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From geochemical to biogeochemical cycles: an organizational view of how (and why) life shaped its conditions of existence

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From geochemical to biogeochemical cycles: an organizational view of how (and why) life shaped its conditions of existence

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ABSTRACT

Since the seminal work of Maturana and Varela, the Organizational Approach (OA) has defended an organism-centered view of life. This paper argues that the OA must be extended to include the historical, ecological and geochemical processes that sustain biological systems across scales. We develop a multiscale account of closure of constraints (CoC) in which localized closures can emerge and persist, and — under specific ecological regimes — stabilize larger-scale networks that progressively transform abiotic geochemical cycling into biogeochemical regimes. On this view, ecological organization is not merely contextual but partly constitutive of biological autonomy: persistence and evolvability depend on how unavoidable interactions are organized into structures that regulate shared conditions. We propose criteria to distinguish closure from mere feedback coupling, and we show how higher-level closures can stabilize non-closed components and structures. This reframing turns OA into a program for explaining living individuals as necessarily embedded in, and partially constituted by, the long-term causal regimes that enable the persistence of life on the planet.

KEYWORDS: Organizational approach; closure of constraints; biogeochemical cycles; biological autonomy; origin of life; Earth system

1. INTRODUCTION

What makes living beings distinct from other forms of organized matter? Since Aristotle, biology has been concerned with what distinguishes living entities from inert systems. A significant part of contemporary philosophy of biology has returned to this foundational question through the lens of biological autonomy and self-maintenance.

In particular, the Organizational Approach (OA) has become a central framework for articulating a naturalistic theory of life, centered on the notion that biological systems are autonomous systems whose identity and maintenance depend on a specific network of interrelated functional constraints. These constraints are not externally imposed but are instead generated and sustained by the system itself, forming a closed and self-determining causal structure, termed "Closure of Constraints" (CoC). This framework

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captures the dynamic, self-constructive nature of living systems, emphasizing their ability to regulate the flows of matter and energy through processes that contribute to their own persistence.

Although this formulation does not make it explicit, the standard interpretation is that the OA focuses on the organizational structure of individuated organisms. Indeed, the OA explicitly aligns itself with the tradition of Varela and Rosen, both of whom place organismal organization at the center of their theoretical frameworks, and considers biological structures such as colonies, ecosystems, lineages, etc., to be constructions derived from the organismal organization.[4] This stance should be understood as a critique of the view that evolutionary mechanisms provide the fundamental explanatory basis of biological phenomena. Since Dobzhansky's (1973) well-known dictum that "nothing in biology makes sense except in the light of evolution," evolution-centered approaches have become so dominant that the concept of the organism has been rendered nearly dispensable (Morange, 2003). In contrast, the OA argues that organization is not merely an outcome of evolutionary processes but a necessary condition for them. Accordingly, for the OA, history is not required to understand what biological systems are, but only to account for where they come from, on the assumption that these two questions are "conceptually distinct," despite being related.

Once life is defined primarily in terms of causal closure, this very definition risks enforcing a logical separation between the organization of living systems and the material processes that realize it, thereby neglecting the definitional relevance of the historical and ecological dimensions that make organizational closure possible. However, precisely because the OA privileges actual organizational self-maintenance as the defining characteristic of life, it leaves a crucial question unresolved: whether the way in which a minimal living organization arises is independent of the historical and ecological conditions that allow for its persistence.

Yet, as we will develop in this paper, the question of which historical and ecological processes sustain and shape the emergence of systems that can be considered alive is deeply intertwined with the nature of their constitutive organization and is therefore essential to understanding life as a robust and continuously evolving phenomenon. This is not merely an empirical question — concerning how biological organization has historically arisen — but also a definitional and conceptual one. Specifically, it concerns whether endurance over time, the capacity for evolutionary change, and the causal relation between individual and collective capacities for ensuring long-term sustainability are merely contingent consequences of being alive, or instead constitutive features of what it means to be alive, and whether the fundamental organization of living beings implies mechanisms beyond their individual dimension. Accordingly, it asks whether what identifies a system as a living entity can be disentangled from its capacity for long-term persistence.

In this work we address this question by examining the conditions and processes that led to the emergence of life on our planet. Drawing on current scientific knowledge, we analyze the successive organizational stages involved in biogenesis, as well as their respective potentials and limitations. To develop our arguments, we will proceed as follows: section 2 examines how prebiotic geochemical cycles created the environmental conditions necessary for the appearance and evolution of organized chemical systems at a microscopic scale. Section 3 analyzes the transition from localized chemical reactions to protocells exhibiting rudimentary metabolic and reproductive capacities. In section 4 we also study the organizational implications of the early invention by protocells of mechanisms to build inter-generational entailments that permitted to accumulate innovations and increase their internal complexity. In this section we also argue why the diverse sets of protocells have at the same time developed cooperative self-sustaining networks ensuring environmental conditions for medium-term persistence and evolution. Section 5 develops the idea that the capacity for long-term persistence — one of the most widely recognized characteristics of life — has required the development of complex proto-organisms that exhibited sufficient metabolic diversity and adaptive versatility to progressively transform abiotic geochemical cycles into

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[4] Consider, for example, Varela's claim that "the maintenance of identity and the invariance of defining relations in the living unities are at the base of all possible ontogenetic and evolutionary transformation in biological systems" (1979, p. 5) and Rosen's argument that "we cannot answer the question (...) 'Why is a machine alive?' with the answer 'Because its ancestors were alive'. Pedigrees, lineages, genealogies, and the like, are quite irrelevant to the basic question. Ever more insistently over the past century, and never more so than today, we hear the argument that biology is evolution; that living systems instantiate evolutionary processes rather than life; and ironically, that these processes are devoid of entailment, immune to natural law, and hence outside of science completely. To me it is easy to conceive of life, and hence biology, without evolution" (Rosen, 1991, pp. 254-55). Following these authors, modern versions of the OA have defended that "we do not need history to understand what biological systems are, but rather to understand where they come from: these two questions are of course related, but conceptually distinct" (Moreno & Mossio, 2015, p. xxxii).

biogeochemical cycles. Section 6 offers a conceptual reassessment of the notion of Closure of Constraints in light of its natural origins. Finally, Section 7 concludes by advocating for a multiscale reformulation of the OA.

