Abiogenesis as the origin of adaptive evolution. An alternative to the Oparin-Haldane model

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Abstract

The emergence of life from non-living matter remains one of the most profound unresolved questions in natural philosophy. Current paradigms largely inherit the Oparin-Haldane assumption that abiogenesis is preceded by a prolonged accumulation of traits through both nonadaptive (e.g. self-organisation) and adaptive (i.e. natural selection) processes. Yet this raises a legitimate question: how can adaptive evolution occur before abiogenesis? Natural selection requires both a persistent resemblance between parental and offspring characters (i.e. heredity) and a source of transmissible variation (i.e. mutation); however the emergence of these properties is itself the central problem of abiogenesis. Here, instead, I describe a spontaneous adaptive evolution model in which heritable variation arises abiotically, and therefore prior to the action of natural selection. The Price equation, although merely a mathematical tool, can help us think about the evolvability of selection itself. Selection is best understood as the non-null covariance between a trait value and its fitness, a quantity that itself evolves. Prior to abiogenesis, this covariance should be effectively zero. By removing the assumption that slow adaptive evolution must precede abiogenesis, this model defines a null expectation in which imperfect heredity is absent in prebiotic systems, a prediction that can be experimentally falsified.

Keywords: origins of life, nonadaptive abiogenesis, dissipative structures, Price equation, molecular bricolage, Oparin-Haldane hypothesis, gradualism, evolutionism, spontaneity

Introduction

Two opposing philosophical views have sought to explain the origin of life. For a detailed account on the historical confrontation among vitalistic and materialistic arguments on the feasibility of this elusive phenomenon (life emerging from inert matter), see [1]. This is not an exhaustive experimental review either. Instead, the purpose of this brief piece is to offer, I hope, a new angle on the problem of tracing the advent of abiogenesis.

L. Pasteur first showed that *generatio aequivoca*, or the spontaneous generation of complex life, was impossible *de facto*. Every biological form known required a pre-existing living propagule (*generatio univoca*) [2–5]. After some intense debate, the experiments were certainly replicated, and the question settled [6]. R.L.C. Virchow's *omnis cellula e cellula* [7], together with the "immortality of the protoplasm" [8], remained dominant principles of biological reproduction for decades thereafter. Thus, although Pasteur's discovery filled an important gap in knowledge, an intriguing question emerged: whence do living things arise, if not from inert matter? [9, 10]

Besides a subtle margin for vitalistic responses –*à la* "life is eternal" [11]–, many experimentalists in that era confronted the question seriously. The general materialist answer was that evolutionism, not spontaneity, led to abiogenesis [4, 8, 12–15]. They argued that only a prolonged chemical evolution could explain the inert-living interface. As stated by A.I. Oparin: "(...) *these polymers, which were already capable of forming poly-molecular systems, were, of course, simpler than living protoplasm. Only later, due to the prolonged evolution of these systems, their interaction with the environment, and natural selection, did the types of organization that characterize living beings appear.*" [14], pg. 230. J.B.S. Haldane shared a similar view [16], and, taken together, these reasonable speculations were formalised as the Oparin-Haldane hypothesis [17, 18], which rendered the best explanation available at the time: a prolonged phase of both, nonadaptive and adaptive evolution, prior to abiogenesis.

Here I argue, however, that this generalised response reflected a false dichotomy, i.e. the spontaneous emergence of life could not be accepted as a valid materialist explanation at the time. This was probably due to a reluctance toward the semantics of "spontaneity" [4]. In addition, I argue that this historical contingency profoundly impacted every theoretical (e.g. RNA world [19–22]) and experimental (see the below section) attempt to tackle the question.

Could we render alternative materialistic models? In this piece, I elaborate on the feasibility of an spontaneous adaptive evolution model, in which the origin of life coincides with the origin of natural selection. In contrast to the Oparin–Haldane model, selection is impossible in inert systems because no mechanism exists to preserve heritable differences. Rather, it emerges *ex novo* when a chemical system spontaneously acquires a channel of inheritance that allows for variation, rendering the transition between non-life and life a discrete (albeit undirected) event.

The assumption of "prebiotic adaptive evolution" in current frameworks

Here I argue how the fields of prebiotic chemistry and synthetic biology, together with the prevailing paradigm (RNA-world [23]), remain conceptually rooted in the assumptions of the Oparin-Haldane model.

The famous triumphs in this regard are found on the side of prebiotic chemistry. If we keep the watchmaker's traditional metaphor, this field is trying to understand how to the plausible components of a primaeval clock (i.e. a first living system) might be produced and self-arranged.

