

Natural Ecosystems and Earth's Habitability: Attempting a Cross-Disciplinary Synthesis



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Abstract There are two contrasting views on life and Earth's habitability. One view is that the program of environmental regulation by life cannot exist, because it is genetically unstable. A program of "common environmental good" cannot be stabilized by natural selection and would have been disrupted by selfish mutants. The ever-changing Earth's environment has remained suitable for the ever-adapting life by chance. The second view is that the Earth could not have remained habitable by chance, because the life-compatible environment is physically unstable. Life regulates the environment, but the program of regulation has persisted by chance (for some reason, the disruptive mutants never spread). Neither view forms a quantitative theory of life-environment interaction. Here I discuss the biotic regulation theory, whereby the genetic and environmental stability are mutually guaranteed: the genetic program of environmental regulation by life encodes such an environment where disruptive mutants cannot spread. The key interdisciplinary question is what these environmental properties are. This is not an academic question: once the natural ecosystems are destroyed, the environment will rapidly degrade even if carbon emissions discontinue. Global change mitigation efforts can be misguided if the key role of natural ecosystems in stabilizing a life-favorable environment continues to be neglected.

Keywords Biotic regulation · Climate stability · Biotic sensitivity · Genetic program · Habitability

1 Introduction

Our civilization is in a global ecological and environmental crisis. Besides accumulation of atmospheric carbon dioxide, a major destabilizing process in the industrial era has been the destruction of wildness, especially the elimination of forests. During the past two centuries, primary vegetation has been exterminated over 40% of the land

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area [19]. Today, the degradation of the natural forests by humans continues unabated. Repeated calls from groups of concerned citizens, including some scientists, do not change the trajectory of our civilization destroying natural ecosystems.

It might appear that this critical situation is due to an insufficient understanding—by the society as a whole and decision-makers in particular—of the scientific arguments for ecosystem protection. The science is settled but the public is lagging behind scientists in the appreciation of an urgent necessity to preserve the still extant natural ecosystems. In that case, scientists could do little more than popularizing their messages more actively [38].

In reality, as I will argue here, the mental inertia of our thinking species appears minimal. The current globally destructive attitude toward natural forests accurately reflects the prevailing scientific paradigms. These paradigms had formed before the humanity began to experience large-scale environmental problems. They do not correctly capture the life–environment interactions and require a comprehensive reappraisal.

Specifically, the *limiting principle* in ecology (Liebig's law) and the *survival of the fittest* paradigm in evolutionary biology (which also underlies the ideology of modern market economy) both formed using evidence from artificial, human-impacted biological systems (agriculture), and processes (artificial selection). At large, these concepts view living objects as existing at the mercy of an external environment, which shapes their functioning and creates a perpetual need to adapt or perish.

However, artificial biological systems and processes differ from natural biological systems and processes in one commonly neglected but crucial aspect: the artificial ones lack sustainability and persistence. Indeed, while natural ecosystems can thrive for millions of years without perturbing their environment, all human-supported biological systems, including the civilization itself, are inherently unstable; they exist as long as there are nonrenewable environmental resources to deplete. Likewise, while natural biological species persist on average for several million years [31], the domestic sorts of plants and animals are unstable. As the human population itself, they are subject to rapid genetic degradation [29, 36].

Historically, people responsible for the development of modern science used to live in artificial biological systems, and continue to do so. Extrapolating knowledge obtained from these unstable systems to the rest of the biosphere resulted in the neglect of the stabilizing impact of natural ecosystems. When environmental science became global, the first indications of the stabilizing influence of life became available for discussion (e.g., [27, 28]). This new evidence was forcefully fitted into the old paradigms. It was misinterpreted as occasional life-mediated negative environmental feedbacks rather than the key genetically encoded principle of life organization [14]. If the stability of the Earth's environment favorable for life is maintained by natural ecosystems, then, even in the absence of direct environmental disturbances like, e.g., carbon emissions, degradation of these regulatory mechanisms presents a major threat to the humanity, and the more so, the longer our species remains unaware of this fact. For the biosphere to preserve a global stabilizing function, the self-sustainable natural ecosystems must be globally protected from exploitation. The biota should

be preserved not in biodiversity hotspots, advanced agricultural systems, or zoos, but on large territories, such that the stabilizing power of these natural ecosystems would compensate for the violation of natural processes that humans perform elsewhere.

2 Life as the Realization of a Genetic Program

Life is a process that transmits genetic information, which is quantum (“digital”), from one generation of classical (“analogous”) objects—living organisms—to another [14, 47]. This information governs all life processes: out of all possible biochemical and biophysical reactions that could occur in the biosphere, only certain non-random processes actually take place at nonrandom rates. Under similar environmental conditions, different genetic programs may govern drastically different behaviors and impacts. For example, while most birds build nests and feed their progeny, the cuckoo does not possess such a genetic program and has to rely on others bringing up its young.

Another conspicuous property of genetically programmed processes is that they, to various degrees, decouple the organism from the limitations of its external abiotic environment. Consider the opening and closure of plant stomata—the microscopic pores that regulate CO_2 uptake and H_2O release by the leaf. The so-called passive component of the stomata closing/opening is governed by ambient relative humidity in a relatively straightforward way: the two guard cells surrounding each pore lose (regain) turgor at high (low) vapor pressure deficit. Depending on the mutual configuration of the guard cells, these turgor changes can mechanically induce either opening (as in *Sphagnum* spore capsules) or closure (as in other plants) of the stomata in dry conditions [4]. A similar passive mechanism determines the shape of dry versus wet conifer cones, modern sustainable architecture uses it in biomimetic hygromorphic materials [18].

However, there is also an active complex hormone-mediated control. It allows plants to sense environmental conditions and regulate the stomata aperture depending on diverse combinations of internal and external stimuli like light, carbon dioxide, and temperature [1, 4]. For example, if the external conditions for photosynthetic CO_2 uptake are unfavorable (low light), the plants can keep stomata closed even at a low vapor pressure deficit. Accordingly, ambient humidity no longer dictates plant functioning.

Parameters of the genetically programmed processes are properties of the biota itself that cannot be deduced from environmental conditions. Compare a poikilothermic animal that lacks a genetic program for body temperature regulation with a homeothermic animal that does possess such a program. The poikilotherm's body temperature can be estimated from environmental parameters (radiation flux) using fundamental physical relationships (Stefan–Boltzmann law) and some simple physical properties of the organism (albedo of the body surface).

The homeotherm's body temperature cannot be specified in this manner but is prescribed instead by complex genetically encoded biochemical processes within

the organism. Similarly, the persistence of organic molecules in the soil cannot be deduced from their molecular properties but is controlled by complex biological and ecological processes in the ecological community [40]. Consider a mite parasitizing on a deer. Despite the flux of solar energy changes radically, from day to night and from summer to winter, the mite barely notices it. The deer maintains a stable body temperature around 37 °C. This stability is of complex nature. Plants absorb sunlight to generate biomass. The deer knows how to find this biomass and eats it up. The food burns within the body in such a manner that the resulting heating precisely offsets heat losses to the environment, irrespective of whether the latter is cold or hot, while the body temperature remains constant. On top of all, this complexity sits the mite and enjoys thermal stability.

What determines the steady-state value of temperature experienced by the parasite? While we cannot deduce its value from the environmental parameters, it is not arbitrary. The information about which body temperature to maintain is contained in the genome of the deer. If one replaces this genetic program with a different one, by transmitting the mite to a different host, the temperature can change too. For example, in passerine birds it will rise to almost 40 °C.