2. FROM ABIOTIC DYNAMICS TO BIOGENIC POTENTIAL: THE ROLE OF GEOCHEMICAL CYCLES – WHY SCALE MATTERS

To understand the origin and persistence of life on Earth we should begin by analyzing the specific features of our planet in the early stages of its history. As is well known, our planet formed ~4.54 billion years ago by accretion from the solar nebula. During metal–silicate segregation and core formation, gases were released from the heated accreting material, generating an early, primitive atmosphere. Much of this first atmosphere was then removed — by hydrodynamic escape and related loss processes — so that it was subsequently replaced by a secondary atmosphere produced by continued degassing of volatile substances from the planetary interior. After the surface cooled sufficiently, water initially bound in accreted materials and released at depth outgassed to the surface and, rather than being lost to space, condensed to form the first hydrosphere 4.4 billion years ago.

Driven by solar radiation and geothermal heat from the Earth's interior[5], recurrent processes of chemical transformations were generated. Since the geological structure of the Earth's crust consists of distinct reservoirs (e.g., atmosphere, hydrosphere, lithosphere), flows of energy and matter were harnessed, forming cyclic processes. Hot, molten materials coming to the surface from the igneous rocks which, after several other processes, were buried deep within the Earth, changed into metamorphic rocks, and were brought to the surface of the planet, or buried so deeply that they were melted and became part of the magma from which igneous rocks were formed once again. These flows of heated and compressed chemical elements and compounds between the deep Earth and the surface reservoirs occurred through volcanism and subduction of tectonic plates, and were harnessed through the surface reservoirs, which include the layer of gases that surround the planet, the liquid water, and the solid – mainly rocky – shell of the interior magma.

These recurrent processes, shaped by the Earth's heterogeneous crust, give rise to what are known as "geochemical cycles." A geochemical cycle is "a system consisting of two or more connected reservoirs, where a large part of the material is transferred through the system in a cyclic fashion" ((Jacobson *et al.*, 2000, p. 10). These cycles consist of a set of recurrent transformations that certain chemical elements (Carbon, Nitrogen, Sulfur, etc.), and compounds (water, carbonates, silicates…) undergo in the Earth's thick outer shell. The Earth's cycles encompass the natural separation and concentration of elements and heat-assisted recombination processes occurring between the hot core and the crust, including the gaseous external surface, which very early was probably dominated by CO or CO_2, as in young Mars.[6] These cyclic exchanges between the Earth's interior and its surface reservoirs enable the ongoing transformation of matter and energy. Without these cycles, all these elements and compounds would be "trapped" in unusable forms or in inaccessible reservoirs (such as deep rocks or undecomposed organic remains). Moreover, geochemical cycles act as the planet's "circulatory system," transporting essential elements through the different reservoirs (atmosphere, hydrosphere, lithosphere, and pedosphere).

One interesting peculiarity of geochemical cycles is their capacity to modify themselves (Hazen et al 2008, Matange et al 2025). Driven by relatively stable "external" sources of energy (solar radiation and heat from the planet's core), a complex set of flows of matter and chemical processes were triggered. These flows affected the formation and transformation of new geological structures, which in turn shaped the dynamics of matter and energy flows, leading to the appearance of spatial and temporal large geochemical cycles affecting mainly the crust. Geochemical cycles progressively accumulated a diversity of chemicals (e.g., in liquid reservoirs) and provided continuous matter and energy flows (Garcia-Ruiz et al 2020)[7]. Moreover, they also generated several physical environmental conditions like temperature ranges, which helped stabilize environmental parameters.

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[5] Earth's internal heat, which is originated by its original formation, radioactivity decay and gravity, drives mantle convection, plate tectonics, rock metamorphism, and volcanism.

[6] It is difficult to reconstruct the pre-biotic geological cycles and global dynamics in our planet, even less in other close planets, like Mars, which seems to have had in that period also interesting geological cycles. We can draw, however, on some aspects of their fundamental mechanisms.

[7] Geochemical cycles evolved dynamically: starting with a very limited "mineral palette" (about 250 minerals), through cyclic processes of cooling, hydration, and plate tectonics, 1.500 mineral types were generated (Hazen et al 2008) thus favoring conditions for prebiotic evolution.

This entire set of factors maintained a complex and dynamic geological process that allowed for astonishing (and persistent) physicochemical diversity in the Earth's crust. Together with exogenous inputs from meteorites, this contributed to the Earth's surface chemical diversity, created a global environment favorable for prebiotic evolution. Geochemical cycles created and maintained the adequate boundary conditions not only for biogenesis, but also provided the physical and chemical framework that allows life to access, use, and return essential nutrients to the planet.

Moreover, these cycles favored biogenesis through different ways: they created concentration traps (evaporative cycles, adsorption on mineral surfaces); thermodynamic gradients (particularly hydrothermal circulation, which created local places of stable pH and temperature gradients (Damer & Deamer 2020); molecular selection, and even compartmentalization (Garcia-Ruiz et al 2017; Jenewein et al 2024), thus operating on a set of much more localized microscopic scenarios. This is of paramount importance, since to understand how abiotic matter came to generate increasingly complex causal loops, it is necessary to consider also a different scenario, one that focuses on processes operating at the microscopic scale. The question, then, is why the organizational complexity required for biogenesis emerged at this scale.

