

Evolution of the Biosphere

By Sergei Doulatov

Abstract

Species are elements of ecosystems that are characterized by a particular structure-function duality. Each species possesses a set of attributes (phenotype) and a set of relationships with other species (role). The combined set of relationships between species defines a topological map of the biosphere. Isomorphic transformations on this map are referred to as variation, while non-isomorphic transformations that add or remove roles are referred to as speciation. Speciation is necessary because propagation of living processes is confined by discrete boundary conditions which conflict with the continuous nature of growth. An inevitable outcome of this is the generation of discontinuities in topological space that must be resolved for further expansion to occur. Evolution is thus directed by functional interrelationships in the biosphere, rather than an inherent design.

The main axiom in biology is the permanent and unbridgeable difference between the living and the non-living. We know of this difference due to a great number of physical effects associated with living organisms that are not observed in the abiotic domain. Even though living matter consists of essentially the same chemical elements as non-living matter, differing only in their relative abundance, their state of organization is entirely different. For that reason, a different thermodynamic field must be associated with the biotic component of the biosphere, in which exist multitudes of compounds that are unstable outside of it. Equilibrium properties of chemical reactions that occur in living organisms are determined by the properties of this field and are substantially different from those carried out in a laboratory. With the advent of molecular biology, it has become customary to regard living matter entirely from the standpoint of abiotic laws of physics and chemistry. Yet, if that were true, biotic and abiotic processes would exhibit the same basic set of properties. While most properties exhibited by living processes, can in fact also be found among inert processes, the former exhibit a propensity to grow and multiply regardless of external conditions, which is never observed in the abiotic domain. A chemical system is passive - it will increase or decrease its entropy depending on external conditions. A biological system is active - it will decrease its entropy regardless of external conditions. This principle of negentropic growth is the most general principle of life, which is reflected in all levels of biological organization, from a single cell to the biosphere.

The main purpose of this work is to create a foundation for evolutionary theory from the standpoint of physical law, which is the main shortcoming of the Darwinian paradigm. A physical theory is based on a hypothesis postulating the existence or proposing a mode of action of some principle in nature. In contrast, an empirical generalization is merely an induction based on a set of observations. A collection of several mutually consistent empirical generalizations, together with a number of assumptions can lead to a synthesis that may appear to be a rigorous scientific theory. An empirical generalization that organisms are in a constant struggle for survival can be inferred from three sets of observations, namely overproduction of offspring, variation and heritability. A number of additional assumptions are then introduced, namely that this struggle for survival is the cause of evolution, that it is the only cause of evolution, and that evolution is continuous in nature. Neither an existence of some basic principle is proposed and justified, nor is a mode of action proposed and justified for any known principles. Natural selection should by no means be confused with such a principle. The fact that certain organisms survive and reproduce, while others do not, cannot be used as its own casual precedent.

First, we must introduce a notion of evolutionary space as a topological construct that should not be confused with fitness landscapes. Here, evolutionary space is a manifold M , which curvature is determined by a set of boundary conditions with a given cardinality N (number of species). These boundary conditions introduce a set of constraints that determine which microstates (unique locations in morphospace) are accessible and which are prohibited. Flatness is the absence of constraint, and consequently flat manifolds display an ergodic characteristic of change, since all microstates are equally probable. In contrast, non-flat manifolds display a directed characteristic of change, since only certain microstates are accessible. Curvature introduces asymmetry into the system, such that individual microstates can be distinguished by their energy (fitness) and the macrostate with lowest energy (set of variants with highest fitness) is chosen at equilibrium. Though all processes tend to equilibrium with time, only ergodic processes are most stable in equilibrium. Non-ergodic processes are most unstable in equilibrium and tend to undergo transformations to higher states of organization.

