at first glance seem to nullify the possible distinction of a local "microcosm" of biocenosis communities. And yet the ability of separate mature trees to form an internal atmosphere of a canopy in which the carbon dioxide gas content, for example, can differ from average atmospheric concentrations, still goes beyond doubt. And the whole problem is in how the biota reacts to such differences.

According to the assessments, the biota's sensitivity to changes in the majority of parameters corresponds to a magnitude of 10^{-2} to 10^{-3} (Gorshkov et al. 2000a: pp. 70–71; Gorshkov et al. 2004). Thus, if a shift in the concentration of carbon dioxide gas detrimental to the community in atmospheric air adds up to less than 10^{-2} —let's say 1/1000 of a percent—then the biota will not notice the change and not react to it. At the same time, a difference in CO_2 concentrations of one percent may be critical for a normal community and lead to its functional restructuring. This restructuring could express itself, for example, by depositing excess carbon in organic soil humus, or, in the case of a CO_2 deficit in atmospheric air, to intensifying processes of destruction and release of inorganic carbon. The same relates to soil quality maintenance and the surrounding air, on which a single tree can exert its influence to a certain extent, either to increase or to decrease. It does this by changes to transpiration, the vertical temperature gradient under the canopy, emission of nutrient aerosols into the atmosphere and other, still little researched, processes (Gorshkov and Makarieva 2007).

In this way, a community, having a sensitivity of $\epsilon \approx 10^{-2}$, acquires a small but noticeable advantage when compared to mutants with a sensitivity point of $\epsilon > 10^{-2}$, unable to maintain the local environment at settings beneficial to themselves. This ability of trees to maintain sensitivity at a level of $\epsilon \approx 10^{-2}$ affirms itself genetically in the process of individual selection. As a result, mutant trees, having lost this ability and now inadequately sensitive ($\epsilon > 10^{-2}$) are gradually pushed from the ecosystem.

Now let us imagine a situation when, as a result of some destabilizing effect, for example, volcanic emissions of carbon dioxide gas, its concentration in the atmosphere materially surpasses the optimal mark for the biota. In that case, with the corresponding level of sensitivity in the biotic communities that make up an ecosystem, this inorganic carbon begins to get absorbed and is converted to an inactive organic form. And if the overall area occupied by such an ecosystem is large enough, a globally significant physical flow of the nutrient comes about from the external environment into the arena of life functions. Obviously, this flow will exist until CO_2 concentrations within and without the ecosystem match each other with the

exactness corresponding to the biota's sensitivity, that is, until the global nutrient concentration in the external environment reaches a value beneficial to the environment. Such is the basic scheme of the biotic regulation mechanism, passed from generation to generation in the process of competition and selection of specific biotic communities.

One argument in favor of biotic regulation of the environment comes in the form of Henry Cowles' discovery of and Frederic Clements' further research into the phenomenon of ecological succession. Succession is the process of an ecosystem's evolution, distinguished by sharply delineated stages and the seemingly pre-programmed replacement of one group of dominant species by another.

So, for example, a newly formed volcanic island is first colonized by blue-green algae (cyanobacteria) and pioneer communities of lichen, which have no need of soil cover. The space of several decades will pass before they form a layer of soil on which more complex organisms can find suitable conditions. At first this could be moss or non-vascular plants, followed by grasses, then still later by bushes, and, finally, trees. And each previous community seemingly leads the following by the hand, surrenders its place and passes along the baton. At the ultimate stage of succession, a sustainable and self-sufficient community forms, which, barring external disruption, is capable of sustaining equilibrium with the environment indefinitely so long as biomass and population density of specifically developed species remains constant. Examples of communities having completed succession, known as climax communities, include oak forests in wet clay soils or pine and fir forests typical of the European north growing in sandy clay and loam.

The successive settlement of a bare volcanic surface introduced above could serve as an illustration of what is called primary succession. But analogous gradations can be observed in the process of secondary succession, during the restoration of a forest after logging or fire, for example.