The microscopic world is a domain populated by entities (molecules and macromolecular structures) where assembling processes and catalytically harnessed reactions could in certain conditions create causal loops, not only among chemical reactions, but also between components and structures that act as boundary conditions on the processes that generate them. Processes unfolded at the microscopic scale allow a high diversity of molecular species to remain in close proximity, thereby enabling dense networks of mutually entailing chemical reactions. Also, at nano- and mesoscales intermolecular forces (Van der Waals, electrostatic, hydrogen bonding) take over, allowing many forms of self-assembly (SA).[8] A substantial part of SA's functional role in biogenesis consists in creating semipermeable compartments that favored the development of more complex and diverse far-from-equilibrium (FFE) chemical organizations. This development depended on the physicochemically active composition of these compartments, and on their nanoscale dimensions, where surface-to-volume ratios, quantum, and interfacial effects become significant.[9]

As it is explained in Ruiz-Mirazo & Shirt-Ediss (2026), the scenario where biogenesis should be search is the nanoscale domain (roughly speaking, from a few to a few hundred nanometers), and within similar energy-exchange thresholds (at most, a few tens of K_BT per elementary process). As these authors argue, "the necessary interweaving between local and global constraints, pushes for a solution in which molecular structures and interactions at the nanoscale become fundamental It is in that context that a material system can (1) harness a set of elementary physical-chemical transformations (taming their intrinsic noise and stochasticity, their asynchronous nature, their spontaneous tendencies to disperse, and their different free energies—provided that they remain within bounds) and, in the same move, (2) extract the work (i.e., develop its own energy means) to bring them together into a spatially and temporarily coordinated autonomous organization" (p. 278). Thus, at the nano- and mesoscopic[10] scale it is possible that *open-ended* recursive feedback can occur, linking FFE self-maintaining processes — such as

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[8] We use SA to denote a spontaneous process in which sets of pre-existing, disordered components, through specific and local physical or chemical interactions among themselves, form complex structures that are at — or relax toward — thermodynamic (or near-thermodynamic) equilibrium. Paradigmatic cases include certain phase transitions and, more commonly, the formation of supramolecular structures that do not involve the creation of new covalent bonds during assembly (e.g., lipid membranes, micelles, supramolecular polymers, and conformational folding of macromolecules). In this sense, SA is typically mediated by many weak, reversible interactions acting concurrently among building blocks — van der Waals forces, hydrogen bonding, medium-range electrostatic/ionic interactions, hydrophobic effects — so that error correction and exploration of configurational space can drive the system toward low free-energy states.

[9] A microscopic scenario is key to explain why, in SA, considerable structural and functional complexity can be achieved "for free," i.e., without external, fine-grained control of each bond-forming event. Both chemical catalytic reaction networks and SA require a nanoscale framework. Only at a nano- and mesoscale, SA processes and catalytically harnessed reactions (along with a host of nanomechanical processes) could easily create causal loops among chemical reactions and components and structures acting as boundary conditions on the processes that generate them. It is in this framework where different hypothesis of how a biogenic process could have started can be formulated.

[10] The mesoscopic scale is an intermediate scale ranging from a few nanometers to a few micrometers. It is a transitional domain where a material's properties are influenced by both microscopic-level fluctuations and macroscopic-level averages. Phenomena at this scale often show a combination of classical and quantum mechanical behaviors.

autocatalytic reaction cycles — that give rise to increasingly complex compounds, which in turn fuel the emergence of new autocatalytic reactions that in turn enter in the loop. In addition, processes of macromolecular SA can further drive the formation of progressively more complex dissipative autocatalytic systems.

Hence, as we will briefly explain next, biogenesis occurred in a framework of microscopic processes, where the conditions for complexification were more favorable, in particular, in a scenario of molecular and macromolecular cyclic autocatalytic reactions, connected with microscopic processes of self-assembly.

3. THE CHEMICAL ORIGINS OF AUTOPOIETIC PROTOCELLS

As argued in the previous section, in the Earth's crust soon appeared favorable conditions for chemical diversification and complexification, which were maintained by geochemical cycles. In particular, in certain places existed more favorable conditions for the spontaneous synthesis of increasingly complex molecular compounds, endowed with catalytic or template properties, and of self-assembling macromolecular structures, in particular, vesicles. Together, the association of these macromolecular vesicles and autocatalytic cycles would have created a diversity of more complex self-maintaining networks (Martin and Russell, 2003). There are increasing evidences that hadean hydrothermal alkaline vents may have provided the necessary chemical gradients and minerals to drive these associations. (Nisbet and Sleep, 2001; Russell et al 2014; Jordan *et al.,* 2019; Jenewein et al 2024). In these prebiotic settings, gradient-harvested work maintains meso-structures – such as surfaces, pores, compartments – that concentrated reagents, reduced effective dimensionality, and enhanced catalytic and templating interactions.

This environment favored the emergence, stabilization, and propagation of *virtuous circles*: autocatalytic processes that generated increasingly complex catalysts, which in turn enabled novel catalytic reactions – involving sometimes self-assembling compartments that enhance autocatalytic reactions – generating a recursive loop. These virtuous circles constitute the starting point that may have led to a type of chemical system capable of using its own (however minimal) organization to remain in a FFE state.

One may envisage heterogeneous populations of relatively simple, self-assembled compartments undergoing successive physical and chemical transformations. These initial compartments or "protocells" would consist of spontaneously formed hollow spheroidal structures containing aqueous microenvironments — that is, prebiotic systems already endowed with the characteristic topology of cells. Garcia-Ruiz's group has argued that in the primitive alkaline hydrosphere liquid water interacted with silicate rocks (serpentinization) favoring the formation of cyanide polymers, capable to maintain a proton gradient between the external and internal environment (Jenewein et al 2024). The problem with this hypothesis is that this type of vesicle is hardly congruent with the phospholipid composition of biological membranes (namely, lack of chemical continuity), and this is why the predominant idea is that the interesting primitive compartments are lipid bilayers. Yet, recently, Sutherland's group has succeeded in simultaneously synthesizing precursors of lipids, amino acids, and nucleotides using only cyanide, hydrogen sulfide, and UV light on mineral surfaces (Sutherland 2025). As Sutherland's chemistry produced more lipids *inside* these poly-HCN compartments, the lipids eventually lined the interior, creating a hybrid membrane. Over time, the organic mineral shell "molted" away, leaving the modern bilipid membrane. This shows that these primitive poly-HCN protocells could have evolved towards biological membranes.