The most celebrated are undoubtedly the Miller-Urey experiments. They demonstrated that sudden changes of potential under feasible prebiotic Earth conditions can produce amino acids within a brownish organic solution with acquired complexity [24, 25]. Many related experiments have been conducted, for example, to form nucleobases [26]. These same arguments extend to the other classic experimentalists, like J. Oró (purines from hydrogen cyanide [27]), or C. Ponamperuma (adenine synthesis and Urey-Miller extensions [28]). After these initial excitements, where inert matter appeared capable of spontaneously increasing in complexity under prebiotic conditions, efforts in this field have moved in multiple directions, providing many solutions to produce interesting reactions. Yet none has succeeded in producing systems with intrinsic heredity upon which "prebiotic adaptive evolution" can act, as envisaged by the Oparin-Haldane model [29–39]. Indeed, under such a model abiogenesis is expected to occur in a rather slow adaptive evolution lasting millions of years [40], with *necessary* steps inferred from modern biology (hence the recurrent "who-first" debates [41–46]).

There are two important consequences. First, the emergence of natural selection is not experimentally sought as a marker of abiogenesis, because adaptive evolution is assumed to precede abiogenesis. Second, attempts to observe abiogenesis directly from inert materials in the laboratory are commonly met with pessimism, given the presumed complexity and duration of the intermediate stages [46]. A related concern was already expressed by Oparin, who noted that: "*the substances that we produce artificially are not exactly the ones which can be isolated from living organisms*, reasoning that "*if such substances were formed now in some place on Earth, (...) they would be eaten, one after another*" [40].

Box 1. Evolution by Natural Selection?

The term "Natural Selection", or simply "selection", is frequently invoked in prebiotic chemistry to describe the differential elimination of chemical species. In this minimal sense, "Natural Selection" amounts to little more than differential frequency of types. Yet, in evolutionary biology, "Natural Selection", or "NS", is generally regarded as the complete mechanism driving adaptive (i.e. Darwinian) evolution [47–53]. Equating these two notions is misleading, as differential survival alone is not sufficient for adaptation, which additionally requires multiplicity, heredity, and variation among replicating agents. Confusion may arise from the fact that even banal enrichment of types is both a natural and a selective process. Indeed, prebiotic mineral types available on Earth were determined by extrinsic constraints. That is to say, the space of chemical species realisable on Earth suffered a series of transformations (i.e. nonadaptive evolution, or non-Darwinian) prior to abiogenesis [54]. Thus, a system can be considered evolvable, natural and selective [55], but not in the Darwinian sense applied in this work.

For example, drastic acidification may alter the composition of a chemical pool in a primaeval ocean through selective elimination of the more unstable compounds, but such a process does not entail adaptation, or memory, at any level [53].

Finally, evolution Darwinian systems is also subjected to non-Darwinian changes (e.g. drift via random sampling, random mutation, etc.) [56–59], but non-Darwinian systems cannot evolve by Darwinian rules.

What if we just search for the parts of the clock that produce its characteristic "tic-tac"? Abiogenesis is often conceptualised as a slow generation of first replicators. An early replicator could have been an RNA autocatalyst, perhaps similar to a ribozyme [23, 60, 61]. Briefly, the current paradigm poses that a ferric impactor led to a reduced environment in which RNA could be formed on a proper geological time [62]. We indeed achieved RNA oligomerisation catalysed by olivine in reduced, alkaline environments [63], and self-reproduction of RNA has been achieved with human engineering [64–66]. Even more: recently, QT45, a self-replicating ribozyme, has been obtained by in vitro selection [67]. The latter still requires a two-step human intervention, but it produces populations of molecules closer to adaptive evolution. Yet this achievement is not interpreted as approaching abiogenesis itself, because the Oparin-Haldane view places the origin of life way beyond the emergence of adaptive evolution.

Finally, the following questions are frequently confounded in published literature: (i) how life emerges (in general), and (ii) historical origins of life on Earth [68]. While (ii) is contingent to the local chemistry and the historical events (impactors, change in orbit, etc.), (i) should be addressed with general principles. General principles that would be dependent on an observational or empirical definition of life [68]. However, they should be attainable theoretically, and, by definition, experimentally.

This piece is focused on question (i). While question (ii) is highly interesting, it is more related to a “molecular paleontology”, or the historical record of evolution on Earth. Scientists working on question (i) are more intrigued on how inert matter can, all of a sudden, behave as living matter (in any given condition) [68]. Note that the Oparin-Haldane model provides neither a general nor a quantitative criterion for delineating abiogenesis (Fig. 1).