So, for 30 years after a forest fire, one can observe on its location total chaos in vegetative cover and maximal entropy in the distribution of productivity to various species of shrubs and trees. In this period, trees grow at top speed, and their ability to regulate the local environment is temporarily at a minimum. Such fast-growing forests, having not yet accumulated the dead organic material through whose decomposition the return of carbon dioxide gas to the atmosphere occurs, are particularly active in depositing carbon, which is very important from a global perspective. At the same time, due to a lack of old, dying trees, the permeation of the matter cycle in such communities can reach levels in the tens of percentage points (Gorshkov 1980).

Only with the passage of several decades after a perturbation does this disruption, as shown by measures of productivity, biomass growth and changes in inorganic substance concentrations in the soil, come down to a few percentage points (Bormann and Likens 1979). And after another 50–70 years, the productivity of the damaged community restores itself, along with its leaf cover and overall nutrient cycle with maximal concentrations in the upper soil horizons. Finally, after a space of 150 years since the damage occurred, the majority of its community characteristics have restored themselves—its biomass, the thickness of soil debris cover, the

content and distribution of chemical substances, and also the impermeability of its nutrient cycle. The ultimate restoration of a forest is marked by the formation of a tree layer of uneven age structure, which occurs only 2–300 years after logging of fire (Finegan 1984).

The chemical makeup of the environment, as well, undergoes material changes in the course of secondary succession. This primarily concerns the soil. Local concentrations of various biogenic elements in the soil may change tens or hundreds of times, conditioned by the life activity of species determining the direction of successive changes. Such species, considering their role in the rebirth of the ecosystem, Gorshkov proposed calling reconstructive.

Among boreal conifer forests, for example, reconstructive species would include the birch, the alder, the aspen, berry plants, mushrooms, and many of the animals that feed on these species. The most notable particularity of reconstructive species is their ability to shift concentrations of environmental food sources in a direction that is disadvantageous to themselves, but beneficial to the incoming generation. It is this that explains the phenomenon of graduated succession—the removal of the presently reigning reconstructive community and the arrival of the next reconstructive generation once it has found optimal conditions for itself, in order to surrender its place to a new dominant group in due time. Finally, at the last, pinnacle stage of succession, the concentration of nutrients in the local environment reaches a value advantageous to the climax species and relatively disadvantageous to reconstructors. In this way, the destroyed community returns to its starting point—the sustainable climax state. Here are some of its features:

- Accumulation towards the end of secondary succession of greater, greater and greater share of available food supplies as community biomass and simultaneous depletion of abiotic system components—water and soil mineral plasts.
- An increased quantity of detritus production.
- Detritus turns into the main source of food supplies in the ecosystem, and detritivores—the main consumers, in place of herbivores (Green et al. 1984, vol. 2, Ch. 12.5.2).

Under these circumstances, climax species acquire maximal competitive advantage, establishing a sustainable population that is capable of maintaining this vigorous regime for an indefinitely long period of time. As regards the reconstructive species, they also remain in the climax community, but only in the form of isolated “marginal” individuals. They make up a decidedly sparse population under the restrictive weight of an environment ill-suited to them. And so it remains until the next cycle.

Such, in general terms, is the process of succession strictly specific to each climax community but unfolding according to the single described scheme, independent of geographical location. However, all this holds true only in the absence of regular perturbations, which can not only put the brakes on secondary succession but cut it off all together. If the perturbations take on a systematic character, then it will cause irreversible harm to the ecosystem, which will forget to program for its restoration and never again return to the climax phase. We observe this, for example,

during regular forest logging for industrial lumber or when it is systematically worked with herbicide to exterminate low-value types of trees, as well as artificially cutting back or clearing mature forests of over-mature trees and fallen or rotting trunks.