By coupling self-assembly with chemical processes, such protocells would allow a richer repertoire of dynamical states, which might alter the composition of the compartment (which in turn might alter their permeability and spatial stability), leading to the appearance of populations of FFE highly dynamical compartments harboring autocatalytic systems (Ruiz-Mirazo, 2011). Chemical reactions intrinsically linked to these dynamics would, in turn, affect both the internal aqueous core and the properties of the compartment itself (e.g., membrane permeability and fluidity) (Ruiz-Mirazo and Mavelli, 2008; Shirt-Ediss et al., 2014, 2015; Piedrafita et al., 2017). So, this gives us a realistic scenario of certain places in the planet where millions of protocells would spontaneously form and disintegrate, which, far from remaining stationary, would grow, shrink, and divide.

A key step in this evolution of mutual dependence between compartments and autocatalytic networks was the appearance of a spatially self-enclosed cyclic organization of material components and transformation processes in which a functional bootstrapping between synthesis and control relationships was established. In other words, the appearance of short-living populations of FFE highly dynamical self-maintaining/self-enclosed systems. These systems likely constituted the first (and minimal) form of a self-sustaining/producing organization, namely, a minimal metabolism, a minimal autopoietic system showing "closure of constraints". Yet, likely, the only way to stabilize this organization required that these protocells achieved a control of growth and fission: in other words, a capacity to self-reproduce.

Accordingly, a plausible scenario for the onset of prebiotic evolution involves non-equilibrium chemistries developing through processes that lead to the emergence of protocells harboring a minimal form of self-sustaining and self-producing organization. Let us analyze next this crucial step.

4. THE ORGANIZATIONAL STRUCTURE OF THE APPEARANCE OF EVOLVING POPULATIONS: PREBIOTIC EVOLUTION AS THE CONSTITUTION OF A MULTI-SCALE FFE SELF-MAINTAINING ORGANIZATION

As said, in this context some protocells would have developed over time molecular mechanisms that enabled them to channel growth and fission, that is, to generate similar protocellular systems. At a given moment, certain protocells were capable of minimally regulating their growth dynamics and dividing in such a way that (at least a percentage of) the resulting 'offspring' closely resembled the original 'mother' protocell. In other words, some protocellular organization became capable of generating controlled cycles of growth and division, including the coordinated duplication of all components and transformations, their appropriate spatial distribution, and their temporal synchronization, such that each cycle culminated in the physical multiplication and subsequent propagation of the original organization[11] (see Mavelli & Ruiz Mirazo 2013; Piedrafita et al 2017; Moreno 2019; Teneja & Higgs 2025 for further details).

This transition had important consequences. When self-producing (i.e., metabolic) protocells develop mechanisms that enable controlled cycles of reproductive fission — thus becoming self-reproducing protocells — they not only extend their identity spatially but also generate a *lineage*: a temporal sequence of ancestry and descent composed of individuals forming a continuous, trans-generational line of historical causal entailments. Through reproduction, distinct groups of individuals arise that are unified by descent from a common ancestor or by participation in a direct line of descent. The generation of lineages and populations[12] is a consequence of the reproduction with heritable functional constraints and of heritable variations.

The appearance of this new collective and transgenerational domain provides a larger spatial (populations) and temporal (lineages) scale, allowing in turn the emergence of a primitive form of evolution by Natural Selection. This development arises from hereditary constraints acting on the metabolic organization of protocells, which, in a given environment, may enhance or impair individual survival and thus lead to differential rates of reproduction. At the population level and over multiple generations, this differential survival gradually biases the population toward those configurations[13] that confer greater viability in a relatively stable selective regime.

Indeed, selection requires processes that occur at the collective and transgenerational level, since evolution requires averaging out a great number of token reproductive processes, and considering at each time the synchronic phenotypic interactions of the individuals. For selection to occur, successful reproductive processes have to persist during many generations within a population. Thus, it is necessary a higher-scale framework, where a high number of individuated organisms interact and reproduce during a high number of generations. But selection does not happen only at the population level and inter-generational scale. In fact, selection results from processes that occur at the level of organisms (more specifically: at the level of how a given (set of) hereditary trait influences the achievement of the life cycle of this organism).

Therefore, in a relevant sense, these processes are key parts of a spatially and temporally wider cyclic causal loop, which connects processes occurring at the organism-environment level and (statistical) processes that happen at the population and transgenerational level. This inter-level scenario may generate non-linear effects or context-dependent changes in the fitness value of each type of organism.

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[11] Since the pioneering work of Segre and Lancet (Segre et al 2000) the hypothesis of the emergence of "lineages" in populations of self-reproducing protocells before the appearance of genetic molecules is explained through the theory of "compositional inheritance", namely, that the organizational specificity of a protocell can be transmitted through the specific ratio of certain molecules, which ensures a "statistical inheritance"**.**

[12] We use the term 'population' in the standard sense: a set of contemporaneous individuals that can interact and reproduce within a shared environment, typically comprising multiple lineages. Yet, strictly speaking, in evolutionary theory a population is defined as a snapshot of a group of interbreeding individuals within a lineage at a given moment. But here we are studying just its first and minimal form.

[13] We use here the term "configurations" to refer not only to the selection of more viable organisms, but also of those ecosystems ensuring global homeostasis.

This entanglement between organismic and population-level scales becomes evident when examining the causal structure of the selective process. Selection should be understood as a circular, interlevel causal mechanism: heritable traits constrain the metabolic organization of individual (token) protocells, which, within a given environment, enhance or impair their survival and, through reproduction, lead to the differential retention of those traits. Because only a limited number of protocells can persist — owing, for instance, to environmental resource constraints — traits that confer higher fitness become increasingly prevalent over successive generations. Thus, if a type of protocells bearing a genetic configuration that produces phenotype X has higher fitness than those expressing alternative phenotypes (W, Y, Z, etc.), phenotype X will come to predominate within the population, provided that the selective regime remains relatively stable for the protocells in question for a number of generations. In this sense, X persists in the population because of what it does.