Here, I propose what I believe is a novel perspective on problem (i).

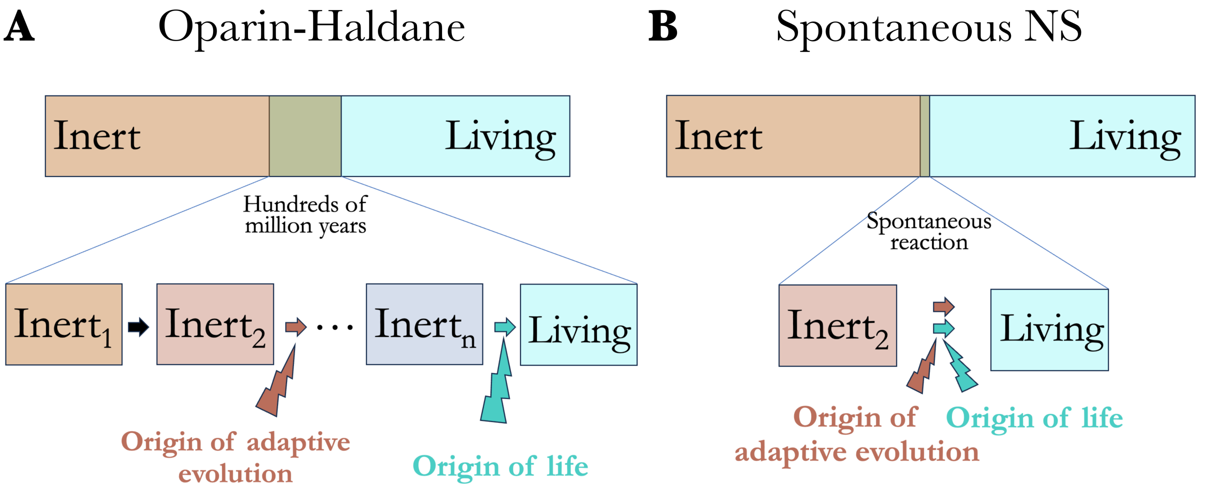

Figure 1: Contrasting views of the living-inert interface. (A) The Oparin-Haldane framework adopts a gradualist perspective in which life-like properties are acquired progressively over extended timescales. Under this view, both adaptive evolution and nonadaptive transformation of types are assumed to operate prior to the emergence of life. Abiogenesis is, at times, identified with the origin of cellularity; other accepted definitions instead emphasize metabolism, replication, or evolution [69, 70]. (B) The spontaneous adaptive evolution, or spontaneous natural selection (NS) as a legitimate a materialist model. Here, timescales of the inert-living interface are those of a single chemical reaction, and most importantly, it is undirected by natural selection. Under this model, adaptive evolution is forbidden prior to abiogenesis.

Evolvability of the trait-fitness covariates

Under the Oparin-Haldane view, abiogenesis requires the gradual accumulation of life-like properties through a sequence of selective events, beginning with simple, nonadaptive symmetry-breaking processes, such as the enrichment of L-amino acids. But, as said, this view also assumes that natural selection (adaptive evolution, Box 1) must operate before abiogenesis, allowing prebiotic systems to overcome the constraints imposed by chance. This assumption is often justified by the observation that selection is a process capable of directing such an unfeasible thermodynamic fate, which regime of possibility is determined by a Boltzmann distribution that includes both state functions, energy and entropy [71–73].

An implication of this view is that selection is expected to operate continuously throughout the transition from chemistry to biology, including the earliest stages of prebiotic evolution, as envisaged by Oparin and Haldane and by many subsequent works [1, 16, 46, 74, 75]. Yet a fundamental question remains unresolved: how did natural selection itself got established? Does it make sense to invoke adaptive evolution before the existence of a system capable of heredity [52]? To assist our thinking, I make use of the Price equation to explore an alternative model in which selection is impossible prior to abiogenesis. The Price equation [76] is commonly expressed as

$$\Delta\bar{z} = \mathrm{Cov}(w, z) + \mathbb{E}(w\Delta z') \tag{1}$$

Where $\Delta\bar{z}$ is the change in the average value of the trait z across generations and can be approximated with the sum of two terms. The first term, $\mathrm{Cov}(w, z)$, is just the covariance between fitness w, and the trait value z, representing the effect of natural selection (i.e. memory of traits that worked better/worse). The second, $\mathbb{E}(w\Delta z')$, is the expected value of the within-group changes in the trait z, and it is weighted by fitness w to impact the number of descendants on the next generation. This reflect neutral (nonadaptive) variation. It can also be related to "noise in transmission" (i.e., mutation), and thus relevant for error thresholds [77]. Although eq. (1) is commonly used to assess selection among conflicting organizational levels [78], it provides a simple mathematical description of any adaptive population, and is therefore most suitable to help a hypothesis on the origins of natural selection. However, these equations are just correlative, not causal. A more proper way to causally isolate the selection would be to remove the influence of fitness w from the second term [79],

$$\Delta\bar{z} = \mathrm{Cov}\left(\frac{w}{\bar{w}}, z'\right) + \bar{\delta} \tag{2}$$