This last factor, by the way, is the most flagrant and dangerous interference in the life of a natural community, since it is the mature forest that represents the healthiest body of the biosphere, in which, when the matter cycle is completely balanced, there is not and cannot be anything “extra.” Foliage growth is limited by fungi and bacteria and all organic components of both strong and over-mature trees go toward the process of life activity of other organisms. In this way, the widespread practice of periodically cutting at a typical interval of 50 years literally severs the process of restoration in primordial climax forests with their closed matter cycle and ability to compensate for environmental perturbations. Therefore, for a return to an unperturbed state of the biosphere, the interval between successive clear cutting of forests should be increased to at least 300 years, that is, slowed by six times. And considering that clearing today usually surpasses the volume of natural growth, we ought to be speaking of a reduction in logging on a global scale by a minimum of eight to ten times. (For more on that, see Chap. 15.)

There’s no need to remind you that the stages of succession described above could not repeat themselves over the course of millennia were they not fixed in the genetic memory of the biota, and that means in the genome of each individual species. So, for example, all reconstructive species within a given succession are programmed to change the environmental parameters toward a direction disadvantageous to themselves and advantageous to climax species. Though, considering the particular role of the latter in maintaining environmental stability, it’s not hard to understand that not only the biota as a whole, but the reconstructive species themselves win on this in the end. Accordingly, the ability of the climax community to maintain beneficial conditions for all living things is inseparably connected to the corresponding genetic informatics and a specific selection of biological species in whose genetic memory it is written.

Genetic memory, however, just like any other ordered information, is vulnerable in time to gradual destruction and collapse. Therefore, when speaking of the biota’s ability to maintain the preferred environmental conditions, we cannot ignore the mechanism that enables the preservation of this genetic program through the process of its inheritance. According to the concept of genetic regulation, this mechanism, as stated above, is the competition and selection of individuals and their communities.

Evolutionary theory, as you know, designates several types of natural selection depending on the tasks that changing environmental conditions put before a population—directional, stabilizing, disruptive, etc. The concept of biotic regulation primarily addresses stabilizing selection, aimed at conserving average phenotypical markers and thus providing populations the fitness for their usual survival conditions. Filtering out individuals with extreme divergences in phenotype, it blocks the

removal of genetic information due to chance mutations at a population level, maintaining the order of the system and preventing the build-up of entropy.

But the selection of individuals is to a certain extent a measure of their quality, that is, their fitness to perform some kind of biological work or another. And, like any process of measurement, it should obviously have some capacity to judge reacting, for example, to mutations of the genome beyond a certain benchmark. Individuals with clearly altered genetic programs and expressed anomalies leading to a decreased competitive advantage are squeezed out of the population, while others, whose changes are below this benchmark, successfully pass through the sieve of stabilizing selection, clearing the ground for intraspecies genetic variation.

The existence of this benchmark of reaction to mutations allows us to explain the phenomenon of *discrete species*. After all, if the course of evolution is uninterrupted in time, and species constantly adapt to changing environmental conditions, then what causes the absence among them of intermediary or transitory forms observed in both modern material and paleontological data? But it all falls into place when interpreted in light of the stabilizing selection described above, which doesn't "notice" immaterial divergence in phenotype, but hems away any that goes beyond a specific species benchmark. At the same time, the existence of this benchmark gives us the key to understanding the surprising persistence of species, comparable in longevity to geological epochs.

There are still possible situations when stabilizing selection seemingly retreats to the background, allowing space for other forms of natural selection to come to the foreground of life. Such occurs, for example, when the regulatory capacities of the biota are depleted at critical stages of its historical development. As we have already noted, a large number of abiotic processes exist both within the Earth and in space that are beyond the scope of the biota's regulatory influence. One of the clearest examples is the transformation, occurring two billion years ago, of the Earth's reducing atmosphere to an oxidizing one, when the biosphere, in the words of microbiologist Grigory Zavarzin, "turned itself inside out," changing fundamentally to a high-nitrogen oxidizing atmosphere with a few oxygen-free pockets where anaerobic micro-organisms found refuge (Zavarzin 2001).