In the presence of a genetic program of environmental regulation by life, humans within the biosphere can be compared to parasites within an animal body. Similar to the mite, humans remain largely unaware of the pillars of our existence and thus misguided about how to cope with unfavorable environmental changes. There is more to it: if the parasites take an excessive share of the animal's resources, the animal dies together with the parasites. If the parasite is a thinking animal capable of rational behavior, it is in our interest not to undermine the system that is regulating our environment and preserve a significant part of the biosphere untouched.

Deciphering what subprograms the big genetic program of life carries allows one to make use of them. One example is the programmed death. The death of an organism can happen "by itself" since all classical objects age. Alternatively, death can be genetically programmed in that sense that it will occur non-randomly at a certain life stage well before the body actually wears out (e.g., Pacific salmon dies shortly after reproduction). If a species had such a program, switching it off would produce a radical increase in longevity. The question of whether death is or can be programmed has been a matter of active and sometimes controversial discussions [23, 24, 26, 45]. Some of this debate, as discussed below, is relevant to conceptualizing the life-environment interactions.

3 "Survival of the Fittest"

All contemporary living beings have a single common ancestor, from which we have inherited its genetic program modified by the four billion years of biological evolution. What is the minimal amount of information that had differentiated life from the inanimate world? For example, the first organism must have possessed the information about how to synthesize a copy of itself. Such information could not evolve,

because the evolution itself is contingent on the ability of living beings to reproduce. Did the minimal genetic information kit include the program of environmental regulation, which then persisted through time maintained by natural selection? Is this proposition necessary to explain life persistence?

Neo-Darwinism answers “no.” Two observed properties of the living beings appear sufficient to understand the phenomenon of life: besides reproduction, living things must be able to mutate such that at least some of the offspring differ genetically from their parents. This naturally happens, because the probability of exact copying of the DNA molecules (the molecular carriers of genetic information) during cell divisions is less than unity. During reproduction, some letters (nucleotide pairs) of the genetic code are copied with errors (mutations).

Neo-Darwinism postulates that if the environment changes, those individuals whose genetic program is better suited to the new conditions will produce more offspring and start dominating the population. Individuals less fitted to the new environment will not leave enough progeny and may ultimately die out. This is the Neo-Darwinist view of natural selection: environmental changes drive genetic changes and, hence, biological evolution.

This “survival of the fittest” principle may seem tautological, since nothing generally defines “the fittest” except its exceptional survival. In fact, however, this formulation reflects a fundamental, if implicit, premise of evolutionary biology: whatever changes life's environment undergoes, there are always some individuals to survive.

Based on this axiom, modern evolutionary biology cannot be qualified as a quantitative theory of life–environment interaction. It leaves the key theoretical questions unanswered, namely how genetic diversity and environmental change are linked. If some environmental parameter (temperature, pH, CO₂ concentration) changes by a certain amount, how much and what kind of genetic diversity must a given species possess to survive in the new environment with at least the same productivity? In other words, what is the probability that among the genetically different individuals composing a species there is at least one individual capable of producing the same or larger number of viable progeny in the new environment as the dominant individuals used to produce in the old one?

If evolution is driven by natural selection in an ever-changing environment that favors the best-fitted genetic variants, the evolutionary tempo and mode should reflect the rate R at which these variants are generated within a species. The larger the value R , the higher the probability of there being an individual fitted to any possible environmental change (e.g., [24]). On the other hand, given the prevalence of the long periods of evolutionary stasis, when species remain morphologically unchanged for the most time of their existence (“punctuated equilibrium”), the tempo of genetic and morphological changes associated with environmental adaptation should be related to speciation rates.

Rate R is proportional to the total number of individuals in a species and inversely proportional to their generation time. Differences in R values between the small, numerous, rapidly growing organisms and the larger, more slowly growing organisms constitute 10–15 orders of magnitude (i.e., 10^{10} – 10^{15} times). Meanwhile, the mean species duration (i.e., the time since origin to giving rise to another species) differs

by two orders of magnitude at most and shows no correlation with R . For example, some of the longest living species (25 million years) are found among lizards and some marine unicells [31].

On the other hand, data from domestic animals unambiguously testify that any features not continuously supported by selection undergo rapid genetic degradation [36]. For this reason, despite possessing high genetic diversity (see Fig. 10.9 in [11]), domesticated species cannot survive when reintroduced to the wild environment. This does not support the statement that a population generally carries individuals capable to survive in any environment.

As long as the question of how genetic diversity and environmental adaptation are quantitatively linked remains open (in evolutionary biology it is not yet posed), the proposition that life has been able by chance to genetically adapt to all environmental changes that might have happened during the last nearly four billion years of life existence, is unjustified.

4 Gaia and Daisyworld

Furthermore, the view of life as a chance-driven genetic adaptation to an ever-changing unpredictable environment comes in conflict with the evidence suggesting that a lifeless Earth should have become unfit for any life long ago because of the destabilizing external abiotic processes. Prominent examples are the increase of solar luminosity and the infiltration of CO_2 from the Earth's core. On a time scale of hundreds of millions of years, either process could have raised the planetary temperature to a life-prohibitive value. Since this did not actually happen, it must mean that life has been imposing some stabilizing impacts on the global environment rather than merely adapting to random environmental changes. Some of such negative feedbacks have been identified: e.g., the biota removed the excessive inorganic carbon from the atmosphere and stored in the form of carbonates and inactive organic carbon in sediments.

Furthermore, the modern environment appears optimized for life—something that cannot be explained by chance. For example, the observed ratio of concentrations of life-important inorganic elements like nitrogen and phosphorus in the ocean is precisely such as they are used by life (the Redfield ratio). This suggests that the physicochemical environment of the ocean was formed and is maintained by life itself.

Considering this and related evidence James Lovelock formulated the Gaia hypothesis (see references for the discussion below in [46] and [7]). It posits that life is shaping and regulating the environment on Earth maintaining it far from the physicochemical equilibrium that would set in on a lifeless planet. In its original formulation—Earth as a super-organism, which regulates its own “internal” milieu—the Gaia hypothesis was intensely criticized by Neo-Darwinists. They argued that environmental regulation on a global scale cannot be maintained by natural selection. Environmental regulation implies that organisms must act in concert for “the

common good” which they somehow “foresee,” while natural selection favors individuals that act on their own (maximize their reproductive success) without any teleological foresight.

In an attempt to refute these criticisms, Lovelock presented his Daisyworld model. The white and black daisies, each maximizing their growth rates in the optimal environment, without “acting in concert for the common good” nevertheless produced a partial stabilization of global temperature in the face of an external disturbance represented by a changing solar luminosity. When the mean global temperature rises above the optimum because of increasing solar luminosity, the white daisies who, because of their higher albedo, enjoy a slightly lower *local* temperature than the global mean, find themselves closer to the universal growth optimum temperature than the black daisies (who, because of low albedo, are *locally* warmer). As the white daisies spread more widely, the planetary albedo increases, and the global temperature declines thus counteracting the initial external perturbation.

The Daisyworld model received considerable attention in the literature, but it did not stand as the intended proof of environmental regulation by life. It was pointed out that there is no mechanism by which the information about environmental regulation, even if it was initially present, could be preserved through evolution by natural selection. For example, the environmental regulation in a Daisyworld is disrupted by the appearance of a mutant gray daisy (a “cheat”) that does not synthesize either of the necessary pigments (black or white) but invests extra resources in reproduction, thus growing faster than either black or white daisies. Such a mutant can spread over the planet forcing out the white and black daisies after which the planetary regulation ceases and life ultimately perishes. “Good guys come last”, i.e., natural selection does not maintain behaviors contributing to the “common good” [5].