Biosphere as a whole undergoes successive transformations collectively known as evolution. Evolution is a hierarchical process that does not fulfill the ergodic hypothesis on any level. On the level of individual organisms, variation is directed via structural constraints on M_i . Ergodic hypothesis fails because not the entire morphospace is accessible to variation. The most crucial reason for this

restriction is the prevalence of geometric regularities in the structure of biological organisms, such as allotaxis in sunflowers and pine cones, which is a manifestation of the Golden Section relationship ($a:b::b:a+b$). Other remarkable geometric regularities include various symmetries underlying the metazoan body plan. For example, bilateral symmetry in higher animals constraints the number of allowable appendages to $2N$, such that each longitudinal axis of the body is a mirror image of the other. On the level of the biosphere, speciation is directed via functional constraints on $M_n \rightarrow M_{n+1}$ transformation. Ergodic hypothesis fails because only certain sets of relationships are permitted, namely the ones that produce coherent ecosystems. Consequently, structural conservation in individual organisms is translated into functional relationships in ecosystems.

The stochastic nature of evolution is commonly argued on the basis of the following logic: only a genotype is heritable; since genotype determines phenotype which determines an organism's niche in an ecosystem, changes in genotype cause evolution; since changes in genotype are random, evolution is random. This logic, however, is flawed due to the failure of statistical hypothesis in evolution. Nor can it account for any macroevolutionary trends, such as an increase in structural complexity, increase in energy-flux density of the biosphere, increase in per capita energy utilization, and so on. Furthermore, it produces a number of curious biogeochemical paradoxes. For example, if the rate of speciation were inversely proportional to complexity, one would expect the rate of speciation for simple species to exceed that of complex ones. Remarkably, the opposite is in fact true, with most species belonging to complex metazoan phyla and the rate of speciation generally increasing with evolutionary time. Also, simple species would be expected to have a greater biomass since they accumulate biomass at a greater rate, while the opposite is in fact true. The reason for these shortcomings is that evolutionary thought to date, as illustrated by the argument for stochastic evolution, has failed to fully consider the most crucial level of biological organization – the ecosystem, and as a result has neglected the possibility that relations between species could channel evolution in a non-random fashion. Since the biosphere as a whole, much like a single cell, organism, or population, strives to expand in accordance with the principle of negentropic growth, it will adopt only those sets of relations between species which permit that expansion and consequently only those phenotypes and genotypes which give rise to those sets of relations. The entire thinking should be turned upside down!

Since we must proceed from the standpoint of the biosphere as a whole, we next consider the notion of a biological species, which is the singular most important element in evolution. Darwin argued that the species as such do not exist, since any two distinct forms merely represent positions along a continuum of variable forms referred to as species, varieties, or individual differences. He cited difficulties in taking lessened fertility in the offspring and sufficient geographic isolation as a guide as to what forms a species. Fortunately, these problems are avoided upon consideration of the biosphere from a physical, as opposed to naturalist, standpoint. The net effect of living matter in the biosphere is to transform the luminous energy of the sun into chemical free energy that enters the biotic cycle and is used to alter the abiotic domain. Therefore each homogeneous type of living matter called a species must be defined according to the unique function or role it plays as part of this process. More precisely, by role we mean a set of relations that an organism has to other organisms and to inert medium, including its resource base. The notion of a biological role is essentially equivalent to the notion of an ecological niche in the strictest sense. It should not be understood as an amorphous description of various properties of a species, such as its space utilization, food consumption and temperature range, but rather an aggregate of its interactions with a subset of other species that collectively determine its potential population density. Whereas a role is a functional characteristic of a species, a phenotype defined as an aggregate of attributes of a species, is its structural characteristic.

As previously noted, evolution is restricted by both structural and functional constraints operating on their respective levels in the biosphere. Two distinct processes that alter the complement of attributes can be identified. One is variation, which operates on the level of individual organisms and thus must conform to the existing set of relations in the biosphere that exist on a higher hierarchical level. The other is speciation which operates on the level of ecosystems and allows for generation of novel roles through the generation of corresponding attributes. The distinction between species and variants is also evident from a genetic standpoint. Variants are always more genetically similar to each other than to any other species and so are variants of variants and so on. On the other hand, a new species when it arises, contains a set of concordant changes in the global geometry of the genome that is qualitatively different from changes that any variant contains, which is related to the novel role that this species plays in the biosphere. An essential characteristic of every variant is its Darwinian fitness, which is determined by the topology of the biosphere, which is a product of constituent roles. The notion of fitness associated with each phenotype is in every way analogous to

the energy associated with each microstate in physical systems. The biosphere will seek to maximize its net fitness, as much as any physical system will seek to minimize its net energy. The fundamental difference between the two systems lies in their equilibrium behavior, as discussed below. A change in topology due to introduction or elimination of roles changes the distribution of fitness values accordingly. Hence, the lawful nature of evolutionary change follows from the lawful nature of topological constraints.