Importantly, this circular causal loop – which is the core mechanism of evolution by Natural Selection (NS) – only works if it involves, along with the population level, an organismic level, namely, the metabolic organization of individuated protocells and their capacity for functional diversification[14], expressed in their phenotypic phenomenology. Otherwise, it becomes tautological or – at most – trivial (Hunt 2014). Although individual organisms disappear before the global causal loop that explains the occurrence of evolution by NS is completed (in the same way as individual molecules are constantly being broken down and reformed in metabolic cycles that once and again constitutes and maintains organisms), they still have a causal role in the maintenance of these loops.

Thus far, we have analyzed evolution within populations in largely abstract terms. However, these evolving populations were composed of groups of protocells competing for the resources required for survival and reproduction. For these population-level processes to persist, protocells must not only reproduce and compete for survival, but also *collectively sustain the material and energetic conditions that keep reproductive continuity viable*. Over time, sustained metabolic activity depleted specific resources and generated waste products, thereby modifying the surrounding environment. At the same time, the spontaneous emergence of metabolic diversity would have enabled the formation and stabilization of cross-feeding networks, preventing both resource exhaustion and the accumulation of toxic by-products. In turn, these networks would have supported further increases in both the size and diversity of protocellular populations.

In other words, from a realistic thermodynamic perspective, for evolving populations of protocells to persist, they must exert specific forms of control over their environment — namely, regulating matter and energy flows in ways determined by their phenotypic traits — so as to constitute a global, self-maintaining causal loop of energy-matter exchanges. Within this interconnected network, each population contributes to the maintenance of environmental viable conditions for the others. The resulting system constitutes a proto-ecological network that remains in FFE conditions by harnessing external energy sources.

This is why, ultimately, biological evolution is generated by a material FFE organization that implements this double (evolutionary and ecological) interlevel causal loop, where the transgenerational changes of individuated proto-organisms are framed into a higher-level FFE "eco-evo" organization. In this interlevel system, the "slow" processes of creation and modification of hereditary constraints take place, and an additional circular relation of cause and effect is established between individual organizations and the eco-evolutionary higher-level organization. In other words, the material implementation of a Darwinian System of evolution by NS implies at the same time the construction of a wider globally self-maintaining organization in FFE conditions.

The following section examines how primitive cross-feeding populations may have evolved into early ecosystems, and how, as these earlier ecosystems expanded and interconnected across the planet, they ultimately gave rise to a biosphere capable of regulating geochemical cycles for its own maintenance, thus creating what we nowadays term "bio-geo-chemical" cycles.

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[14] This role is already clear in the famous case of the "evolution" of the "Spiegelman's Monster" (Kacian *et al.* 1972), which shows an almost trivial expression of the theory if we leave out the implicit functional diversity provided by the organism's phenotypes (see for details Moreno & Ruiz Mirazo, 2009). In other words, for the theory to avoid tautology or triviality, it should include in the loop the organismic source of functional diversity (i.e., phenotypic diversity).

5. BIOGEOCHEMICAL CONTROL AND THE LONG-TERM PERSISTENCE OF LIFE

As these proto-ecological networks develop, they begin to modify broader environmental conditions in ways that sustain and propagate an increasingly diverse and complex ensemble of interrelated protocellular communities. The increase in the growth and diversity of protocell populations gradually began to alter their local environmental conditions, achieving local sustainable systems for recycling food and waste. In fact, as Dagg (2003) has argued, ecological networks are not pre-given entities but patterns that emerge from routine interactions among metabolic systems. When distinct organisms share an environment, each one's uptake, transformation, and release of substrates creates by-products and resource flows that become inputs for others. The recurrent coupling of these local exchanges yields stable pathways of matter and energy which, in aggregate, constitute a network. In this sense, the network is an emergent side-effect of interactors' activities (Dagg, 2003).

These collective self-maintaining webs can be interpreted as the earliest steps in the appearance of a full-fledged global ecological domain. This, however, required that protocells developed more diverse and complex metabolisms, somatic-time adaptive mechanisms (including life-cycles), which in turn requires more accurate (probably, genetic) heredity, so that primitive living systems could thrive to such an extent that they became so numerous that they could affect the other geospheres (atmosphere, hydrosphere, lithosphere, and pedosphere).[15]

This complexification and diversification of metabolism in prebiotic evolution were likely especially important for the transition from locally modulated geochemical cycles to a global system of biogeochemical cycles that constitutes the biosphere. As life spread and evolved on Earth, biotic systems caused profound changes in the physicochemical nature of the planet and its geospheres, becoming major participants and effectively taking over former abiotic geochemical cycles, turning them into biogeochemical cycles. Thus, the emergence of these collective self-maintaining webs is another equally important prerequisite for the long-term sustainability of the process of biogenesis.

We must realize that this transition was not a succession of merely quantitative increases in the biological impact on the geochemical cycles, but a radical qualitative change by which earlier organisms took full control of these abiotic cycles.

It is difficult to tell when this global control happened, but it is likely that this did not happen until the prokaryotic organisms colonized the whole planet, as suggested by the diverse roles played by microorganisms, particularly bacteria, in biogeochemical cycles. Only when life became sufficiently adaptive and metabolically diverse so as to colonize the whole of the Earth's crust and achieved a critical mass, the global amount of living entities reached a threshold of ecological expansion: the geochemical cycles began to be dominated by living organisms and became biogeochemical cycles. Since the first prokaryotic organisms thrived and diversified, biological processes have become increasingly important in the determination of the distribution of chemical elements and the compounds into which they are incorporated in the planet's geospheres, driving the interactions between the biosphere and the other geospheres, through the appearance of processes like fermentation, photosynthesis, Nitrogen fixation, and others.[16]

How this transition happened needs further inquiry. Yet, very likely, two important stages must have previously occurred. First, in order for life forms to thrive to the extent necessary, they would have to exhibit a life-cycle and, ultimately, an ability to control their reproduction and proliferation. And second, the gradual geographical expansion of the coupling between the biotic and abiotic components of the local ecosystems, evolving initially in more confined environments, in which living systems were eventually able to control the abiotic components. In these confined environments, both the mechanisms for controlling life-cycle stages and the mechanisms for coupling with abiotic components could evolve, laying the

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[15] It is worth mentioning here the difference and relationship between the concepts of "geosphere" and "reservoir". A geosphere is a segment of the Earth system that compartmentalize the larger Earth system into more manageable parts, while a reservoir is an amount of material defined by certain physical, chemical or biological characteristics that can be regarded as reasonably homogeneous (Jacobson *et al.*, 2000). Reservoirs can be located within geospheres or other manageable units: as examples of reservoirs, we can mention "Oxygen in the atmosphere", or "Carbon monoxide in the southern hemisphere", or "Carbon in living matter in the ocean floor".