This type of arguments proved to be near fatal for the Gaia hypothesis. The only thing that the mainstream science took from Gaia was the explicit recognition that life does impose a certain non-negligible impact on the environment (with several documented examples of a stabilizing impact like carbon deposition in sediments). On the other hand, life is thought to adapt to the biotically mediated environmental changes in very much the same manner as it adapts to random abiotic changes. This *co-evolution* of life and its environment allegedly explains why the life-mediated environment seems to be optimized for life (because life has adapted to it).

In other words, one can say that Gaia, in its original formulation, succumbed to Neo-Darwinism, while the idea of environmental regulation by life for life succumbed to the idea that life on Earth has persisted by chance. Indeed, one could argue that, inasmuch as Neo-Darwinists presume that environment has remained suitable for life by lucky chance, the defenders of Gaia should be allowed to presume that, by another lucky chance, some stabilizing biological processes that did occur in the biosphere were allowed to operate for considerable periods of time and were not disrupted by either biological mutants or any abiotic processes (Table 1). Similarly, for yet another chance, the biotic impact has not driven Earth's environment to uninhabitability—i.e., among the biotic impacts the stabilizing ones dominated. Such an admission would, however, mean that both concepts agree that the persistence of life on Earth could not be ensured by the inherent properties (information) encoded in life itself.

Table 1 Different approaches to the problem of environmental and genetic stability

Concept/issue	Environmental stability	Genetic stability
Neo-Darwinism	Earth's environment may have remained suitable for life by chance. Life adapts to environmental change	The program of environmental regulation by life cannot exist, because it would have been genetically unstable. Such a program of "common good" could not have been stabilized by natural selection and would have been disrupted by mutants
Gaia/Daisyworld	Earth's environment could not have remained suitable for life by chance, because it is physically unstable	The genetic program of environmental regulation by life may have persisted by chance. Disruptive mutants have never appeared or spread
Biotic regulation	Genetic and environmental stability are mutually guaranteed: the genetic program of environmental regulation by life encodes such environmental properties that make the spread of a disruptive mutant impossible. What are these properties?	

At this point, we note once again that neither Gaia nor Neo-Darwinism represents quantitative theories of life–environment interaction. Neo-Darwinism (and generally theoretical evolutionary biology and genetics) is concerned about how to explain the observed patterns of molecular evolution and speciation but is largely agnostic with respect to the environment, including the problem of its stability. Gaia, on the other hand, considers the geophysical and biophysical processes in the environment but has no quantitative clues to the genetic and evolutionary peculiarities of life and their dynamics. Accordingly, models aimed to bring the two concepts together operate with arbitrarily chosen timescales of genetic and environmental change. For example, the so-called “guild” model illustrating the evolution of a closed matter cycle with different trophic groups (guilds) of organisms, allows the matter cycles to remain open for an arbitrary time—until there appears a mutant able to (partially) close them [8]. That the environment can meanwhile degrade for a state unfit for life is not considered.

5 Biotic Regulation

The concept of biotic regulation of the environment aims to reveal and quantitatively describe how the inherent properties of life ensured its persistence on Earth [11, 14]. In such a setting, we must first describe what kind of information life must contain to secure its existence through time. Second, it is necessary to explain how this information can be maintained by natural selection (i.e., why no disruptive mutants could ever conquer the biosphere).

Let us discuss the first question and see how the regulation of the environment by life demands a nonrandom correlation in the functioning of different organisms. Life is based on the continual recycling of chemical elements like carbon, nitrogen, phosphorus, etc. Of these, carbon is the most abundant. Some organisms (plants) can synthesize organic matter from inorganic compounds like CO_2 and all living organisms are able to decompose organic carbon back into inorganic constituents. Other conditions being favorable (sufficient sunlight, water, other nutrients), functioning of the biota ultimately depends on the availability of CO_2 . Atmospheric CO_2 also happens to be a second important greenhouse gas. It is well suited for a brief illustration of the biotic regulation principles.

In the steady state in a closed system, synthesis $P^+ > 0$ (which produces organic carbon and reduces the amount of inorganic carbon) and decomposition $P^- > 0$ (which does the opposite) must coincide (Fig. 1a). If M^- occasionally increases from M_0^- to $M_0^- + \Delta M$, $\Delta M > 0$, to bring it back to the original value the difference $P^+ - P^-$ must be positive. This can be achieved in several ways: either the decomposers reduce P^- relative to P_0^- , or the synthesizers elevate P^+ relative to P_0^+ , or both.

While in heterotrophs the energy and matter stores partially coincide in food (oxygen comes from the atmosphere), in autotrophs the energy and matter stores are decoupled (Fig. 1a). Energy for autotrophs comes with solar photons that have zero mass and thus, unlike organic or inorganic matter, cannot be accumulated. The instantaneous rate of photosynthesis per unit area is limited by the flux of solar radiation and photosynthesis efficiency. Conversely, the instantaneous rate of decomposition per unit area grows with increasing biomass of heterotrophs and, provided oxygen for its burning is abundant, can be arbitrarily high. Accordingly, heterotroph functioning should be the primary source of internal perturbations in the organic and inorganic pools. This asymmetry can be compared to the asymmetry in the dynamics of atmospheric water vapor. While evaporation ("synthesis") is a slow, widely distributed process governed by solar energy, condensation ("decomposition") can occur at an arbitrarily high rate depending on the local value of vertical air velocity [33]. Condensation of water vapor stands behind such extreme weather fluctuations like hurricanes and tornadoes.

Given this asymmetry in the organization of synthesis and decomposition, the program of environmental stabilization should include compensatory reactions to disturbances from both autotrophs and heterotrophs. If one block functions erratically, the other can be damping environmental perturbations in the meantime.

First, at an elevated CO_2 plants may increase their P^+ , which will lead to the appearance of excessive organic matter. (This part of the biotic response is often discussed in the literature in the context of "carbon limitation" of plants.) However, there is another side of the coin that is equally crucial: while P^+ is elevated above its equilibrium value, the decomposers (i.e., all the other organisms) *must ignore* the excessive organic carbon (which is their food) and keep the value of P^- unchanged. If the absolute value of P^- equally increases with P^+ , no net sink of CO_2 may appear.