Where the first term is now the covariance between the relative fitness and a given trait, and $\bar{\delta}$ is the average transmission bias. Although this equation is still just a mathematical tool, it helps to trace, quantitatively, the infinitesimal appearance of the selection, that is, the inheritability of the trait's value fitness,

$$\lim_{t\to t_1^+} \mathrm{Cov}\left(\frac{w}{\bar{w}}, z'\right) > 0, \quad \text{where } t_1 \text{ is the first occurrence of selection} \tag{3}$$

In practice, however, hinting the first instance of selection (eq. 3) could be an extremely difficult task, because many relative measures (e.g. fitness) are hard to quantify. A more tractable approach is to focus on the emergence of a persistent inheritance channel, which may serve as a proxy for the onset of selection. Whether such a channel has been established can be assessed through the regression slope h between a parental character value z and its offspring value z'. In quantitative genetics, h provides a standard measure of heritability and is defined as

$$h = \frac{\mathrm{Cov}(z', z)}{\mathrm{Var}(z)}, \tag{4}$$

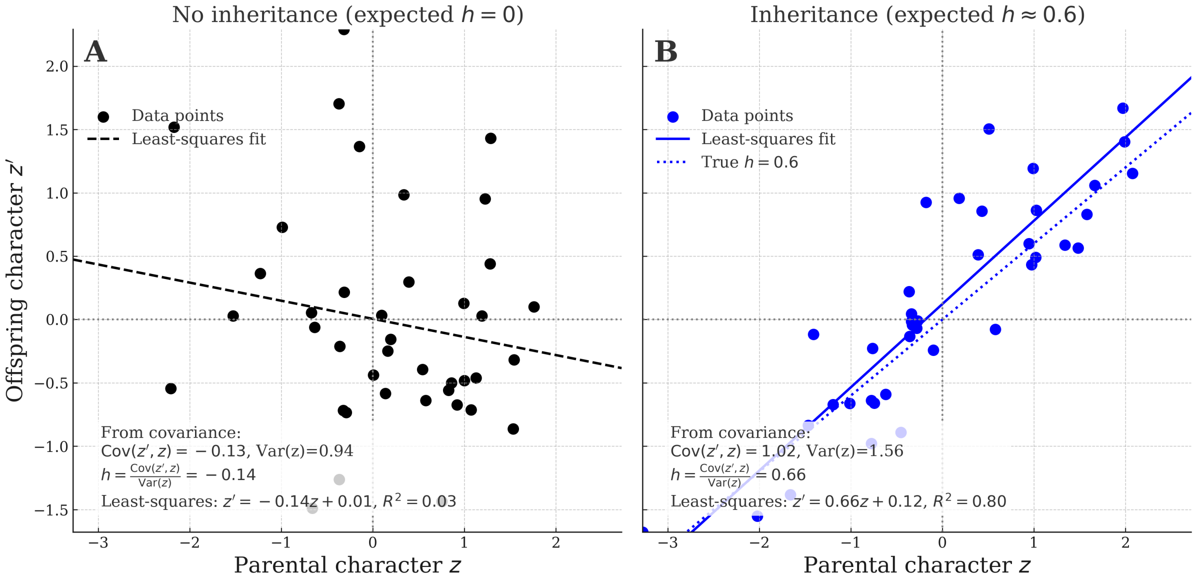

Figure 2: Two illustrative examples showing the expected behaviour of an inert (A) and a living (B) system, as quantified by the heritability coefficient h. In both cases, assuming that multiplicity and self-reproduction are present, a population of parental character values (z) gives rise to a population of offspring character values (z'). Here, h captures only the phenotypic variance in transmission, and it does not allow us to access the genetic basis of heredity. In (A), the inheritance channel is absent or prevented by mutation beyond error threshold [52, 77]. The covariance between z and z' is therefore expected to be approximately zero. Consequently, parental character values do not predict offspring character values and adaptive selection becomes impossible. In (B), parental character values predict offspring character values, yielding a positive covariance between z and z'. Variability around this relationship may arise from transmission bias (δ) or from differences in relative fitness ($w/\bar{w}$).