As an example of variation, consider a frequently cited case of the English moth (*Biston betularia*). In this moth there are two color morphs, light and dark. In the initial state of the biosphere, white variants were predominant due to their cryptic coloration. However in the subsequent state marked by the advent of industrial revolution, an additional interaction with man was introduced into the manifold causing a change in the relative fitness values. Thus, the essential nature of the moth has been preserved while selecting a set of attributes that best conforms to the novel state of the biosphere. Therefore, while fitness is a property of individual variants, it is determined by the state of the biosphere as a whole.

As an example of speciation, consider evolution of fermentation in yeast. The divergence of fermentative yeast from its non-fermentative ancestor is a result of acquisition of a set of genes involved in fermentation, such as alcohol dehydrogenase and pyruvate decarboxylase. Other genes, such as membrane transporters, sensor kinases and gene expression regulators are also required for proper regulation of the flux through the fermentation pathway. In addition, a multitude of seemingly unrelated changes in the genomic organization, gene rearrangements, inversions, duplications and translocations of chromosomal fragments, as well as point mutations in a vast array of genes accompany this speciation event; some segments of the genome are acquired, others permanently lost. The totality of these changes enables the yeast to perform its novel unique role in the biosphere. The fermentative yeast is a fundamentally different organism than its ancestor and will under no condition revert to its original role because the state of the biosphere in which it exists and which came about because of its speciation is different from that in which its ancestor had existed. Therefore, any successful theory of evolution must account for higher order causal hierarchical origin of speciation.

Heterogeneous living matter of the biosphere is composed of homogeneous types of living matter termed species. Each species is defined by its unique set of relations to other species which are part of the biotic cycle, as well as to processes of the abiotic cycle. This set of relations called a role is a subset of a much larger set which is formed by the unity of all distinct subsets and which is referred to as the macrostate of the biosphere. Therefore, every species is indirectly related to every other through intermediate interactions between species for which reason there exists no local process in the biosphere that does not in some way affect its entirety. For that reason, it is most natural to believe that the causal locus of evolution occurs on the level of the biosphere rather than its subordinate parts. That does not imply, of course, that there exist no sufficiently isolated subordinate levels of organization where such relations can be elucidated experimentally. The biosphere is in equilibrium relative to its thermodynamic field, but it is precisely in this equilibrium where it is most unstable. Inert abiotic processes strive to equilibrium with respect to their entropic thermodynamic field in which they are most stable; living processes strive away from equilibrium relative to their thermodynamic field in which they are most unstable. This highlights perhaps the most crucial difference between macrostate transitions in inert processes, such as expansions of gas, and living processes. Equilibrium and stability are synonymous only under an entropic directionality of change. The state of the biosphere is not fixed in time, but undergoes a succession of discrete equilibrium states through discontinuous transformations referred to as evolution. Evolution on the most fundamental level is the change of the set of relations among species in the biosphere. The tendency to evolve is inherent in all living things because it is inherent in the principles of the negentropic thermodynamic field that defines them. The equilibrium instability of that field, which results in its propensity to continuously expand, is the *vera causa* of evolution. As a consequence, the rate of formation of free energy has increased significantly in evolution as a result of the increase in state variables, such as mass of living matter relative to non-living (i.e. net biomass), rate of multiplication (i.e. biotic potential), number of interspecies interactions and potential volume that could be occupied by living organisms (i.e. field of vital stability). These macroevolutionary processes coincide with the changes in attributes of organisms to allow for increased metabolic rates and per capita energy use.