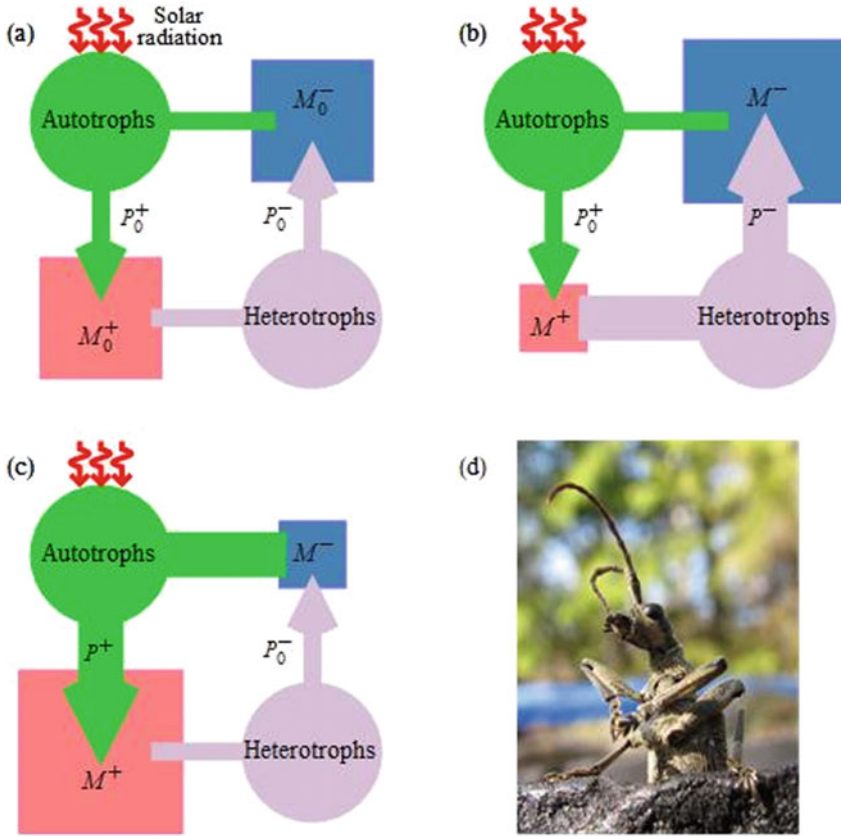


Fig. 1 A schematic representation of a closed ecosystem: autotrophs and heterotrophs synthesizing and decomposing organic matter at rates P^+ and P^- , respectively, and their environment represented by pools of organic matter M^+ and inorganic matter M^- ; $M^+ + M^- = \text{const}$. **a** The equilibrium state with optimal magnitudes of $M^+ = M_0^+$, $M^- = M_0^-$ and coinciding rates of synthesis and decomposition $P^+ = P_0^+ = P_0^- = P^-$. **b** Ecosystem perturbed by an instantaneous rise in the rate of decomposition $P^- > P_0^-$: the organic pool $M^+ < M_0^+$ declined, while the inorganic pool $M^- > M_0^-$ increased. The compensatory reaction of the ecological community will be to increase synthesis rate $P^+ > P_0^+$ to diminish M^- and bring it back to the optimum. This genetically encoded compensatory rise in primary productivity upon addition of inorganic nutrients is interpreted as a nutrient limitation (Liebig's law) in disturbed ecosystems. **c** Ecosystem perturbed by an instantaneous rise in the rate of synthesis $P^+ > P_0^+$: the inorganic pool $M^- < M_0^-$ declined, while the organic pool $M^+ > M_0^+$ increased. The compensatory reaction of the ecological community will be to increase decomposition rate $P^- > P_0^-$ to diminish M^+ and bring it back to the optimum. This compensatory reaction of heterotrophs can take the form of an insect outbreak destroying the excessive "wrong" plant biomass perturbing the optimal ecological community structure (e.g., on tree plantations). **d** A representative of the family of longhorn beetles, some of which are serious pests of tree plantations. Photo by Anastassia Makarieva. Note that in an open ecosystem there must be a third, environmentally neutral reservoir present such that external disturbances in M^+ were not translated to M^- or vice versa (see Fig. 3 in [15])

Another opportunity to ensure a biotic sink of excessive CO_2 is for plants to keep P^+ unchanged (despite the allegedly limiting nutrient increased), while for the decomposers to reduce their consumption P^- in the meantime (despite the food abundance is unchanged). In this case, P^- decreases and the condition $P^+ - P^- > 0$ is met as well.

If, on the other hand, the inorganic carbon stock diminishes from the equilibrium amount M^-_0 to $M^-_0 - \Delta M$, then to restore the equilibrium we will need $P^+ - P^- < 0$ (decomposition exceeds synthesis). Again, two stabilizing responses are possible. Plants may keep P^+ constant despite the decreased amount of an allegedly "limiting" nutrient, while the decomposers raise P^- despite the is no increase in their food abundance. Alternatively, plants may reduce production P^+ while heterotrophs increase their consumption P^- .

This consideration of the mechanisms of environmental stabilization reveals two things. First, we can see that the stabilization of the carbon pool is a community-level reaction. It rules out the limiting principle as an explanation of a possible stabilizing biotic sink (or source) of inorganic carbon. Negative feedbacks of the biota cannot be explained assuming that plants are limited by inorganic carbon (CO_2), while decomposers are limited by organic carbon (food). A compensating sink or source appears in the result of nonrandom, *correlated* changes between the rates of synthesis P^+ and decomposition P^- , not in the result of *independent* changes in either P^+ or P^- . From the conventional biology viewpoint, when plants elevate their production P^+ while heterotrophs keep their consumption P^- unchanged despite the greater food availability, the latter "sacrifice" their immediate profit for the "common good" of a stable environment (see discussion in [21]). These complex reactions account for the fact that the persistence of organic matter in the ecological community is less a chemical property of molecules than dictated by the state of the community itself [40].

Since there are many chemical elements used by life and all of them must be regulated, the biota should be able to separately react to disturbances in each pool by changing the stoichiometric ratio of the synthesized organic matter. For example, if inorganic carbon is in excess due to an external environmental disturbance, while the remaining nutrients remain optimal, the biota should synthesize organic matter containing just carbon and no nitrogen or phosphorus and keep this excessive organic carbon in an inert state in a refractory pool [10]. A conspicuous example is the elevation of the proportion of carbohydrates that are difficult to digest in the organic matter of plants grown under conditions of elevated CO_2 [6].

The second conclusion is that in a stable environment production rates P^+ and P^- cannot be maximized simultaneously. In other words, it is not possible that the equilibrium value of $P_0 = P^+_0 = P^-_0$ is the maximum possible value of both P^+ and P^- . Any perturbation in a stable environment necessarily entails a nonrandom change in the production rates of either plants or decomposers or both. In some conditions, either P^+ or P^- must be higher than the equilibrium value. An optimal environment can, therefore, be defined as a stable environment where the *equilibrium* values $P^+_0 = P^-_0$ are maximized.

6 Rethinking Liebig's Law and Pest Attacks

Thus, that some groups of organisms can at times develop a higher productivity than in the long-term mean is not a proof that the environment has not been optimized for the ecological community as a whole. Environmental disturbances may bring about an increase in productivity in some species of the ecological community in very much the same manner as an infection of a mammalian body by viruses elevates its temperature and metabolic rate. Such an elevation of metabolic power above the optimal value is necessary to cope rapidly with the infection. It does not mean that the body's functioning is "limited" by the absence of viruses. Likewise, increased plant productivity in the ecological community can be an indication of environmental problems rather than well-being (Fig. 1b). Prolonged maintenance of the community in the state of such "environmental fever", e.g., by continuous fertilization, can lead to environmental and ecological degradation. For example, as long-term studies of tundra ecosystems indicate, continuous nitrogen fertilization results in a progressive loss of soil organic matter [30].

Attacks of insect pests on disturbed ecosystems represent a similar "fever" response of the heterotroph block of the ecological community to a situation when some kind of organic matter is present in excessive quantities (Fig. 1c). In natural ecosystems, a disturbance is followed by the process of succession that involves a nonrandom sequence of ecological events and implies a nonrandom species composition and energy flow structure at each stage of the recovery. Tree plantations, where the species composition does not match the genetic program of natural succession, represent a perturbed state. The "pests" try to destroy this unhealthy biota such that the normal succession process could start. Thus, while nutrient fertilization is perceived as positive for human-controlled biological systems, and pest attacks are perceived as negative, the two phenomena are in fact two sides of the same coin—the genetically encoded program of environmental regulation by the biota.