and captures whether offspring traits z' statistically resemble parental traits z. This definition does not involve fitness w directly, but rather formalizes the existence, and the reliability, of the inheritance channel for the examined character. In contrast, this form of the Price equation (eq. 2) isolates the effect of selection as the alignment between relative fitness and offspring traits. Thus, when $\bar{h}$ is higher than 0 (eq. 4), it is allowing for offspring traits z' to have statistical memory of the parental traits z. This in turn makes it possible for z' to covary with relative fitness in eq. 2, thereby establishing the first conditions under which natural selection can operate. On the other hand, when $\bar{h} = 0$, the system does not have any statistical memory, and thus adaptive heredity is forbidden. An example is shown in Figure 2.

Thus we expect an increase in h distributions over time, in which heredity beings to be further controlled by the incipient living form. Figure 3 shows two mock distributions of h for the above example regressions. Nevertheless, that z' is more or less invariant to z does not give us any direct insight about the fitness of z', nor its selective coefficient, because changes in average h can be also due to transmission bias δ besides to fitness changes. To test whether transmission bias is affecting h fluctuations, the environment of the interrogated chemical system should suffer a change, and be controlled by an experiment in which environment does not change. The expected deviance on h caused by transmission bias δ will be exposed by the control experiment, and be different than that caused by the loss-of-fitness Δw, that will be exposed by particular environmental changes.

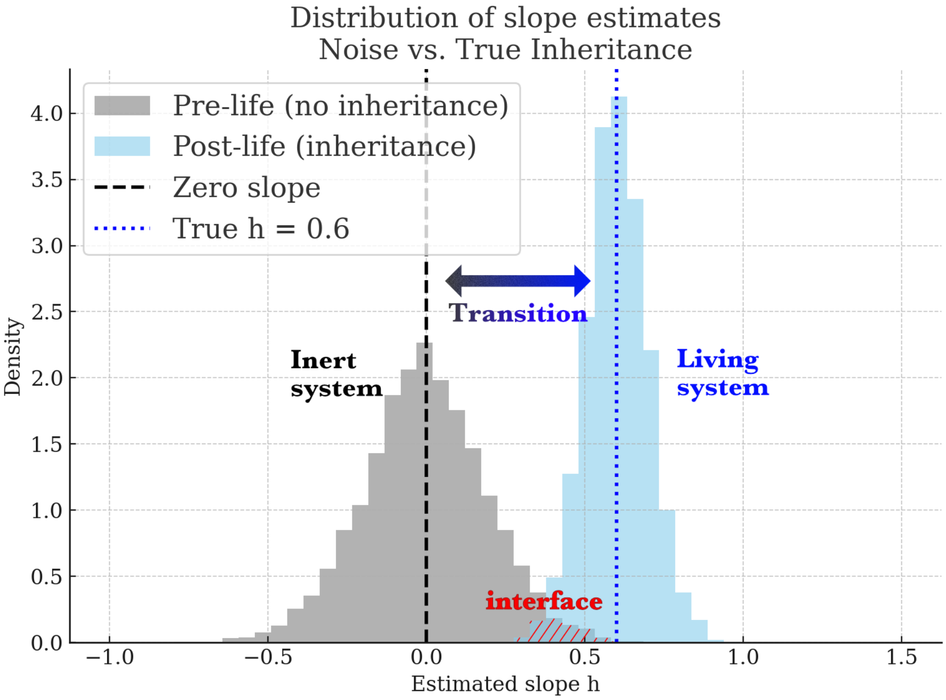

Figure 3: Mock h distributions for the examples shown in Figure 2. Values are just for illustration purposes and they do not retain biological significance. Interface regions where h values could be part of both distributions may exist. In this way, it is shown that the Price equation can be a good mathematical tool to trace abiogenic products, assuming that abiogenesis requires no prior adaptive selection of molecules.

Imperfect heredity is required for adaptive evolution

The notion that life originated with a replicator exhibiting perfect heredity is difficult to reconcile with this model of abiogenesis. We know of some artificial replicators like the Rebek system [80] that do not allow for selection by applying Eq. 3. That is to say, the ability to storage substantial information on them is absent, and they do not allow for variability in the produced offspring [81], as aperiodic crystals growing. Indeed, this Rebek system experimentally behaves much more like a perfectly faithful replicator than a Darwinian replicator. Thus, these are considered *trivial* replicators, since their information cannot change the character value in which it is encoded [82, 83].

