

# Autopoiesis and Natural Drift: Genetic Information, Reproduction, and Evolution Revisited

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Arantza Etxeberria

Logika eta Zientziaren Filosofia  
Saila

(Department of Logic  
and Philosophy of Science)

Euskal Herriko Unibertsitatea  
(University of the Basque  
Country)

Avenida de Tolosa 70  
20018 Donostia-San Sebastián  
Spain

ylpetaga@sf.ehu.es

**Abstract** The contribution of the theory of autopoiesis to the definition of life and biological theory affirms biological autonomy as a central notion of scientific and philosophical inquiry, and opposes other biological approaches, based on the notion of genetic information, that consider reproduction and evolution to be the central aspects of life and living phenomenology. This article reviews the autopoietic criticisms of genetic information, reproduction, and evolution in the light of a biology that can solve the problem of living organization.

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## Keywords

Autopoiesis, evolution, genetic information, history, materiality, organization, reproduction

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## 1 Introduction

Maturana and Varela (M&V) proposed the term autopoiesis, a neologism that means self-production,<sup>1</sup> as a theory of the living organization behind the biological autonomy of organisms [29, 30, 57–59]. This notion and its development have strongly influenced some perspectives in theoretical biology, artificial life, and cognitive science, although as yet it has had no comparable effect on mainstream biology<sup>2</sup> (e.g., molecular and evolutionary biology). Autopoiesis makes a significant contribution to science and philosophy in the introduction of a new subject of inquiry along with a new scientific concept: autonomy from a biological perspective.<sup>3</sup> It is expected that its influence will grow and expand considerably as systemic approaches in biology progress.

The theory,<sup>4</sup> as it appears in the primary literature, offers guidelines (and a model) to understand biological autonomy and opposes certain directions in theoretical biology. Hence, autopoiesis is defined both in positive terms (autopoiesis is the organization

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1 “The autopoietic organization is defined as unity by a network of productions of components which (i) participate recursively in the same network of productions of components, and (ii) realize the network or productions as a unity in the space in which the components exist” [59, p. 188]. In the new prefaces incorporated in a recent edition of [29] the authors state that the name occurred to them in the context of a discussion on the Aristotelian distinction between praxis and poiesis.

2 This is likely to change: for example, Weber and Depew [65] think that autopoiesis can help broaden the Darwinian approach to evolution.

3 The biological notion of autonomy is different from older political or moral notions in that instead of looking at autonomy as a quality of action (an autonomous city or agent is self-determining and in control of its own actions or its own life, whereas a heteronomous one is in control of another), it considers the processes able to originate this capacity or its conditions of possibility, together with their characteristic actions. Thus, autopoiesis accounts for the identity of the individual who can be autonomous. The actions of an autopoietic individual are characterized in terms of structural couplings with the environment (and later as enaction [60]), that is to say, changes in the plastic structure of the unit are not instructed by inputs from the environment, but generated according to an internal dynamics.

4 Work on autopoiesis has inspired other approaches to the notion of autonomy for biology [5, 25, 45]. Some articles discussing this can be found in the collection [14].

defined by a recursive network of component production), and in negative ones (autopoiesis *is not* a result of the properties of certain cellular components, such as genetic materials). The negative presentation of the theory involves a criticism of the role played by biological concepts such as genetic information, reproduction, and evolution<sup>5</sup> in the explanation of life.

Consequently, under the lens of autopoiesis, the theory of life takes a new form as regards information, reproduction, and evolution. In the *received view* of biology [50] genes are leading constituents of biological ontology, and most living phenomena are explained according to the behavior of genes in reproduction (mainly abstracted as gene replication) and evolution (mainly studied as differential gene selection). In the autopoietic perspective, the three of them are secondary or derived, not primitive or constitutive of the organization.<sup>6</sup> Information is an observer-dependent term, not operationally active in the system. Reproduction is a possible (not necessary) outcome of the organization mode of living systems, giving way to a historical sequence of individuals, which in the long term, and through variations, will result in evolution.