7 How is the Information About Environmental Regulation Maintained?

Suppose that we have an environmentally competent ecological community. The genetic program of species that compose this community encodes the behavior of individuals in such a manner that the community as a whole exhibits a compensatory reaction to any disturbance of its optimal environmental conditions. But the cumulative genetic program of the community is subject to errors that accumulate during its copying. With a low probability, a disruptive mutant ("gangster") species can appear which is productive enough to force out the normal ("regulator") species but at the same time is unable to regulate the environment. As soon as such a gangster invades the entire biosphere forcing out the normal communities, the biotic regulation ceases. Ultimately, the gangster perishes once the uncontrolled environment degrades to a

state unfit for any life. How can be the biosphere protected against such gangsters? Below I provide a brief sketch of the main concepts.

We first need to formally define a gangster. As discussed above, a normal community reacts to a small environmental perturbation ΔM as $\Delta P = k\Delta M$, where $\Delta P \equiv P^+ - P^-$ is the difference between the rates of synthesis and decomposition and ΔM is the deviation of parameter M from its optimum value M_0 . Thus, in an optimal environment, the biochemical cycles are fully closed: $\Delta P = 0$. For the gangster $\Delta P = \text{const} \neq 0$: in other words, the environmental impact of the gangster is independent of the state of the environment within a relatively broad range of environmental conditions. For example, even when a resource is declining due to overconsumption, the gangster will continue to deplete it.

When the gangster starts colonizing the biosphere, the linear size L of the area occupied by the population of gangsters increases, while the environmental conditions in this area deteriorate. The condition for life to be protected against gangsters can be therefore written as

$$S_{\max} < S_E \quad (1)$$

Here S_{\max} is the area colonized by the mutant by the time when its environment has degraded to a state unfit for the mutant: i.e., to a state when the gangster is no longer more competitive than normal individuals and $S_E \sim L_E^2$ is the total area occupied by life. When condition (1) is fulfilled, the mutant goes extinct before it succeeds to colonize the entire biosphere. Let us now estimate S_{\max} .

Suppose the mutant population originally occupying a small area of radius $L \ll L_E$ depletes its life-important resource (food) M (kg m^{-3}) at a rate ΔP ($\text{kg m}^{-2} \text{s}^{-1}$). The influx F of this resource into the area from the global environment is, in the linear approximation, $F = \Delta MD/L$, where D is turbulent diffusion coefficient and $\Delta M = M_l - M_0$ is the difference between the local and global concentrations of the resource. By equating $\Delta P = F$ (which means that the gangster's life is sustained by the influx of food from the yet undisturbed environment), we find how the relative degree $\varepsilon \equiv \Delta M/M_0$ by which the mutant destroys its environment depends on the radius L of the area that it currently occupies:

$$\varepsilon \equiv \Delta M/M_0 = \Delta PL/(DM_0); \quad (2)$$

$$L_{\max} = \varepsilon_{cr}DM_0/\Delta P = \varepsilon_{cr}D\tau/H. \quad (3)$$

Here, $\tau \equiv M_0H/\Delta P$ is the turnover time of resource M_0 found in the biosphere in a layer of thickness H due to its depletion by the gangster at a rate ΔP .

We can see from Eq. (2) that the gangster's environment deteriorates (the absolute magnitude of ε grows indicating deviation from the optimum environmental value M_0) with increasing linear size L of the area occupied by the mutant. As soon as ε reaches a critical value ε_{cr} (3), the mutant loses its competitive advantage as compared to normal individuals/communities that are able to drive the degrading environmental

conditions back toward the optimum. This critical value of ε_{cr} in (3) determines the maximum size L_{max} of the area that can be colonized by the mutant. If $L_{max} > L_E$, the biosphere is unprotected against mutants. Eqs. (1) and (3) illustrate those major factors that control the spread of gangsters in our example. First, other conditions being equal, a larger planet (with large L_E) is better protected against gangsters than a smaller one. Second, the larger the turbulent diffusion coefficient D of the physical environment, the greater territory can be invaded by the mutant before it goes extinct. Indeed, rapid mixing prevents local resource depletion and offsets local environmental degradation for the mutant. Third, the higher rate ΔP at which the mutant destroys the environment, the smaller area can be invaded by the mutant before it goes extinct. The narrower the range of environmental conditions within which the mutant remains competitive (the lower the value of ε_{cr}), the sooner the mutant goes extinct.

Finally, perhaps the most important message to take from Eq. (3) is that the smaller the optimal concentration M_0 of resources in the biosphere, the smaller L_{max} and *the more protected life becomes* against gangsters/mutants. Resource abundance (a large value of M_0) undermines life stability providing opportunities to gangsters and lazybones. This is one of the key principles of biotic regulation.

8 Fundamental Constants Guarding Life on Earth

Let us now discuss some particular examples of the numerical relationships (1)–(3) using the available crude estimates of the relevant parameters. In the ocean, small unicellular organisms (phyto- and zooplankton) mostly perform the synthesis and decomposition of organic matter. Such organisms spread by the process of turbulent diffusion. Consider a zooplankton species consuming phytoplankton biomass at twice the mean global rate of decomposition P_0^- , such that for this gangster $\Delta P = P_0^+ - 2P_0^- \sim -P_0^-$. Thus, this gangster destroys its life-important resource (phytoplankton biomass) with a power coinciding in the order of magnitude with the mean power P_0^\pm of the existence of life on Earth. This is about 100 GtC/year for the planet as a whole.

Global phytoplankton biomass, which is concentrated in the oceanic layer of thickness $H \sim 100$ m, is remarkably small: about 1 GtC [2]. For the turnover time $\tau = M_0 H / \Delta P$ in (3) of phytoplankton we have $\tau \sim 10^{-2}$ year. A characteristic value of the turbulent diffusion coefficient on the oceanic surface is about $D \sim 10^3$ m²/s = 3×10^{10} m²/year. Assuming generously, that our gangster loses competitiveness as compared to normal species only when its food is *totally* depleted, $\varepsilon_{cr} = 1$ in (3), using these values in (3) we obtain $L_{max} \sim 3 \times 10^3$ km. Considering that the area of the Earth's ocean is $S_E = 4 \times 10^8$ km², we find that the maximum area occupied by the gangster, $S_{max} = \pi L_{max}^2$, is still one order of magnitude smaller than the total area occupied by the oceanic life, such that condition (1) is fulfilled even if not by a large margin.

This estimate uses an unrealistically high value of ε_{cr} corresponding to complete resource depletion. The value of ε_{cr} in (3) is related to the sensitivity of competitive interaction in the biota ε_b . This sensitivity characterizes the magnitude of a local deviation from the optimal conditions, which makes the local ecological community appreciably less competitive than its surrounding neighbors who continue to enjoy the optimal conditions. Based on various approaches, the value of ε_b was estimated to be in the range of 10^{-4} – 10^{-3} [11]. That is, even a relatively small environmental degradation is noticed and acted upon by natural selection. Even if for the mutant this range is significantly broader, the value of ε_{cr} should nevertheless be appreciably smaller than unity. For $\varepsilon_b \ll \varepsilon_{cr} \sim 0.1$ we obtain from (3) that a gangster can at maximum occupy one-thousandth part of the oceanic biosphere before it goes extinct.

Among the parameters entering Eq. (3), the ratio $M_0/\Delta P$ deserves a special consideration. Here M_0 (kg m^{-3}) is the resource concentration in the environment, in our example—phytoplankton biomass; ΔP is the rate at which the gangster can potentially destroy the biosphere. For $|\Delta P| \sim P^\pm$, the ratio $\tau = M_0 H / \Delta P = M_0 H / P^\pm$ characterizes the turnover time of the considered resource owing to its synthesis or decomposition by the biota, where $M_0 H$ (kg m^{-2}) is the resource abundance per unit area.