[16] For instance, the Carbon cycle is influenced by a diversity of metabolic processes, including Carbon dioxide fixation, carried out by photosynthetic and chemoautotrophic organisms; aerobic respiration; organic decomposition (or mineralization); and methane production. To cite another example, the Nitrogen cycle is influenced by Nitrogen fixation, nitrification, denitrification, and ammonification, among other processes (see below). A wide diversity of living beings, especially bacterial clades, are involved in these metabolic processes. For a useful discussion, see Staley and Orians (2000).

foundation for subsequent interaction between the biosphere and the other geospheres, which would enable the transition from abiotic to biogeochemical cycles.

The biogeochemical cycles now constitute a complex, interactive, and dynamic system driven by energy from the sun and by the heat of the Earth's interior, related to radioactive decay processes (Jacobson et al., 2000). Millions of species that appeared along the evolution of life on Earth influence the biogeochemical cycles, each adapted to survive and thrive under particular ranges of conditions, each using environmental resources in a particular way, depending on the ecological interactions and processes in which they are involved. As an outcome, living systems are capable of a rather diversified set of influences on the biogeochemical cycles (see, e.g., Staley and Orians, 2000). The combined effect of cyclic dynamics of transport and transformation of chemical elements flowing in and between the geospheres results in a planet in a continuous state of physical, chemical and biological change, in a FFE condition that fundamentally depends on the metabolic processes in the biosphere, which influence and are influenced by the physicochemical conditions of the environments where living beings maintain themselves.

Once life colonized Earth, it became a dominant controlling factor, along with continental weathering, substantially contributing to the dynamics and stability of the cycles of these elements. The stability of the concentrations of many elements in the present-day oceans is probably due to balanced conditions between input and removal fluxes, with living beings being often involved in such fluxes. For instance, depositions of biogenic sediments are one of the primary oceanic sinks for P, amounting to an important removal flux.[17] The Boron cycle provides a dramatic example of how biotic mediation changed the cycling process. Continental weathering is the dominant input flux of B to the ocean, but this is mostly due to the enrichment of this element in continental soils as a consequence of biological processes. This is a clear case of control of geochemical cycles by biotic systems and processes, as B-enriched soils are fundamentally controlling the input flux of this element to oceans (Kakegawa et al., 2002). We can conclude, thus, that the dynamics of B concentrations in oceans depends on stabilization by fluxes due to terrestrial biota and continental weathering, resulting in a present-day biogeochemical cycle that is different from the pre-biotic geochemical cycle (Kakegawa et al., 2002).

Most naturally occurring organic molecules contain, besides Carbon and Hydrogen, one or more of four key elements: N, O, P, and S. These were, therefore, the most affected geochemical cycles on Earth once life thrived, but they were not the only ones. Early in the history of our planet the atmosphere was probably dominated by CO or CO_2, as in Mars and Venus, but as life thrived on the planet, the atmosphere came under the control of biological processes, mostly as an outcome of metabolic evolution. To consider one example of how life changed substantially the geochemical and geophysical dynamics of Earth, let us briefly refer to the case of the O cycle.

Oxygenic photosynthesis, for instance, whose oldest possible signs date back to 3.8 Gyr (Buick, 2008), with a minimum hypothetical age of 3.0 Gyr (Crowe et al., 2013; Planavsky et al., 2014), led to a rise of oxygen since it first evolved in the Archaean eon. Oxygen then caused the "Great Oxidation Event" (GOE) around 2.4-2.3 Gyr, approached modern levels during a brief "O_2 overshoot" between 2.3 and 2.05 Gyr, and declined afterwards (Bekker & Holland, 2012). Atmospheric pO_2 probably reached near-modern levels during the "Neoproterozoic Oxygenation Event" (NOE) between 0.8 Gyr and 0.65 Gyr (Kah & Bartley, 2011; Och & Shields-Zhou, 2012). This has been the final step in the oxygenation of Earth's surface. The Oxygen cycle is, thus, an obvious example of a geochemical cycle that came under the control of living systems.

Nowadays biogeochemical cycles are entangled with one another. As material cycling on Earth is to a large extent mediated by the biosphere, these entanglements typically involve metabolic activities of organisms. Yet, at the beginning, things would have been different. In the primitive biosphere biogeochemical cycles were driven by anaerobic prokaryotes living in an atmosphere dominated by Nitrogen, Carbon dioxide, and methane, with almost no free Oxygen. According to Moody and colleagues (2025), an anaerobic Carbon cycle was established early in life's evolution, whereas biological cycling of elements such as Nitrogen and Sulfur began later, though nonetheless early in the Earth's history. More recently, Stüecken (2025) has argued that the early biosphere should probably "have been fueled by hydrothermal injections of H_2 and FE_2^+, making volcanically active basins at least 2-8 times more productive relative to background" (see Horne et al. 2025). Biologically-mediated processes that made the Nitrogen cycle to be under biotic control may be also very old. In rocks dated between 3.8 and 3.5 Gyr, i.e., between the Eoarchean and the Paleoarchean, Nitrogen isotopic data have been interpreted as evidence of hydrothermal assimilation by thermophilic microbes (Pinti *et al.*, 2001, 2009) and biological N_2 fixation (Zhang *et al.*, 2014).[18]

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[17] Sources and sinks are fluxes of materials *into* and *out of* a reservoir, respectively.