It seems plausible that ecological succession could serve as an excellent paradigm of a local transformation that occurs in a succession of equilibrium states. Many properties of successions make them amenable to experimental investigations. Because of their smaller scale and shorter time

between successive transformations, the state can be more easily defined in terms of constituent roles and their interrelations and change in relations can be more easily calculated. Moreover, principles valid for successions will hold approximately valid for the evolutionary process on the scale of the biosphere and geological time. The reasons for this equivalence are manifold, the most primary being that in both instances, species will alter their habitat and the resources available in it by doing work on the abiotic in the directions determined by their respective roles. These alterations will create the necessary conditions for generation (or invasion) by other species and the continuation of that process. This dynamic of waves of generation (or invasion) by new species combined with extinction (or replacement) of old ones, is a crucial aspect of both ecological and evolutionary transformations. For our purposes, it will suffice to mention several dynamic aspects of this process. Early succession stages are characterized by invasion of simpler organisms, such as bacteria, lichens and mosses, which roles are more tolerant of the harsh conditions in barren areas. These organisms facilitate invasion by more complex species in part through changes in the abiotic, such as availability of minerals and soil deposits, but also directly as a source of food. As the species diversity (i.e. number of realized roles), biomass, and productivity increase, conditions are created for invasion by yet more complex organisms, such as angiosperms and vertebrates, capable of sustaining multi-trophic ecosystems. Some of them inhibit growth of simpler organisms by replacing and altering their roles. Kinetics of these transformations is decisively non-linear. The rate of transformation increases hyperbolically as a function of time, with the initial transformations infrequent in occurrence and increasing in frequency as the productivity of the system increases. This is analogous to the aforementioned speciation-rate paradox. These preliminary observations support our assertion that the dynamics of this process are similar to evolutionary dynamics, as both are caused by the propensity of the biosphere to expand by generating and occupying all potential roles the conditions for which have been created by previous transformations.

All species are connected through respiration, feeding, and excretion. Every species is characterized by a particular intensity of multiplication also known as its biotic potential (ω). A given population produces n progeny at regular intervals determined by the rate of population growth r . The progeny move outwards, either passively through diffusion or actively using motility, at a rate k to establish new communities. Spatial distribution of organisms is bounded by their field of vital stability, beyond which growth cannot be sustained. As the density ρ increases within the bounds of that field,

the potential to sustain further growth decreases. Spreading organisms will also come in contact with other species with overlapping fields of vital stability, which will either interfere or alleviate their spread, so that both their own density and the combination of other densities will determine potential for further growth. If these density-dependent effects did not exist (for an infinitely large field of vital stability), r would remain constant and equal to ω . Thus, we are dealing with two variables, one pertaining to the present number of organisms N and the other to the potential to support further number of organisms P . In the ideal case, spatial effects do not matter and the growth function has a form of a simple wave with a frequency ω and an amplitude n/N . If, however, spatial effects are taken into consideration, the amplitude n/N will decrease with constant ω . In order for this to be valid we must assume synchronized replication, which will generally hold true as long as a population expands from a single source. Consider the ideal growth law:

$$\frac{dN}{dt} = rN, N = e^{rt} \quad (1)$$

The most general form of this law can be stated as follows:

$$\frac{dN_1}{dt} = rN_1(1 - a_2N_2 - a_3N_3 - \dots - a_nN_n) = rN_1 - ra_2N_1N_2 - ra_3N_1N_3 - \dots - ra_nN_1N_n \quad (2)$$

where $a_2 \dots a_n$ are the effects of species 2, ..., n on the rate of multiplication of species 1. These equations are not readily solvable analytically because of the second order dependence on N . Even though, this seemingly presents a difficulty to our analysis, we shall soon realize that it leads us to most intriguing results. Due to a constant propensity for multiplication, organisms will exert pressure on their environment resulting in an increase in the area occupied by them at any time. Since organisms propagate through a medium that exerts resistance on their propagation, defined boundary conditions will exist for both r and k depending on the state of the biosphere. Since different organisms multiply at different rates, the boundary conditions for each organism must accordingly be different. For $r(t)$ the boundary condition is known as biotic potential ω , for $k(x)$ it is known as dispersion potential κ , and for $N(x,t)$ it is known as carrying capacity K . To address the problem, we substitute invariant potential quantities for r and k , and define M in terms of potential wave functions $P_i(x,t)$. Since ω , κ , and K are invariant, there exists a linear complex operator that assigns an ordered pair $(r, i\omega)$ for every r and $(k, i\kappa)$ for every k , such that $(r, i\omega)$ and $(k, i\kappa)$ are the bases for \mathbf{C} . In other words, we