The maximum surface-specific rate P^\pm of equilibrium life functioning (when the rates of synthesis and decomposition coincide) is determined by the flux of solar radiation and the biochemical efficiency of converting the energy of light into the energy of organic matter. Vertical size H of phytoplankton abundance is determined by the characteristic length of light penetration into the ocean. But how can turnover time τ be a fundamental property of life on Earth rather than a random value characterizing a given state of the biosphere?

The fundamental nature of τ follows from the universal biochemistry of life, which in its turn dictates a universal metabolic optimum rate of existence for all living beings. The metabolic rate per unit of living matter (the rate at which organisms consume energy) is broadly universal at around $q_0 \sim 4 \text{ W}/(\text{kg live mass}) \sim 4 \times 10^{-2} \text{ W/gC}$ for a vast majority of living beings from bacteria and plants to higher animals [32]. Total biomass of all phytoplankton cells per unit area, $M_0 H$, is determined by the condition that their cumulative energy consumption does not exceed the biotically available energy flux $K P^\pm$, where $K = 42 \text{ kJ/gC}$ is the universal energy content of organic matter:

$$M_0 H q_0 = K P^\pm; \tau \equiv M_0 H / P^\pm = K / q_0 \approx 10^6 \text{ s} = 3 \times 10^{-2} \text{ year.} \quad (4)$$

We can see from (4) that the turnover time of live biomass in the ocean, which depends on primary productivity and live biomass abundance, is equal to the ratio of two fundamental constants: the energy content of organic matter K and the universal metabolic rate of living beings q_0 . The optimal ambient concentrations of life-important elements like carbon (both dissolved organic carbon and CO_2), nitrogen, phosphorus, etc., are linked to the optimal concentration of living cells that is determined by H , P^\pm , and τ .

The above considerations are aimed to illustrate that a particular set of values of fundamental parameters of Earth and life itself plays a crucial role in life stability. Similar to how a particular value of the fine-structure constant—a fundamental physical constant—allowed for the formation of the main chemical elements used by life, the long-term persistence of life on Earth is contingent upon several major parameters of our planet and life itself. We still do not know many of these critical parameters. But clearly, their investigation will shed light on the principles of life organization as well as on many important problems of modern humankind.

9 Life as a Potential Destabilizer of the Environment: No Genetic Adaptation Possible

A crucial property is the ability of life to transform the environment more rapidly than any geophysical processes. Transpiration of water by terrestrial plants amounts to about one-tenth of total solar power absorbed by the planet. (For comparison, global atmospheric circulation power is about an order of magnitude smaller—only about ~1% of solar power.) Likewise, the global rate of synthesis and decomposition of organic matter P^\pm is several orders of magnitude higher than the rate of any geophysical processes. Net primary productivity of the biosphere is about 10^2 GtC/year—compare this with the rate of carbon emissions from the Earth's core that occurs with an average rate of 10^{-2} GtC/year, i.e., are ten thousand times slower.

In other words, life itself is the most important potential destabilizer of the environment—a fact that has not been emphasized in the studies of Gaia where the focus is instead on the abiotic environmental perturbations. In the original numerical Daisyworld models, the main environmental parameter controlled by the biota was albedo (a static parameter) rather than concentrations of life-important elements that strongly depend on the system's dynamics.

In biotic regulation, compensation of abiotic disturbances (which are central to both Gaia and Neo-Darwinism) is a by-product of the inherent process of compensating for the more significant fluctuations within the biota itself. Biotic processes are significantly more powerful than abiotic processes. Being able to compensate for the internal life-induced disturbances, the biota is automatically able to compensate for all the weaker disturbances like the geophysical processes.

On the other hand, the short time scale of potential self-degradation of the biota given by turnover time τ of major life constituents testifies that genetic adaptation to changing environmental conditions has not played a significant role in life's survival. This is because new genetic information (which could possibly help the organisms in a changed environment) takes a very long time to arise. A characteristic time of evolutionary change is about $\tau_{sp} \sim 3 \times 10^6$ years—this is the meantime of species existence, after which a new species possessing new properties can be produced from the old one (Table 2). So if the biotically controlled environment fluctuates on a time scale of $\tau \sim 10^{-2}$ – 10^2 years (Table 2), $\tau \ll \tau_{sp}$, no genetic adaptation can take place.

Table 2 Some key biological and environmental time scales

	Time scale (years)	Comments
<i>Biology</i>		
Metabolic turnover time τ	3×10^{-2}	$\tau \equiv K/q_0$, where $K = 4.2$ kJ/g is the energy content and $q_0 \sim 4$ W/kg is the characteristic mass-specific metabolic rate of living matter, see text
<i>Genetics</i>		
Characteristic species duration τ_{sp}	3×10^6	Leopold [24], Makarieva and Gorshkov [31]
Time scale of genetic information “melting” τ_m	3×10^8	$\tau_m \equiv \tau/(v n_d n_p)$, $v \sim 10^{-10}$ (n.p. div) $^{-1}$ is the probability of mutation per nucleotide pair (n.p.) per cell division (div), $n_p = 1$ n.p., $n_d = 1$ div; it is assumed that living cells on average divide and copy their genetic information each $\tau = 3 \times 10^{-2}$ year. In time τ_m , mutations will have occurred with a probability close to unity at all nucleotide sites in all genomes. In the absence of natural selection, this would erase all genetic information
<i>Environment</i>		
Carbon turnover time via inorganic and metabolically inactive organic pools τ_c	10	$\tau_c \equiv M/P$, $M \sim 10^3$ GtC is the store of inorganic (atmosphere) or organic (soil, wood, dissolved organic matter in the ocean) metabolically inactive carbon, $P \sim 10^2$ GtC/year is the global rate of biological synthesis and decomposition
Surface fresh water turnover time on land via runoff τ_w	10	$\tau_w \equiv W/R$, $R = 2.5 \times 10^4$ km ³ /year is the global river runoff, $W \sim 2 \times 10^{-4} \times 1.4 \times 10^9$ km ³ is the surface fresh water pool assumed to be of the order of 0.02% of oceanic water
Ocean warming by 10 °C by full sunlight absorption τ_o	30	$\tau_o \equiv H_o c \rho \Delta T / I$, where $H_o = 3.8$ km is the mean oceanic depth; $c = 4.2$ kJ/kg/°C is the specific heat capacity of water; $\rho = 10^3$ kg/m ³ is water density; $I = 150$ W/m ² is the mean solar radiation flux absorbed at the surface; $\Delta T = 10$ °C

Biotic regulation offers a new interpretation for the evolutionary changes known from the fossil record. Random changes of the genetic program of biotic regulation in most cases produce defective mutants, but in some very rare cases can produce improvements in the efficiency of biotic regulation. RNA viruses that have mutation rates six orders of magnitude higher than the DNA-based life [14] generate new meaningful genetic information. Basic calculations show that the intraspecific genetic polymorphism generated by mutations (errors) during DNA copying is insufficient to describe the observed rates of generation of new genetic information in the biosphere [31].

The new genetic fragments generated by viruses are then “offered” to other species in the biosphere via horizontal gene transfer along this “evolutionary highway” from viruses to the rest of life. If upon incorporation into the genomes of the “existing” species such fragments make the biotic regulation program more efficient, new species may evolve and compose a new community with a new program of biotic regulation. Since a new program can imply a new set of optimal conditions, such an evolutionary change can entail a major environmental change—not vice versa. Thus, the environment will change, but remaining under biotic control at all times. The spontaneous evolution of life drives environmental change. The most dramatic shifts of this type should be very rare: one possible example is the transition from anoxic to oxygen-breathing biota. More regular evolutionary events like the appearance of new species in a given ecological community can be interpreted as minor improvements in the biotic regulation program.

