Chapter 12
Is Natural Selection Physical?

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Abstract Biology, in contrast to other historical disciplines such as cosmology or geology, is not explicitly articulated with physics. More specifically, its unifying principle, evolution by natural selection, is currently not formulated in physical terms. This hinders any attempt to explore whether this principle may apply to other physical systems, beyond life as we know it, or to understand the origin of life in a physico-chemical framework. To better understand whether an explicit articulation is achievable, we first aim to clarify, on the basis of examples, how principles are articulated within the physical sciences, or between the physical sciences and other scientific fields. This leads us to establish a typology where we emphasize that physical principles involve both "rules" in the form of mathematical relationships between concepts, and "premises", defining the conditions and objects to which they apply; articulations may take place at these two levels. We then ask whether the principle of evolution by natural selection may fit in such a typology of articulations. We contend that addressing this question is made difficult by an apparent but ineffective distinction between rule and premises in current accounts of the principle of natural selection. These reduce evolution by natural selection to the iteration of a constant rule, thus failing to recognize that biological evolution is a process that recursively modifies its own modes of operation, e.g., through changes in inheritance systems or levels of individuality. While this may be ignored when focusing on paradigmatic cases of natural selection (as formalized by population genetics, where connections with physics are recognized), it becomes a patent

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problem in more general formulations of natural selection. We conclude by discussing whether this problem could be resolved, through a formal and general description of this principle, where rules and premises would be truly independent or, alternatively, whether its heuristic value, within biology or beyond, is just of a different nature than that of physical principles.

12.1 Introduction

Insofar as living beings are recognized as physical objects, the principle of evolution by natural selection must be physical in some sense. Yet, despite its 160 years of existence, it has not become part of the physicists' toolbox, which makes it non-physical in practice. Going beyond these two obvious but contradictory assertions is the objective of the present essay: trying to clarify in what sense (if any) may natural selection be seen as physical, with at least three underlying motivations. One is to assess the possibility of applying this principle to physical yet non-biological systems (Charlat et al., 2021), that is, beyond living beings and their derivatives, from languages to computer programs. A second, related, motivation is to clarify whether natural selection, in its present formulation, may be appropriate to understand the continuous transition from inanimate to living matter. A third motivation, stemming from a physicist's perspective, is to put it on par with other physical principles. These endeavors would greatly benefit from an explicit articulation of the evolutionary theory with physics and, reciprocally, may be substantially hindered if such an articulation turns out to be unachievable.

Our analysis begins with a survey of the various means by which principles are articulated within physics, or between physics and other scientific fields. We emphasize that physical principles involve "rules" (analogous to mathematical functions) as well "premises" (defining their conditions of applications) and that articulations may take place at both levels. We then discuss whether the principle of natural selection may fit in this typology of articulations. Our analysis suggests that, to some extent, this principle is already articulated with physics, for instance through shared mathematical concepts, notably in its well circumscribed and formalized version developed within population genetics. However, current accounts, when formulated in terms of rules and premises, face a fundamental limitation: the phenomenon of biological evolution inevitably provides examples where the "rules" are themselves evolving and thus indistinguishable from the "premises", as previously emphasized (Godfrey-Smith, 2009). It thus does not seem reducible to a standard recursive function, that would remain constant across time steps. In the concluding section, we discuss whether such a difficulty could be resolved and to what extent it impedes the search for evolution by natural selection in other physical systems.

12.2 What Is Physical

Considering how concepts and principles are articulated within physics, the first articulation to come to mind is one by derivation, where a principle is explained as an application of more general principles. A textbook example is Kepler's laws of planetary motions, that were explained by Newton as a consequence of his law of gravitation and his laws of motion. This may be symbolically represented as $k = m \circ g$, where a principle is written here as a function $f : P \rightarrow I$, from a set of premises P to a set of implications I, and where the premises can be instantiated by $x \in P$ to lead to predictions $f(x)$. The notation $k = m \circ g$ refers to function composition, i.e., $m \circ g(x) = m(g(x))$, where k represents Kepler's laws, m represents the laws of motion and g the law of gravitation. Another example would be the derivation of the classical laws of motion from special relativity in the limit where velocities are small compared to the speed of light.