The cause of this was the formation process of the Earth's core, where, by force of gravity, the majority of the planet's iron displaced itself, consequently reducing sharply concentrations in seawater of iron oxide (FeO). And, while in the previous 1.5–2 billion years, all of the oxygen formed by the life activities of anaerobic prokaryotes had been expended on oxidizing atmospheric gases (NH₃, CH₄, CO, H₂S) and iron oxide diluted into seawater, then the liberated oxygen began to accumulate in the atmosphere, which told upon nearly the whole prokaryotic biota, which in its masses was unadapted to life in an oxidized environment. As a result of these cataclysmic events, a global transition occurred in the species makeup of the Earth's biota, and the place of the previously dominant anaerobic microorganisms was taken by the at that time relatively scarce photosynthesizing cyanobacteria (blue-green algae, the most ancient of prokaryotes), which used water and carbon dioxide gas to construct organic molecules, and for an energy source—the visible part of the solar spectrum.

But even incomparably smaller-scale transformations of the environment, accompanied by mass-extinctions of species, have not occurred too often over the course of Earth's history—on average, once in a hundred million years over the last half-billion year period (Raven and Johnson 1998; Jablonsky 1994). Meanwhile, the time required for a transition in the biota's species makeup is calculated in millions of years and takes up whole geological periods.

Unfortunately, the process of environmental degradation and accompanying loss of biodiversity as a result of human economic activity that we observe today has already become comparable to the rate of biota transformation in past geological epochs. But the time frame is incomparable, distinctive by several orders of magnitude. How on Earth can the biota respond to this? Perhaps through the development of new species, which, according to paleontological data, requires tens of thousands of years of evolution? Obviously not, though the theoretical possibility of new species development, especially among bacteria, in response to anthropogenic change to the environment cannot be ruled out. Far more real today is the threat of genetic disorganization in existing species and consequent loss of genetic memory of the biotic regulation mechanism passed from generation to generation.

This is because stabilizing selection is truly effective only under conditions of a natural ecological niche for each species. Individuals with a normative or insignificantly changed genetic program possess the greatest competitive advantage and form a population whose genetic memory saves information of species' properties corresponding to the interests of environmental preservation, as well as of the environment itself and its provision of the species' survival needs.

As natural habitat conditions disappear, however, and genetically programmed methods of responding to external pressures become inadequate to the new reality, such individuals quickly lose their competitive advantage, giving them a green light to disrupt the genome and change genetic memory. This relates not only to domesticated animals or cultivated plants, already long torn from their natural roots, but also to a multitude of *synanthropes*, species closely linked to humans whose ecological niche has been deformed by conditions civilization has brought about. Such, for example, is the house mouse, now incapable of returning to its natural state, or sparrows, having increased their numbers by several orders of magnitude and also almost never encountered outside the zone of human habitation.

We see a clear analogy in forests intensively exploited by humans, which are already practically incapable of returning to climax phase since genetic information of the optimal environment for climax species has been irretrievably lost. And as humans artificially maintain reconstructive species they find pleasing, the community truly loses its capacity for biotic regulation. Should humans "conquer" the whole biosphere, this mechanism could be lost on a global scale. Then, clearly, nothing will be left to us, we "lords of the planet," but to take environmental management into our own hands. That is, to replace biotic regulation with technological. But how much does this correspond to our real capabilities? This is how we must interpret the question of biotic regulation of the environment.

Life, as you know, is a process characterized not only by the acquisition and reworking of matter and energy, but of information. In both the rate of information flow and the efficiency with which it is reworked, there exists between the biota and civilization an impassible abyss. Thus, for example, the flow of information (matter exchange) in a given bacterial cell (10^8 bits/s) could be compared with the information flow of a personal computer. Let the molecular “memory units” play the role of logical operators, and the cell itself serve as control panel. For each square micrometer of the Earth’s surface, there are several living functioning cells—Plankton in the ocean, plants, bacteria and fungi on land—that non-randomly react to local changes in the environment. The overall quantity of bacteria on Earth is estimated at 3×10^{27} , and the number of cells in the biosphere is roughly on order of magnitude larger. Thus, the flow of information processed by the Earth’s biota adds up to $10^8 \times 10^{28} = 10^{36}$ bits/s. This process of data conversion takes place with nearly no energy usage, i.e. with an energy conversion efficiency close to 100% (Gorshkov et al. 2000b: pp. 211–212).