take the complex quantity to be invariant with respect to time, so that the real component corresponds to measurable quantities, while the imaginary component corresponds to potential quantities. Other physical parameters that enter into the equations, such as density, can be similarly defined in terms of complex magnitudes. These quantities are state variables and are invariant with respect to a single state of the biosphere. As such, they define the role of a species through its interaction with a subset of other species and must necessarily change upon any transformation, that is to say any evolutionary event. We can now analytically determine the potential function for the propagation of each type of homogeneous living matter.

$$P'(x, t) = \frac{\partial N}{\partial t} + \frac{\partial N}{\partial x} = i\omega N - i\kappa N = i\omega - i\rho \quad (3)$$

$$c = \frac{dx}{dt} = \frac{\partial x}{\partial N} \frac{\partial N}{\partial t} = \frac{1}{Nk(i\omega e^{i(\omega t - \kappa x)})} = \frac{\omega}{\kappa}$$

$$\frac{\partial^2 N}{\partial t^2} = -\omega^2 N, \quad \frac{\partial^2 N}{\partial x^2} = \kappa^2 N$$

$$\frac{\partial^2 N}{\partial x^2} = -\frac{1}{c^2} \frac{\partial^2 N}{\partial t^2} \quad (4)$$

where $i\rho$ is the potential population density, and c is the phase velocity. Thus, the general form of the wave equation is satisfied exactly. On the most fundamental level, wave properties of propagation of living processes are a manifestation of their self-similar growth. Next, we re-introduce the additional quantities that determine the magnitude of density-dependent interaction of a given species with all other species, or in other words that define the role of that species as it is done in Equation 2, but in terms of imaginary potential coefficients.

$$P'(x, t) = \frac{\partial N}{\partial t} + \frac{\partial N}{\partial x} = i\omega N - i\kappa N(1 - i\kappa_2 - \dots - i\kappa_n) = i\omega N - i\rho_1 \sum i\kappa_n \quad (6)$$

$$P(x, t) = e^{-(\kappa_2 \dots \kappa_n)\kappa_1 x} e^{i(\kappa x - \omega t)} \quad (7)$$

Based on these conceptions, each species in the biosphere acts as a single wave source, which may be treated as complex vectors in an n -dim manifold. Based on this construction, we can apply the entirety of developments in wave theory to the analysis of relationships between species in the biosphere. Of particular interest would be using wave interference to define relationships between species. Constructive interference results in mutualism or cooperation. For example, consider the process of facilitation in ecological succession where a species promotes the production of compounds

that positively affect the growth of another species. Destructive interference results in competition or parasitism. For example, consider the process of inhibition in ecological succession, where a species promotes the production of compounds that negatively affect the growth of another species. Accordingly, the expansion of M can be defined in terms of the potential functions as $P_M = P_1 \bullet P_2 \bullet \dots P_n$. It can be shown that given a wave propagating through a medium that exerts resistance in the direction of propagation and given that velocity of propagation is non-uniform, the wave will eventually transform into a shock-front, as it approaches the boundary conditions. Both of these conditions are satisfied for P_M , however it is beyond the scope of this paper to rigorously prove that the expansion acquires non-linear properties. The ultimate reason for this is that P_M , much like P_i , is restricted by a set of boundary conditions that limit its continuous expansion. This limitation, however, is opposed by the negentropic growth law, which states that the biosphere must continuously strive to higher energy states. Under these conditions, continued expansion of the biosphere is possible only due to introduction of new roles $\{\kappa_1, \dots, \kappa_n\}$ (i.e. speciation) or removal of existing roles (i.e. extinction). In other words, macroevolution is constrained to allow further expansion of the biosphere. Consequently, only those roles which conform to this criterion are permitted; and thus, only those sets of phenotypes and genotypes which give rise to these roles are permitted.