Many physical principles are, however, irreducible even though they concern emerging phenomena whose constituents are fully described by lower-level principles (Anderson, 1972). Many examples can be found in the field of condensed matter physics; thus, the absence of a critical point on the melting curve of any substance is explained by the impossibility to change symmetry gradually, a basic principle that is not derivable from other physical principles. This principle can be instantiated: the liquid phase is isotropic while the solid phase has the discrete symmetry of a crystal, and this symmetry can itself be derived from properties of the constituent molecules. Symbolically, the fundamental principle $f : P \rightarrow I$ is articulated to lower-level concepts $C \in P$ or/and to lower-level principles $g : Q \rightarrow P$ such that we may consider $f(x)$ for $x \in C$ or $f \circ g(y)$ for $y \in Q$.

Notably, we find these two types of articulation not only among physics-born principles, but also when considering how a principle originating from outside physics has become articulated with physical ones. An example is information theory, which we understand here in its broadest sense, as the study of phenomena involving the transmission, processing, extraction, and utilization of information. Information theory includes mathematically well formulated principles among which Shannon's theorems, which set fundamental limits to the rate at which data can be compressed and communicated (Shannon, 1948). These theorems have a status analogous to that of fundamental principles of condensed matter physics (Anderson, 1972): they stand on their own and are not reducible to other physical principles, but their premises can be instantiated with physical concepts that are themselves subject to physical principles. For instance, bits can be realized with magnetic materials and their processing is subject to Shannon's theorems. The other type of articulation, by derivation, has also been proposed by considering that physical principles may follow from more general informational principles rather than the opposite. A well formulated case is Jayne's derivation of statistical mechanics from a principle of statistical inference (Jaynes, 1957) and a more speculative one is Wheeler's proposal to derive 'It from Bit' (Wheeler, 1989).

The most fruitful articulations between information theory and physics are, however, of different natures. The major one is the formal articulation between Shannon's theorems and statistical physics, coming from their common reliance on asymptotic principles (law of large numbers). Symbolically, this articulation can be represented as $f = l \circ g$ and $\varphi = l \circ h$ where f is an information theoretic principle, φ a physical principle and l a common underlying principle. In practice, this implies that the two fields share common methods and common concepts, for instance the same concept of entropy.

Finally, another kind of articulation, also exemplified with information theory, is more conceptual. The concept of information appeared in physics first informally, in Maxwell's thought experiment of a demon violating the second law of thermodynamics (Leff & Rex, 2003). The resolution of this paradox involved recognizing which information processing steps are subject to physical constraints, i.e., recognizing which concepts C from information theory were subject to a physical law $\varphi : C \rightarrow I$. A solution is provided by Landauer's principle which establishes an equivalence between logically irreversible operations (e.g., data erasure) and thermodynamical irreversible operations (dissipative processes). Another example of a formal articulation between physics and information theory is the development of the field of quantum information (Nielsen & Chuang, 2010), which now finds instantiation in the engineering of quantum computers.