[18] This interpretation should be taken at this point with a grain of salt, as secondary alteration through metamorphism cannot be ruled out, making it hard to reach any firm conclusions about the Paleoarchean

The global sum of the ecosystems emerged as a geosphere in its own right — the biosphere – one that operates across and within all others, as the continuous and strong interactions between living systems' metabolic activities and all parts of the Earth system led to the emergence of a single complex, coupled, and evolving system, in which all parts are dependent to some degree on all the other parts, as proposed in the Gaia theory and other frameworks (Lovelock, 1972; Lovelock & Margulis, 1974; Vernadsky, 1998). As Jacobson and colleagues (2000, p. 6) observe, "the biosphere is ultimately what ties the major systems of the Earth together." Once the biosphere was substantially interacting with the other geospheres, a turning point from geochemical cycles to biogeochemical cycles was a necessary consequence. The picture that emerges from duly considering the feedback processes connecting the biosphere and the other geospheres is an integrative view of the Earth system as a set of coupled biogeochemical cycles, which is now part of the received knowledge in Earth System Science.

Today it is widely accepted that the specific Earth's FFE conditions are due to the activities of living systems, but the acceptance of this view is rather recent, with high levels of controversy marking the appraisal of the Gaia theory by the scientific community since James Lovelock and Lynn Margulis, building on Vernadsky's theories, proposed it. With the advent and growth of Earth System Science, the acceptance of this view became widespread but its relations with the Gaia theory took longer to be vindicated (see, e.g., Margulis, 2004).

6. RETHINKING ORGANIZATIONAL CLOSURE IN LIGHT OF ITS NATURAL ORIGINS

Previous sections have shown that the long-term persistence — and hence the evolutionary potential — of prebiotic systems depended crucially on their collective and intergenerational dynamics, which progressively modulated geochemical cycles in ways that enhanced their continuity. As their organizational complexity increased, prebiotic systems gradually developed the ability to modulate geochemical cycles for their own benefit. This capacity was mediated by the construction of increasingly diverse and extensively collective long-term networks of populations, whose global dynamics was powerful enough to exert a significant influence on the geochemical cycles. In turn, the individual viability of the new and more complex proto-organisms depended on the new conditions of the collectively constructed environmental niche.

It is well established that prokaryotic life (bacteria and archaea) was already capable to colonize and modify a wide range of environments, as well as that it can modulate geochemical cycles to turn them into biogeochemical cycles, as explained above. Yet, it remains unclear to what extent more ancient proto-organisms already participated in environmental regulation. This capacity likely emerged gradually: proto-organisms may have initially exerted only localized effects, but these interactions could have reinforced their persistence, enabling metabolic evolution and diversification, and increasing their ecological influence.

This calls for rethinking biological organization as a multiscale phenomenon. As explained in the introduction, the OA has focused primarily on the self-production/maintenance of individual organisms. The term "self-production" was conceived rather as an actual organismic-like process of "self-constitution", where the causal circularity was maintained by the constraints (enzymes, membrane, etc.) created within this process of material production of self-individuated entities. Within this framework, if a system internally "produces" and recursively maintains the functional constraints that sustain it, it constitutes a biological system.

The approach we propose here differs in that it explains the specificity of biological causal structure not only in terms of the constraints internally produced and maintained within individuated organisms, but within spatially and temporally larger processes involving millions of organisms of differentiated populations which collectively interact and evolve during thousands and millions of generations, also involving controlled cycles of environmental processes. First, because stabilization of a "minimally metabolic" system requires invention of re-production and therefore historical entailments. In other words, when considering the material conditions of its realizability, the appearance of a minimal system that harbors a closure of constraints (this is what is meant by the aforementioned definition of minimal metabolism) is not intrinsically stable at the strict organismic individual level. And second, because history requires inter-generational persistence of populations, which in turn requires certain ecological capacity to actively ensure suitable environmental conditions.

Nitrogen cycle (Stüeken et al., 2016). It is likely, anyway, that biological Nitrogen consumption had already evolved at this time, as evidenced by NH_4^+ concentrations in metasedimentary biotite grains at ~3.75 Gyr (Stüeken et al., 2016). What is harder to establish is, in fact, which particular metabolism was responsible for such concentrations.

As the earlier self-reproducing protocells evolved into primitive true organisms, their internal organization became increasingly dependent on *spatially and temporally broader organizations that include inherited and ecologically stabilized constraints and recurrent feedback pathways operating across levels (lineages, populations, ecosystems, and, ultimately, biogeochemical cycles).* We call 'supporting regimes' those durable historical-ecological regularities that (i) stabilize boundary conditions, (ii) secure sustained material throughput, and (iii) make the recurrent re-instantiation[19] of organismic CoC viable across evolutionary timescales.

This collective dimension is reflected in the organization of individual organisms: certain fundamental constraints — such as genetic constraints — are not fully generated within the circular logic of the individual metabolic organization. Although organisms are autonomous systems because they produce the constraints (i.e., enzymes, membranes, etc.) that control a cyclic process of material and energetic processes of self-production and self-maintenance, these processes – and ultimately the fabrication of the whole machinery – require an inherited constraint – the information recorded in the specific sequence of nucleotides of inherited DNA — which comes from the parental organism(s), and ultimately is generated at the population level (more precisely, in an interaction between the population and organismic levels).[20]

Thus, a more comprehensive view recognizes that biological autonomy instantiated in individuated organisms is not only a structural or functional property, but also a historically and ecologically constituted one. The organism's capacities for self-maintenance, reproduction, adaptation and agency are shaped and sustained by long-term processes of selection, ecological interaction, and environmental structuring. Although the organizational core of this entire collective system is embodied in the metabolic organization of highly integrated individual entities — which are ultimately the protagonists of evolution and niche construction —, it is impossible to understand the persistence and robustness of life by considering their organization in isolation. Organisms are autonomous not despite their evolutionary and ecological embeddedness, but precisely because of it. A robust theory of life must therefore integrate the logical structure of the individual organisms with the multiscale processes that sustain and transform it. This perspective highlights the importance of tracing how a full-fledged organizational closure emerged and stabilized as a complex set of entangled multiscale causal networks, involving specific environmental and selective conditions.