On the contrary, to start the algorithm of natural selection unfaithful transmission is a prerequisite. Thus, information cannot be 1-bit. This is deduced from the Fundamental Theorem of Natural Selection [48, 51] and thus reflected in the Price equation (Fig. 2B). However, excessive mutation might erode the statistical link between traits and their past competence; that is, when the second term of the Price equation exceeds the mutational error threshold [77]. Abiogenic replicators, under the spontaneous selection model, should have been multiplicative and variable, while approaching unlimited heredity [52], causing open-ended evolution.

Alternative frameworks that formalise selection among populations of early replicative systems, such as the entropic selection principle [84, 85], could in principle be accommodated within the spontaneous adaptative evolution model, provided that variation and heredity are already present.

Coupling of adaptive selection and abiogenesis

In the Oparin–Haldane view, the emergence of selection and the emergence of life remain decoupled in time. A.I. Oparin clearly stated that natural selection occurred in non-living molecules [40], but also that the first "living thing" is not a poly-molecule, but probably a "slime": "*with certain reservations we can even consider that piece of organic slime (...) as being the first organism*" [40]. J.B.S. Haldane, contrary to A. I. Oparin, recognised that "*the first living, or half-living things were probably large molecules synthesised under the sun's radiation*" [16], thus treating life as a continuum rather than as a discrete quality. This is an important discrepancy [86] that has been largely neglected in posterior literature. However, Haldane also acknowledged: "*clearly we are in doubt as the proper criterion to life*" [16].

For the sake of clarity, we can consider this classical scenario depicted by both scientists, and imagined by many [46]. A pool of chemicals, of distinct nature and stages of aggregation, populate the prebiotic oceans. The pace and causes for the compounds to aggregate are uncertain.

The pool of molecules herein suffer a slow transformation. In an adaptive-sequential model (Oparin-Haldane), this process will be arranged by nonadaptive transformation (self-organisation) and adaptive evolution. Under such a model, tracing the trait-fitness covariance won't be useful to hint abiogenic reactions, since adaptive changes are expected within non-living compounds.

However, at the time of elaboration of the Oparin-Haldane narrative, neutral forces of evolution were largely neglected, maybe with exception of the Fisher-Wright models in population genetics [48, 87]. Now, we do acknowledge that a substantial portion of the variation found in extant populations is due to nonadaptive processes [57, 59]. It is sensible to think that the generation of variability in non-living compounds, which are not purified, was not directed by any adaptive forces (memory of traits that worked better, or eq. 2), because there were, by definition, no available channels of inheritance to allow for selection (eq. 4, Figs. 2& 3). That is to say, variability in the pool of compounds will be determined, contingently, by the local chemistry and the events disturbing that chemistry. This concept is very similar to Prigogine's *historical element* [71], in which the past states of molecules determine their present state, acquiring a probabilistic, or historical character. Thus, under the spontaneous adaptive evolution model, the first occurrence of natural selection occurs at the time of the first abiogenic reaction (or the origin of life).

The latter, however, it is just a description and does not say anything about the validity of the models. However, abiogenic reactions will be untraceable under the Oparin–Haldane model, unless defined by a feature obviously besides natural selection.

The problem of spontaneous complexity

A problem, in appearance, with the above is, how the emergence of life-grade complexity can be attained in absence of selection? Could teleonomic principles be acquired by chance, all at once? [88]. The history of this issue is indeed tortuous [54]. Here, instead, I invite the reader to consider the familiar tangle of wires and cords that tends to form around old computer hardware. Such tangles arise because disordered configurations are overwhelmingly probable, not because they confer any adaptive advantage to the computer. "Selection" of tangles does not equate to natural selection (Box 1).

This is a common premise in modern evolutionary biology, exemplified by frameworks such as Constructive Neutral Evolution [89]. The latter is a model in which complexity is attained nonadaptively but it is subsequently maintained by purifying selection [90]. There is some evidence that these processes are common in biological systems, specifically, regarding the overcomplicated kinetoplastid regulation of a protist and gene scrambling, among others [89, 91]. It was formulated for biological systems with "excess capacities"; we here invoke it as a way to understand nonadaptive coalescence under conditions of free energy excess [72] – i.e. self-organisation [92]. Furthermore, molecules of very high complexity can be attained abiotically by this means [93].

These findings simply instantiate that life-grade chemical complexity could be attained spontaneously, in the absence of adaptive selection. This interpretation is in line with the Prigogine's *Theory of Dissipative Structures*, in which the "order through fluctuations" is a mechanism (not reducible to the equilibrium principle) leading to "inhomogeneous spontaneities" [94].