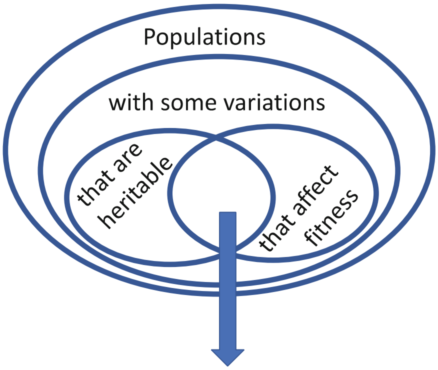
To sum up, the relationships between physics and information theory illustrate four types of articulations that we may divide in two classes. Starting from a well formulated mathematical principle, we may have the first type, *articulation by derivation*. Noteworthily, this can go from physics to another field but also the other way round (e.g. Jaynes' derivation of statistical mechanics from the principle of maximum entropy). Within this first class, we also have a second type, which we call *formal articulation* (e.g. the common asymptotic principles behind Shannon's theorem and thermodynamics). Alternatively, a second class of articulations starts from a concept that may or may not be formalized (i.e., may or may not be the premise of a mathematically formulated principle), which includes the third type, *articulation by instantiation* (e.g. the application of Shannon's theorem to physical information processing systems) and the fourth type, *conceptual articulation*, involving the formulation of a new principle (e.g., Landauer's principle).

Before considering which of these four kinds of articulation(s) may be relevant to describe the relation between the principle of evolution by natural selection and physics, it is also worth noting that an informal concept, even if it originates from physics, may find no clear articulation with physical principles; in that sense, it may be considered as 'non-physical'. For instance, the concept of dissipative structure was proposed to explain a broad range of far-from-equilibrium systems exhibiting spatial or/and temporal patterns, including biological evolution (Prigogine, 1969). It has however been shown that no general principle (technically, no variational principle) can cover all these phenomena (Landauer, 1975). This does not mean that no physical prediction can be made by analyzing a particular phenomenon representing a dissipative structure, but that no new prediction can be made from recognizing that this physical phenomenon is an instantiation of the concept of dissipative structures. In other words, dissipative structures can be regarded as "non-physical" since they are not the premise of any physical principle. This example illustrates again that we are taking the question "is *x* physical ?" in an epistemic sense, without questioning the materiality of the entities at play. It also illustrates that articulation by instantiation in absence of a rule is not sufficient to make a concept physical.

12.3 The Case of Evolutionary Theory

To discuss if and how the principle of evolution by natural selection may be articulated with physics under the above-described typology, it is first necessary to review how it is usually formalized. One of the most cited formulation takes the form of premises, through a list of necessary conditions for evolution by natural selection, as given by Lewontin (Lewontin, 1970) and many subsequent authors (e.g. (Godfrey-Smith, 2009)). These may be hierarchically organized as illustrated in the upper part of Fig. 12.1. First, "populations" are required: evolution by natural selection does not apply to individual entities, but to collections of such entities. Second, these populations must be heterogeneous, i.e., harbor some variations in properties that are often denoted as "traits". These variable traits must further fulfill two conditions: (1) be somewhat stable over time, or heritable in systems where reproduction takes place, and (2) affect the stability or the reproductive success of their carriers (their "fitness").

One the other hand, another common formalization, the Price equation, is more akin to a rule (lower part of Fig. 12.1). In contrast to many models from populations



$$\Delta E_{i \in I}(z_i) = \mathrm{Cov}_{i \in I}(w_i, z_i) + E_{i \in I}(w_i \Delta z_i)$$

Mean change in trait value

Covariance between trait and fitness

Individual change (0 if perfect inheritance)

Fig. 12.1 Evolution by natural selection, in its currently most general formulation. The upper part is a hierarchically organized list of premises. The lower part is the Price equation, the rule according to which those premises give rise to evolution, that is, to a change in the mean value of any trait genetics, which may also be taken as rules, the Price equation appears most general, not relying on restrictive assumptions such as a particular mechanism of inheritance (Frank, 2012; Gardner, 2020; Luque, 2017; Price, 1970). This equation simply expresses the change in mean value of a trait between two time points as resulting from the "co-variance between the trait and fitness", but not only so if the trait value also changes at the individual level (that is, if the trait is not perfectly heritable). In Steven Frank's words (Frank, 2018): "*The abstract Price equation describes dynamics as the change between two sets. One component of dynamics expresses the change in the frequency of things, holding constant the values associated with things. The other component of dynamics expresses the change in the values of things, holding constant the frequency of things*". Through its covariance term, this equation formalizes a "rule" according to which the above-defined premises should produce change over time in the population mean of a trait value.