Modern computers, whose aggregate storage space allows us to preserve all of humanity’s cultural information, are marked by their speed and high energy conversion efficiency. Nonetheless, next to molecular technologies, their capabilities stand abysmally low. If you gave a computer performing 10^{11} operations per second to every person on earth, the total flow of processed information would not exceed 10^{20} – 10^{21} operations per second, which is 15 orders of magnitude lower than in the biosphere. As regards energy efficiency, the most powerful modern computer, capable of performing 10^{16} operations per second, uses about 10^7 watts, and energy usage comes to 10×10^9 J—12 orders more than in the biosphere. If you covered the whole Earth in supercomputers, each of them occupying an area of 100 m^2 , the total information processing flow would add up to 5×10^{28} bits/s—20 million times less than in the biosphere. And the energy used by such a computer network would go a hundred thousand times beyond that used by the biosphere (Makarieva et al. 2014).

In all likelihood, given the current rate of technological progress, the gap between information flows in the biota and civilization could be reduced by five to six orders of magnitude in the foreseeable future as computers grow faster and more numerous. But even if we managed to close the gap entirely, it would still not solve the problems or allow us to create a technological management system for the environment equivalent to biotic regulation. In part, this is because interaction between next-generation computers and the environment would be qualitatively different from what happens in a living cell, where molecular memory units are integrated into their environment. And this holds true not only for unicellular organisms, but for fungi and higher plants that sustain this quality due to their highly efficient surfaces—spindly, branching fungal hyphae, high leaf indexes, extensive root systems, etc.

But, that’s not even the most important part. What’s most important is the limited potential of the human brain, particularly sharply illustrated by our interaction with computers. To demonstrate this thesis, let us recall the well-known problem of automatic and manual control.

Manual control takes place on the basis of inborn and acquired information, as well as peripheral impulses coming in along feedback channels from the sensory organs, and is limited by the information processing speed of the central nervous system. Automatic control, based on computer programs, takes place at a speed a million times surpassing human potential. At the same time, the latter must be absolutely sure of correct input in the computer program, testing it many times in the course of preliminary experiments. And, nonetheless, various unforeseen situations often force a person to take control into their own hands, leaning on personal experience, knowledge and intuition, even at the expense of speed to the operation.

From this perspective, you could view the biosphere as a globally distributed system of microscopic computers, with biotic regulation equivalent to a control panel, in which the rate of information processing surpasses human mental capabilities by 30 orders and change, and by ten to fifteen orders—computerized control capabilities. In essence, it serves as the environment's automatic control system, based on programs developed over the course of several billion years. Paleontological data bears witness that roughly once in a hundred million years, a transition of the Earth's biota occurs, accompanied by a mass extinction of old species. Gorshkov supposes geophysical and extra-planetary factors created conditions for these changes. That means that over the past billion years, environmental control programs have been tested no more than ten times. Each program was unique in its epoch, supported by the biota for the longest possible period of time. New biotic programs underwent, through the process of evolution, an experimental trial of many thousands of years, at once preserving the continuity of life's universal biological organization.

Humanity, therefore, according to Gorshkov, in seeking an adequate replacement for biotic regulation of the environment, would need tens if not hundreds of thousands of years, since testing and correction of such programs necessarily comes into being under manual administration. But people do not have the kind of time on their hands that they would need to create a technological control system for the environment. The process of anthropogenic degradation of the biosphere is unfolding far faster, counting down years in the hundreds.

And people shouldn't be setting such goals for themselves anyway. Just the opposite, doing justice to the biota's great perfection, we ought to do everything in our means to preserve it and restore as much as possible of what we have destroyed in our millennia-long barbarity against nature. Then we wouldn't need a technological medium for environmental regulation at all. And we could find more reasonable uses for our growing power.