The spontaneous adaptive evolution model

Considering the above, I propose a model of abiogenesis in which life-grade complexity may arise spontaneously, prior to the conditions that make adaptive evolution possible. This does not require the preceding nonadaptive regime to be instantaneous, as chemical complexity may accumulate slowly. Yet the rupture between this regime and an adaptive one is discrete (spontaneous), because abiogenesis coincides with the first appearance of persistent selection. The latter is granted because of the fortuitous establishment of the inheritability channel (Fig. 3), where parental traits begin to control heredity of traits over noise (Fig. 2), thus hinting the advent of adaptive evolution (eq. 4).

This view rejects the intuition that chemical systems achieve life-grade complexity in a slow sequential fashion and that this process is adaptive and necessary. In such model, gradual evolution and assembly of parts (e.g. metabolism, genetic code, compartments) is paradoxical. The acquisition of parts is, by definition, not a continuous event, but a limited set of discrete transitions towards complexity. The features of coalescent structures are achieved by nonadaptive transformations, before natural selection exists. Thus, evolution may later purify any nonadaptive trait z that was required to achieve abiogenesis, since, again by definition, such traits were acquired before life began and may carry a substantial cost on fitness w.

Two recent contributions not only strongly support the experimental validity of this model's narrative, they also constitute notable developments toward the resolution of the challenge in recent years [95, 96]. I briefly summarize the main findings by publication date. The first experiments show that a variety of semihollow structures, with distinctive morphology and thickness, were achieved spontaneously in a Miller-Urey experiment [95]. The latter consist of silicon-enriched HCN polymers, a kind of compartment not present in modern-day biology. Instead, the second experiments show how photo-RAFTs, or reversible addition–fragmentation chain transfers driven by light pulses, lead to the polymerization-induced self-assembly (PISA) of some components, selected *ad hoc* [96]. These, importantly, are not based on modern-day biological parts, but they spontaneously form micelles that "self-reproduce". Although molecular changes that occur in these micelles over time are the result of contingency rather than natural selection, as they have no possibly enabled inheritance channel and thus they follow the nonadaptive regime (Fig. 2), this could be an interesting result to be falsified by the latter model.

Other recent study has also pointed out the fundamental historical limitations of sequential models, particularly in the context of the RNA-world hypotheses [97]. The authors presented a compelling perspective of the field, while adhering to a concept similar to Jacob's "molecular bricolage" [98]. In their view, the acquisition of parts remains constrained by biochemical features akin to extant life (eg. the need of a protein coding system). In addition, natural selection is invoked to facilitate the assembly of parts, whose chemistry is necessarily similar to that of modern life. This may be a legitimate model for abiogenesis on Earth. However, a more generalist model for abiogenesis must not rely on strict biochemical continuity with known life. Here, a generalist model is proposed instead, in which abiogenic conditions are most varied when natural selection is null (possible interactions are maximal because they are uncontrolled by selection coefficients in prebiotic conditions), and that this list of conditions must be not limited to Earth's prebiotic environment. Possible interactions between parts on the successful molecule populations would be rapidly constrained by selection, explaining for example the *post-hoc* generality of the genetic code. But, importantly, the achievement of a rudimentary code is not necessarily time-placed at abiogenesis, as there could be other ways to control heredity and fulfil eq. (4) [53, 55, 99].

But how could the spontaneous adaptive evolution be tested?

Under this model, abiogenesis can be abstracted as a rare, undirected, mineral, spontaneous (favourable), and complexifying reaction; and, once it occurs, the abiogenic products are forced to store information of the outcomes of the interaction between their characters and the environment.

Let us consider, once more, the classical Oparin-Haldane example [16, 40], where UV radiation and other abiotic processes will ensure a concoction of different chemicals within the primaeval oceans, and the former will act upon the latter with certain periodicity (e.g. day-night cycle). In this scenario, the falsification of a spontaneous selection model is easy to design, as it just requires monitoring the relevant parental character values z over time (e.g. half-life of an amphiphile, aromaticity, molecular weight, self-catalytic activity, etc.), and to stipulate the measurements of the offspring character values z' (i.e. change in the selected parental character values). If the model is accurate, the origin and maintenance of very simple life forms will be observable starting as soon as (i) z and z' begin to correlate; (ii) this correlation is governed by multiplicity and imperfect heredity, thus maintained even in unfavourable environmental conditions (Fig. 2); and (iii) once h distributions are shown adaptive (Fig. 3). On the other hand, if abiogenesis requires slow adaptive evolution prior to its occurrence, this model would be useless to hint for abiogenic reactions.

In light of the above considerations, should some effort be directed toward screening chemical self-assembly reactions for their capacity to sustain imperfect heredity?