10 Life on Land

Life on land differs from oceanic life in several crucial aspects. First, life on land could originate several times from oceanic life. If the first local ecological communities on land were poorly organized, they could perish without driving the whole life on Earth to extinction. In contrast, oceanic life originated only once.

Second, diffusion of many life-important chemical elements in the terrestrial biota occurs much more slowly than in the ocean—because of the high viscosity of soil it occurs by molecular rather than turbulent diffusion. For example, for soil nitrogen and phosphorus the diffusion coefficient is less than 10^{-2} m²/year, i.e., D in (3) is practically zero.

On the other hand, the locomotion of large animals on land is less costly than in the ocean. Large animals are able to consume biomass at a high rate and to migrate quickly over large areas. Their migration rate (analogous to diffusion coefficient) can be very large. Also, plant biomass on land is about three orders of magnitude larger than in the ocean (where it is of the order of 1 GtC), which results in a higher value of carbon turnover time $\tau \ll \tau_c \sim 10$ years (Table 2). Accordingly, during its invasion the gangster on land will have a significantly larger resource than in the ocean.

These considerations show that life on land is potentially unstable with respect to the destabilizing impact of large animals: they are the main candidates for terrestrial gangster species [34].

Ecological communities on land evolved, perhaps by trials and errors (the latter leading to extinctions), several measures against such vulnerability. While the store of biomass on land is very large, it mostly consists of biologically unavailable wood. Wood becomes available for decomposition only after the tree is dead. Wood in a living tree is defended biochemically against being eaten by animals. Among the many millions of biosphere species, only a few are able to destroy living wood and kill trees. Large animals normally consume no more than about 1% of primary productivity in undisturbed terrestrial ecosystems like forests: i.e., the resources available for them are much smaller than the total biomass store (unlike the situation in the ocean).

Humans are a gangster species, but an unusual one. Unlike the “normal” gangsters who based their invasion on the available stores of resources, humans, owing to our ability to accumulate cultural heritage, learned how to use fire. We thus could increase the available resource abundance and increase turnover time τ in (3). This allowed for a global expansion of our species in the past. The spread of humans with their primitive agriculture impaired the regulatory capacity of the terrestrial biosphere, but did not fully destroy it. Humans still did not eat wood and depended on soil fertility (low D for soil biogens in (3)), such that when the natural ecosystems were totally degraded in one place, humans went away and let them to recover.

However, recently the store of energy resources available to our species grew by additional one-two orders of magnitude with the discovery of fossil fuels— 10^4 GtC compared to 1 GtC of live biomass in the ocean or ~ 10 GtC of edible biomass on land. Using this energy, humans have almost completed the colonization of the entire biosphere simultaneously destroying all natural ecosystems everywhere in the world. Humans have been able to do it very quickly—apparently, before our environment has deteriorated to a state prohibiting further expansion.

In the now globally disturbed terrestrial ecosystems, synthesis and decomposition proceed in an uncorrelated manner, such that carbon pools can be depleted or doubled in just a few years. An example of such decoupling is soil erosion (i.e., the depletion of the soil organic carbon pool)—depending on the intensity of anthropogenic pressure, soil degradation occurs on a time scale from 1 to 10^3 years. If in the past a degraded agricultural field had a chance to be recovered via being colonized by natural species, now, when the natural ecosystems are globally lost, and our soils fully degrade, they will not have such a chance. The same concerns other life-essential resources like freshwater on land that is characterized by a transient store (Table 2). Water cycle is heavily impacted by the presence of natural forests and deteriorates if those are replaced by plantations [35, 41].

11 Conclusions

Functioning of living objects depends on environmental concentrations of life-important chemical elements in organic and inorganic form. Their pools are finite and their turnover times are small on the evolutionary scale. Thus, a genetic program of environmental sensing and control must have been included in the minimal genetic information kit that had differentiated life from non-life.

We have considered what environmental characteristics the genetic program of environmental regulation by life must encode to make this program maximally genetically stable (Table 1). The conclusion is that the environment must be such that when left without regulation it locally degrades at a maximally possible rate. This means that the local abundance of energy and matter resources and their global mixing must both be small. In such a case, any mutant not contributing to the “common good” of keeping the environment stable will deteriorate its own local environment and perish before it could have conquered the biosphere.

This conclusion formulated by Gorshkov [13] forms the basis of the concept of the biotic regulation of the environment. Other authors later arrived at similar conclusions in different, but related contexts (although not in the original Daisyworld studies). Generally, maintenance by natural selection of any property that restricts individual performance like resource consumption for the “common good” requires that the resources are limited and their global mixing is small.

Kinzig and Harte [21], see also [17], showed that limited resources in spatially structured environments with little mixing favor “less voracious” microbes (the “strategists”) who, in contrast to the “voracious tacticians,” sacrifice the maximal possible rate of resource consumption to the long-term persistence. The implication is that in stable ecosystems consumption of the resources by heterotrophs does not proceed at the instantaneous maximal possible rate (which can be infinite depending on heterotroph biomass).

Studies of programmed senescence found that a very long lifespan is associated with the production of numerous progeny and thus resource depletion is selected against under conditions of low resource abundance and low mixing, favoring instead a shorter lifespan and programmed death [25, 42]. In this context, mixing also includes the dispersal of living individuals. Interestingly, in their critique of the programmed aging concept Kirkwood and Melov [23] did not present any objections against the maintenance of such a program in spatially heterogeneous environments with limited resources and limited dispersal but called such conditions “special.”

However, rather than being special, strict limitation of energy consumption and mobility is in fact at the core of life organization. Getting their energy from massless solar photons plants do not need to move [14]. Any local environmental perturbation by an incorrectly functioning tree will be inherited by its progeny. Furthermore, since energy consumption by autotrophs per unit area is limited by the incoming solar radiation, natural selection for maximization of mass-specific metabolic rate will lead to a proportional decrease of area-specific plant biomass store thus reducing τ

in (3). While oceanic and land biota have comparable areas and equal total net primary production (50 GtC/year), there is only 1 GtC phytoplankton compared to about 15 GtC of green leaves [2]. This is because the small phytoplankton has metabolic rates about ten times higher than the larger green leaves, see [32] and Fig. 1 in [15].

It might be instructive to discuss how the original Daisyworld model could be reformulated to make transparent the above fundamental patterns. In the Daisyworld, a constant global temperature under changing solar luminosity implies that any given value of luminosity determines a fixed steady-state ratio of black to white daisies [44]. The same effect would be reached if one seeded the entire planet with just one species of daisies able to change their color depending on temperature—darkening when it is cold and whitening when it is hot. It is clear then that if the solar luminosity remains constant or changes very slowly, this property of temperature-dependent color change will be subject to genetic decay. Daisies of the same brightness as the “regulators” but lacking the ability to change color will ensure the same optimal global temperature. They will not have to invest resources into maintaining the temperature-control mechanism. Using the spared energy to reproduce more vigorously, they will outcompete the regulators globally thus doing away with the planetary temperature homeostasis. Then when the solar luminosity ultimately changes, slowly as it will, the biota will be unprotected.

This once again illustrates that there cannot be a genetic program for regulating a physically stable environment. The environment must be rapidly changing toward unfavorable life condition if left without biotic control [34]. For example, the temperature “regulators” will have an advantage if the temperature of the abiotic environment fluctuates widely around the optimum (e.g., during the day). Then by changing the color it would be possible to keep the local temperature close to the optimum at all times and have advantage over those who cannot regulate. The role of the time scale τ (3) of resource depletion (environmental deterioration) in this case will be played by the time scale of the characteristic local temperature fluctuations.