It would be hard to find a serious ecologist unwilling to subscribe to these words. And nonetheless, in finishing this section which illuminates the key ideas of the concept of biotic regulation,² we would err against truth if we limited ourselves to only one side of the coin. Because not all biologists and evolution specialists,

²We will say more on the biotic regulation concept's handling of the biosphere's carrying capacity in Chap. 14.

unfortunately, share this view. Many look upon it with circumspection, seeing a certain tendency for oversimplification.

Biologist Nikolay Marfenin, in a letter to one of this book's authors, wrote, "The theory tacitly implies that after the biotic processes, the abiotic are all clear and accounted for. But no, it is the abiotic processes that are the greater quandary, still researched very inadequately and so not accounted for. You can't make conclusions about the role of the biota from calculations of the carbon cycle, because the role of the *abiota* remains insufficiently clear." Famed microbiologist and member of the Russian Academy Grigoriy Zavarzin, in his article, "The Antimarket in Nature," while in many ways showing solidarity with Gorshkov ("The description of the community as a holistic evolutionary unit closely coincides with my own understanding of macroevolution's central issue"), nonetheless characterizes his approach as "an attempt to translate the processes of evolutionary biology into the language of university physicists (Zavarzin 2007).

Academy member Nikita Moiseyev addresses nearly the same point in his article, (from "Ekologia i zhizn'," 1998, No. 2), where he characterizes Gorshkov as "a remarkable researcher, having developed a grandiose theory of 'biotic regulation' parameters for the biosphere within whose bounds (quite broad, by the way) it is necessary to support life. But, as often happens with leading scientists, his own scholarly interests fill up the horizon, leaving out many important circumstances in the biosphere's development... And if we look (at it) from the overall systems point of view that we need to, inherent to the process of self-development of such a complex non-linear dynamic system, which the biosphere is, then we see a picture that doesn't look much like the one drawn only through the use of biotic regulation theory."

The majority of evolutionary biologists also do not share the view of the hyper-trophic role it assigns to stabilizing selection at the expense of other evolutionary mechanisms (see, for example, (Lima-de-Faria 1988; Chaykovsky 2010; Markov 2015)). On the other hand, it hardly satisfies to explain evolution by way of influence only from external factors on the biota, whether extra-planetary or geophysical. And if you start from the proposition that biotic community functions as a whole submit to the interests of maintaining "determined" conditions of life on Earth, then how do you explain, for example, the origin of the unbelievable variety of species, or such phenomena as preadaptation?³

And yet it is for good reason that we have assigned such a substantial portion of our book to this concept. It comes down to the fact that there are not many theories in our day that we might call so essential as the concept of biotic regulation of the environment or the "Gaia Hypothesis." Both one and the other contain no shortage of productive ideas, and even if they are not the ultimate truth, they nonetheless bring us materially closer to it, or at the very least allow us to come closer. Beyond that, each of them presents a fresh, substantive look at the processes of transforming

³An evolutionary paradox linked to the functional reconstruction of organs that, at the time of appearance, do not have the adaptive value that they receive in the course of further evolution. For example, the swim bladder in fish reconstituted itself as the lungs of land animals.

matter and energy in the surrounding natural world, providing us plenty to ruminate upon. This relates in part to the idea of sustainable development, which within the framework of the biotic regulation concept receives new reinforcement, especially with regard to the preservation of natural ecosystems and forests in particular (more on that in Chap. 15). Perhaps for the first time in the history of scientific thought, the role of inviolate ecosystems is being assigned the pride of place that it rightfully deserves.

Only one thing stirs a reflexive sense of perplexity. However you may relate to Viktor Gorshkov's theory, hiding it under a bushel is unacceptable under any circumstances. Truth, as you know, is born of argument, but no serious discussion has of yet touched upon this theory, though 20 years have passed from the moment of its publication. Such a state of affairs could hardly be called rational. And so we'd like to think that this book will make a contribution to overcoming the incomprehensible "conspiracy of silence." The more this work becomes known, not only to specialists but to everyone concerned with the worrying state of the environment, the better. The wealth of ideas laid forth within it provokes serious consideration forcing us to look upon the delicate natural world that surrounds us in a new way and to recognize the fateful role that humanity's prodigal attitude may play in its fate.

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