In this line of action, R. Hazen argued that mineral evolution and its reactions are inherently governed by a regime of chance [54]. He proposed a semi-quantitative estimate of the feasible prebiotic reactions leading to the origins of life on Earth-like planets, calculated with time and surface areas for mineral reactions. His result, an upper limit of 2×10^{53} serendipitous abiogenesis "experiments", is the number of distinct mineral-surface reactions that could have taken place on the Hadean Earth. This number is way beyond of any human laboratory setting, insofar these consist of nonadaptive–nonsequential reactions that we have to test by combinatorics. However, reaching abiogenesis might be inevitable over planetary timescales in Earth-sized natural laboratories [54]. Despite being a simplistic demonstration, we may consider it a good proxy for the upper limit of uncontrolled reactions needed to achieve abiogenesis (in Earth-like planets). Hazen further expressed: "*strategies exist to increase the likelihood of observing improbable chemical reactions in the laboratory. One can work backwards from modern biochemistry to focus on key molecular species and their products. New approaches in combinatorial chemistry, coupled with computational chemistry, hold the promise of quickly narrowing the search.*" [54]. I agree with this. However, brute-force computational chemistry does not seem practical to screen such large quantity of reactions. Indeed, if we consider all the physicochemical combinatorics needed, it is a daunting computational task. The more interesting question is whether we can use the spontaneous adaptive evolution model to further delimit the regime of chance. We could limit the computation to those chemical compounds and conditions (reaction experiments) that fulfil the premises of the model.

A compatible idea has been recently reviewed by Barlett *et al.* [100]. They propose to examine the increase in information processing over time, using the internal complexity of the system as an indicator. In fact, this effect could be best captured by quantifying $\mathrm{Cov}\left(\frac{w}{\bar{w}}, z'\right)$ over time, as this provides a quantitative proxy to assess whether selection has emerged and heredity is controlled (Fig. 3). In relation to this, some authors investigated how to search for group selection on chemical systems [101, 102]. One recent attempt to do this is promising [103], but this still remains a theoretical and logistical challenge. Finally, although I have not disclosed any efforts on how "computational life" might help falsify or not any model of abiogenesis, self-replicating programs have been running a lot lately. Recently, we have some examples of how the choice of the programming language – extended brainfuck, SUBLEQ, or Forth (family of languages) – does exert a defining outcome on the rise of computational "self-replicators" [104]. These kind of conclusions could be more useful to solve natural questions if matched correctly with what we know so far about evolvability and heritability of biochemical traits [105].

Final notes

I make no claim that this model provides the correct explanation for abiogenesis. Rather, I argue that it is a legitimate materialist alternative, and that it generates experimentally distinguishable predictions from those of the Oparin-Haldane framework. Under the Oparin-Haldane view, abiogenesis is expected to result from a prolonged sequence of adaptive and nonadaptive transformations, and consequently, the precise moment of abiogenesis is vaguely defined. Under the spontaneous adaptive evolution model, abiogenesis should instead occur as an undirected yet spontaneous event from non-living precursors, with adaptive selection appearing only once life has arisen. Including these assumptions is thus helpful (1) as a null, (2) to test a broader range of chemical reactions that were precluded in the Oparin-Haldane view, and (3) to quantitatively trace inheritability of parental characters z as the first instance of selection, and thus abiogenic reactions.

Resource endowment, for instance, drives important nonadaptive changes in the frequency of prebiotic types [55, 85], but adaptation to resource dynamics is allowed only when those changes become coupled to fitness.

It could be argued that this model merely sets a very low complexity threshold for the origin of life. For instance, a group of simple replicators lacking proper environmental isolation might satisfy the model's conditions, even if such a system would be classified as "infrabiological" in the sense of [70]. Yet our intuition about what life should be is strongly biased by modern cellular organisms, which are highly derived products of billions of years of evolution. Hence, regardless of where one chooses to place the definitional threshold for life, the present model provides a quantitative criterion for tracing a discrete origin of adaptive evolution in the lab.

In fact, other commonly accepted definitions of life [69] are, under the proposed view, based on emergent properties that the most simple adaptive system already will tend to acquire, for example an efficient genetic code, persistent compartmentalisation, or certain metabolic complexity. Interestingly, viruses are not self-replicators, and would not be considered alive under this framework unless they are allowed for reproduction and imperfect heredity by cellular machinery [106]. Self-replicators, by contrast, maintain this channel autonomously.

In the end, the quest might still be to figure out the material rules governing a (very) elusive *generatio aequivoca*. What an irony!

Conflict of interest

I declare no conflict of interest.

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