Natural ecosystems exert a strong control on local surface temperature, via transpiration on land and control of water transparency in aquatic ecosystems [20, 39], as well as via cloud formation [16, 41]. The presence of an ocean with its nearly infinite store of atmospheric moisture results in a major thermal climatic instability: the concentration of water vapor, the major greenhouse gas, doubles per every ten degrees of temperature rise, thus increasing the greenhouse effect and further increasing the temperature. This intrinsic physical instability, along with abiotic temperature perturbations, creates favorable conditions for the maintenance of biotic temperature regulation by natural selection. (It cannot be excluded that the ocean itself might be of biogenic origin [14]). The problem why despite the destabilizing moisture feedback the Earth's climate remains stable has not received considerable attention in atmospheric sciences even if it is key for understanding Earth's climate [3], see also Fig. 2.

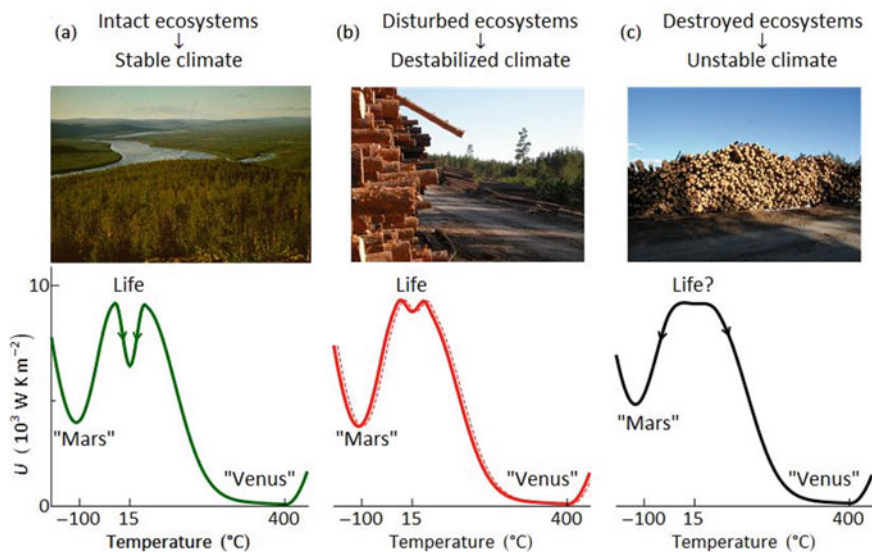


Fig. 2 Climate stability, carbon emissions and biotic regulation. Potential function U (W K m^{-2}) for the thermal stability of the Earth's climate versus planetary temperature T , $dU/dT = -c_s dT/dt$ (W m^{-2}), where c_s is heat capacity per unit surface area, t is time (after [12]). The slope of the U curve (dU/dt) shows how fast the climate system tends to return to a stable state when perturbed. The steeper the curve, the greater the time it will take for a given radiative forcing $F > dU/dt$ (W m^{-2}) (or the greater the forcing required for a given time period) to drive the climate away from the stable state. **a** The relatively unperturbed (preindustrial) biosphere is characterized by the deepest central pit (maximum stability) corresponding to modern global mean surface temperature ($+15^\circ\text{C}$). The left and right stable states correspond to uninhabitable Mars- and Venus-like climates at around -100°C and $+400^\circ\text{C}$, respectively. **b** On modern Earth with the biosphere significantly perturbed, the life-compatible potential pit is shallower. This means that any forcing in a given time, including radiative forcing from excessive carbon dioxide, will lead to a greater deviation from the preindustrial stable state than it would in an unperturbed biosphere. The dashed line shows global warming estimated neglecting changes in climate stability—the central pit just shifts to the right by about 1°C . **c** Totally destroyed natural ecosystems correspond to the disappearance of the life-compatible potential pit. In such a case even with a negligible external perturbation, or complete lack thereof, the climate spontaneously and irreversibly can precipitate to either Mars- or Venus-like states, with greenhouse gas emissions making the latter outcome more probable. Photos by Victor Gorshkov (**a**) and Anastassia Makarieva (**b**, **c**)

Since carbon dioxide is needed for the biotic matter cycle and is at the same time a greenhouse gas that affects temperature, the biotic controls of temperature and productivity could have come into conflict. The presence of atmospheric moisture as a major substance controlling both albedo and greenhouse effect on Earth allows life to avoid possible conflicts decoupling temperature and productivity controls—rather than the former being a by-product of the latter as sometimes proposed (e.g., [37]). In

other words, if a favorable for productivity CO_2 excess would entail an unfavorable increase in temperature, this could be compensated for via a biogenic reduction in the greenhouse effect or increase in albedo, i.e., by the biotic control of moisture.

The fact that only physically unstable environment can be regulated by the biota has direct implications for the humanity concerned about global change. This means that once the regulatory mechanisms (natural ecosystems) are destroyed, the environment will rapidly degrade to an unfavorable state irrespective of whether humans directly contribute to environmental deterioration, e.g., via carbon emissions, or not.

If the biotic impacts are responsible for the apparent thermal stability of the Earth's climate, the global destruction of natural ecosystems should have resulted in a decrease of this stability and growing climatic fluctuations on a variety of timescales. In the absence of external forcings, such destabilization alone could have produced either global cooling or global warming. Carbon dioxide emissions should have pushed the system toward global warming. However, even if the emissions stop and all the excess carbon is removed from the atmosphere, climate stability will not be regained as long as the natural ecosystems continue to be destroyed.

The common neglect of the genetic program of climate control by life has led to a troubling situation when natural ecosystems are evaluated in the most primitive terms according to their mean steady-state properties. Forest recovery is exclusively discussed in terms of carbon storage or the mean local temperature impact via albedo and transpiration [43]. But the main issue about natural ecosystems is not what they are but how they react to environmental perturbations. In simple terms, natural forests neither cool nor warm the Earth. They warm it if it is too cold and cool it if it is too warm compared to the optimal steady state thus ensuring climate stability, Fig. 2. That the precise biological mechanisms of this control have been so far too complex for us to find out, does not mean that they do not exist or that we will be spared if they disintegrate.

Finally, forest ecosystems consist of some of the longest lived species—trees. Once destroyed, they will recover their function through the natural process of forest succession in hundreds of years from now. Thus tree planting by itself, while having a wide appeal due to its conceptual simplicity, does not offset or compensate the destruction of natural forests, even if it could make total wood loss zero or even lead to a biomass increment. Tree plantations and young regenerating forests are not environmentally functional as they lack the needed genetic information about how to control climate. Diverting resources and attention from the protection of natural forests, tree planting may even have an adverse effect on climate stability. However, it can make a huge positive impact if the newly planted trees are cut instead of natural forests thus reducing anthropogenic pressure on the latter. Also, tree planting and generally restoration of land fertility can allow people to grow more food on restored lands without extending agricultural lands into the extant natural forests.

To conclude, contrary to what is sometimes opined in the Gaian context (e.g., [9, 22]), whether or not life regulates its environment is not an academic issue of little relevance to the current climate problems of the humanity. Neglecting or, conversely, taking into account this regulation implies distinct, sometimes opposing strategies of mitigating global change and preserving ourselves as a species. There is urgency associated with the fact that biotically unregulated environment should be inherently unstable and rapidly degrade. If science is to contribute to preventing the global ecological and environmental collapse rather than facilitating it, a multidisciplinary effort is required to build a coherent and comprehensive picture of life–environment interactions.

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