Following the above-established typology, let us now try to clarify how evolution could be articulated with physics, starting with the possibility of an articulation by derivation. Strictly speaking, the proposal of deriving the Price equation from a more general principle is meaningless, because this equation happens to be a mathematical identity (Frank, 1995). Yet we note that, independently of the Price equation, multiple proposals have been made to express evolution by natural selection in a physical framework, (e.g. (Bernstein et al., 1983; Lotka, 1922)), although none has been conclusive. Notably, Prigogine and co-workers proposed to view evolution as a particular instance of dissipative structures (Prigogine, 1969) but, as noted above, no general principle applies to dissipative structure, so that evolution cannot be meaningfully reduced to this concept.

A second possibility is that of a formal articulation, where common principles would be recognized as underlying natural selection and physical principles. Here again multiple proposals have been made. Some work follows the goal of identifying common underlying mathematical principles behind Price equation and physical laws (Frank, 2018). Several formal mappings have been found between models of populations genetics and models of statistical physics, which follow from common mathematical principles (Barton & Coe, 2009). These mappings, however, are only established for specific models of population genetics, that is, to formal accounts of particular cases of evolution by natural selection, that may be considered as "paradigmatic" (Godfrey-Smith, 2009).

A third possibility, that we now discuss in more details, is that of an articulation by instantiation, where a physical realization of the premises is formulated: are Lewontin's conditions amenable to physical implementations? A potential problem in addressing this question is that evolution by natural selection, as it can be currently witnessed in biology, applies to objects (traits within individuals within populations, etc.. . .) that are also its *products*: owing to its multigenerational component, evolution is recursive. In principle, this should not constitute a fundamental impediment to its articulation by instantiation with physics: recursive processes may be well formalized through recursive mathematical functions. Yet, we encounter several difficulties when trying to formalize evolution by natural selection along those lines.

A first difficulty comes from the ‘dynamical insufficiency’ of the Price equation: formally, it cannot be iterated because it requires in its premises more than it delivers in its conclusions (it requires a covariance and delivers only a change in mean trait) (Frank, 1995; Lewontin, 1974). More circumscribed models in populations genetics avoid this caveat, but as noted above, they cannot be taken as general descriptions of natural selection. A second difficulty relates to the fact that recursive functions require a starting point to be effectively iterated: objects that satisfy the conditions but *are not* the products of evolution. One may think for example of clay crystals (Bedau, 1991). However, Lewontin’s conditions are at best loosely met in such systems where, in particular, a clear description of individuality is lacking. Computer programs or polymers subject to in vitro evolution can be seen as more satisfactory candidates: they can clearly be formulated in physical terms only, despite being themselves a product of evolution by natural selection. A third and major difficulty comes from acknowledging that no formalization of the principle of natural selection has yet been proposed where it cannot be argued that the rule itself may be subject to change by natural selection. For example, inheritance systems or levels of individuality can be considered as fixed in the short term and part of the rule but are also subject to evolution in the long run. A similar argument has led Goldenfeld and Woese to propose that evolution is “self-referential” (Goldenfeld & Woese, 2011).

In fact, the above listed first and second difficulties may be symptoms stemming from this more general problem: current accounts of evolution cannot be formally framed as rules and premises, because they fail to capture that the plasticity of the phenomenon of biological evolution, where examples are always found where the rules themselves are evolving. No formalization is currently available of a general principle that would apply to the diversity of forms that evolution by natural selection can take. The view of evolution as happening in populations of well-defined individuals harboring well defined traits (that underlies Lewontin’s formulation or Price equation) is in fact an idealized account of an end-product of evolution, which is to be explained as much as it is an explanation. This conclusion relates to the previously emphasized argument that even within the biological world, many border-line cases (as opposed to “paradigmatic” ones) can be found, where this framework does not apply straightforwardly (Godfrey-Smith, 2009).