This is not to deny that an early and minimal form of CoC may have arisen early in primitive protocells. Yet, these hypothetical systems would have been extremely fragile, and lacked organizational continuity. The appearance of the first reproductive protocells (initially non-genetic) must have been also the first way to stabilize the CoC, since each new protocells was warranted to include those components ensuring organizational continuity. Later, with the appearance of the earlier form of genetically-based

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[19] By re-instantiability we mean the capacity of an organizational pattern (e.g., a network of constraints) to be reliably realized again in new tokens across time, so that the organization remains continuously achievable across generations and changing conditions. Importantly, this does not imply that the organization must first collapse and then be rebuilt; rather, it tracks the repeatable realization of organizational configurations under historically and ecologically stabilized enabling conditions. Nor does re-instantiability presuppose organizational stasis: it is fully compatible with — indeed meant to capture — the fact that organization can expand, complexify, and extend across levels over evolutionary and ecological timescales. On the present view, early protocellular and infrabiological organizations can progressively become paradigmatic biological organisms precisely by acquiring and integrating extra-organismic constraints (lineage-stabilized templates, population-level retention dynamics, and ecologically structured recycling relations) that stabilize boundary conditions and throughput, thereby enabling increasingly robust and scalable forms of closure. The term has an established usage in bioinformatics infrastructure discussions (see Tan *et al.*, 2010), where "re-instantiability" is invoked (together with terms such as persistence and reproducibility) to denote the capacity to recreate a resource/tool/database instance from standardized specifications so that results and infrastructures remain repeatable over time; we adopt the term in an analogous, organization-centered sense to capture cross-temporal reliability of organizational realization.

[20] Organisms may be said to realize autonomous CoC because, "materially" speaking, all the processes are dynamically governed by self-fabricated constraints: in fact, DNA is a dynamically inactive component – transcription and translation are entirely carried out by proteins (or RNAs). Thus, materially (metabolically) the cell is a CoC, since all the enzymes, membrane and other constraints necessary to the ongoing cyclic re-production of the cell are generated. In this sense, the informational causal role of DNA occurs only because it is materially achieved by the enzymatic control of a host of proteins and RNAs within the cell. The fact that proteins cannot be fabricated without this information has been called by H. Pattee "semantic closure" (1982), although in reality at the level of the cell, this is not a complete form of closure because the genetic information is not generated within the cell.

reproduction, selective pressures could shape inter-generational inherited constraints (which require population-level variation and intergenerational dynamics, as well as proper integration with the environmental conditions under which its self-maintenance materially takes place).

Also, long-term maintenance of diverse lineages is impossible without the formation of self-maintaining webs among these different populations. Multiscale nested organization enables high degrees of internal integration, including metabolic complexity, regulatory control, and ecological sustainability. This gives rise to individuated agents capable of modulating their environments in real time, but with long-term consequences. Such capacity to functionally modulate the environment is central to the evolutionary success and ecological entrenchment of living systems and, therefore, to constitute life as a robust, long-term, evolvable phenomenon.

7. CONCLUSIONS: FROM MINIMAL ORGANIZATION TO MULTISCALE CLOSURE OF CONSTRAINTS

In sum, we argue that a revised account of the minimal requirements for biological autonomy is necessary, one that recognizes that the viability and adaptive potential of organismic organization are grounded in integration within larger ecological and evolutionary systems. Key features such as evolvability and agency cannot be adequately explained by an abstract, implicitly isolated notion of CoC alone; they require a multiscale framework in which closure emerges from historically accumulated and ecologically extended interactions.

Under this multiscale interpretation, the OA retains its central insight — organismic autonomy as an organizational achievement grounded in constraint-based, far-from-equilibrium self-maintenance — while extending its explanatory scope to encompass the durability and planetary consequences of life. In this view, individuated organisms represent the organizational core that actively builds this temporally and spatially larger organization. The foundational insights of the OA remain indispensable, as they capture the unique integration and complexity *that appear in the organization of individual* living systems, which are the key support of this global organization.

Individuated organisms are central in this global concept of Multiscale CoC, because they are uniquely constituted by strongly interdependent components that form a coherent, operational self-maintaining unit, where the high degree of interdependence of the different parts and processes is needed to coordinate the distances, times, rates, and energies involved in all of the living processes. This integration is inherent in any system whose identity is based on a FFE cyclic set of synthetic processes, namely, on a logic of self-construction that depends on the specific energy requests and the actual rates of their (always precarious) constitutive/interactive dynamics harnessed by a hierarchy of regulatory constraints (Ruiz Mirazo & Moreno 2024). This is why we maintain that this new account of the OA is right in the focus on organisms, and we still consider that their organization is the fundamental basis of the entire multilevel phenomenon of life.

In this expanded view, the OA becomes not only a framework for identifying the minimal features of life, but also a research program aimed at explaining its long-term persistence as a planetary phenomenon through the construction of a robust biosphere. Still, this new view raises further questions, such as how the global biosphere has evolved while maintaining stability despite radical external changes (such as large meteorite impacts) or internally induced changes (such as major oxygenation events and mass extinctions), and while biodiversity has been continuously increasing. This requires answering questions about the mechanisms through which the biosphere (or "Gaia") has maintained global viability parameters for nearly four billion years, despite radical external perturbations and internally driven changes, while maintaining the narrow range of conditions compatible with complex life forms[21].

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[21] We suggest that our multiscale CoC approach can help develop an intermediate explanatory view on the debate between "Darwinized" and "Cybernetic/TD" mechanisms to explain why and how the biosphere has shown adaptive robustness throughout its long history (see Donoghue et al. 2025 for details).

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