Finally, let us consider more briefly the fourth possibility, that of a conceptual articulation of natural selection with physics, where informal concepts are formalized and shown to be subject to physical principles. In fact, many physical principles have been formulated to apply to biological systems, constituting the field of biophysics; but this discipline tends not to refer to evolution. Several recent works in stochastic thermodynamics may be seen as filling this gap, including for instance efforts to identify thermodynamic limits to replication (England, 2013). More broadly, biological evolution has long been an important source of inspiration in physics and engineering. Current work on functional, “adaptive” or even “intelligent” matter, which can modify its internal structure in response to external stimuli from the environment (Kaspar et al., 2021) may thus be expected to unravel new physical principles pertaining to the evolutionary notions of function and adaptation.

12.4 Perspectives

Our analysis suggests that some articulations are already effective between evolutionary theory and physics. A formal articulation takes place when common underlying principles are shared, which permits methods to be transferred between physics and population genetics (Barton & Coe, 2009), a particular branch of evolutionary biology, grounded in a particular inheritance system, where the "rules" are regarded as constant. A conceptual articulation is also effective when concepts originating from evolutionary biology are inspiring new physics (e.g. England, 2013; Kaspar et al., 2021). However, no articulation by derivation has been achieved, where the principle of natural selection would follow from more elementary and general physical principles (or reciprocally). This is not unexpected, considering that even within physics, many emerging principles are irreducible. Maybe more surprisingly, even an articulation by instantiation, whereby the premises of evolution would be formulated in physical terms, encounters difficulties. In our view, this arises from intricacies between the rule and the premises: evolution not only applies to its own products, which may be captured by a recursive mathematical function, but also changes its own rules of operation, like a recursive function that would change itself across time steps. In other words, given a precisely defined rule, e.g. a population genetics model, we can find examples in biological evolution where elements of the rule are themselves considered as subject to natural selection.

Could this problem be resolved? We can at least speculate on what its solution would look like. One possibility would be to stick to the rule/premises framework but noting that the rule of natural selection should be a "meta-rule", a rule-changer, describing how modes of evolution by natural selection are evolving themselves, through changes of features such as inheritance systems, rates and modes of mutation, or levels of individuality. Another possibility would be to recognize that a satisfactory description of the evolutionary process may take a radically different form. As previously argued (Goldenfeld & Woese, 2011), we may even need different mathematical concepts to formalize evolution *in general* (Fontana & Buss, 1994), which may in turn suggest new modes of articulations with physics.

It may also be that natural selection *in general* cannot be mathematically formalized, just as dissipative structures cannot be associated with a unifying principle. This would arguably hinder the search for natural selection beyond life, as well as the integration of natural selection as an essential component in the physico-chemical emergence of "lifeness". But would it necessarily imply that natural selection cannot be of any heuristic value outside of its original field? Within biology, natural selection serves as a general and often implicit explanation for adaptations, and thus as a justification for "functional thinking": the heuristic assumption that many features of biological systems are *best understood* as fulfilling roles within complex ensembles that constitute a living whole, the individual, the organism. Here, *best understood* means that capturing the function of a feature provides a mean to summarize its important properties, its "evolutionary causes", without focusing on unnecessary details: a wing is a feature that allows flying, regardless of what molecules it is made of. This type of reasoning is reminiscent of the application of variational principles to describe physical phenomena. For instance, the laws of refraction (a local property) can be derived from a principle of least action, namely the extremization of the time taken by light to join two points (a global property), or the equilibrium states of matter can be derived from the minimization of an appropriate thermodynamic potential. This has inspired past attempts to derive a general physical principle related to that of natural selection, as typically illustrated by works on dissipative structures, but so far to no avail. While an explicit articulation of natural selection with physics may still be sought along those lines it remains possible in the meantime to explore whether the particular kind of explanations it provides to biologists could be relevant elsewhere.

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