In sum, the main motivation for this theory is a need to attend to the problem of living organization, left behind by a scientific practice in biology that is more interested in experiment and manipulation than in developing the right epistemological framework for inquiry into living organisms (the theoretical biology of von Bertalanffy, Weiss, Woodger, Waddington, and so many others). However, although the main consequences of autopoiesis for a renewed view of evolution are concurrent with other movements within the field (there is an ample group of researchers and perspectives pushing towards an expansion of evolutionary biology so as to integrate organizational and developmental aspects not included in the modern synthesis [4, 8, 21, 24, 35, 40, 46, 64, 66]), some of its specific proposals leave questions open for philosophical debate.

In the following section some of these questions are made explicit, and they are pursued further in the sections thereafter, which analyze the views of the proponents of autopoiesis on information (Section 3), on reproduction (Section 4), and on evolution (Section 5). The aim of this article is not, however, to provide a systematic discussion of these difficult problems, but to comment on some friction arising in theoretical biology between two conflicting views on the nature of life—the primacy of organization and the primacy of evolution—from the perspective and with the guidance of the theory of autopoiesis.

## 2 Primacy of Organization: Materiality and History

For the proponents of autopoiesis, living organisms and their functional structures are not *designed* by evolution. Neither reproduction nor evolution can have a role in the generation or origination of autonomous individuals, since they are not mechanisms<sup>7</sup>

5 The way in which autopoiesis deals with genetic information, reproduction, and evolution has been a subject of controversy and debate since it was first proposed. This can be noticed even in Beer's original preface to the English translation: "All of this is totally alien to what we (most of us working in cybernetics) have believed. Information, including codes and messages and mappings, was indeed for us the whole story of the viable system. If one thinks of reproduction, for example [...] then the survival of the code matters. The tissues of each generation are subject to aging and finally death, but the code is transmitted. The individual becomes insignificant, because the species is in the code. And that is why identity vanishes in an ageless computer program of bits. [...] Nature is not about codes: we observers invent the codes in order to codify what nature is about. These discoveries are very profound" [30, p. 69].

6 "We assert that reproduction and evolution are not constitutive features of the living organization and that the properties of a unity cannot be accounted for only through accounting for the properties of its components" [59, p. 187].

7 Probably M&V have in mind the distinction between whys and hows (ultimate and proximate causation), which has become standard in the philosophy of the modern synthesis, according to which evolutionary explanations only refer to the ultimate causes of living organisms. From this point of view, although the evolutionary process of variation and selection is sometimes said to be a *mechanism* (a perspective enhanced by algorithmic approaches to artificial evolution), in fact it is quite dubious that it involves one, devoid as it is of actual mechanical causes, because of its separation from proximate causes. In contrast, autopoiesis is a mechanism. For

to produce autopoiesis, but processes that occur in systems already formed and that derive from their properties. Standard evolutionary thinking, where it is considered that reliable reproduction and evolution take place at the genetic level, blurs autonomy to the point of obscuring it, because living organization is made dependent on an “organizing agent” transmitted in reproduction and transformed in evolution. Thus Varela writes:

I maintain that evolutionary thought, through its emphasis on diversity, reproduction, and the species in order to explain the dynamics of change, has obscured the necessity of looking at the autonomous nature of living unities for the understanding of biological phenomenology. Also I think that the maintenance of identity and the invariance of defining relations in the living unities are at the base of all possible ontogenic and evolutionary transformation in biological systems. [55, p. 5]

Perhaps this intuition sounds too radical, but it is not to be understood as meaning that evolution never took place or denying that most of the characteristics of life as we know it on Earth can be traced back to an evolutionary history, but as suggesting that all the generative processes depend on the self-organizing and self-producing processes that constitute organisms in their space, together with the interactions with their environments. These processes change in the long transgenerational sequence of reproductive events, that is to say, concrete forms change in the course of history. M&V characterize evolution as a “natural drift,” a process not driven by any *mechanism* of its own, but a result both of certain self-organizing deterministic processes and of many contingencies in the interaction of organisms with the environment, selection being an effect of all of them.

This is something that stems from the very characterization of life as autopoiesis, which has, in my view, two main epistemological features. One is the primacy of life, with a focus on individual organisms as whole identities that we, as living creatures, apprehend directly. Hence, the living state does not derive from the properties of its components<sup>8</sup>; the organization is primary. However, its authors consider that autopoiesis offers a *mechanistic* vision of life, as opposed to vitalistic versions, so that “no nonmaterial vital organizing force is necessary” [29, p. 137]. They even talk of an “autopoietic machine,”<sup>9</sup> although it is quite clear that their goal is not the reduction of biology to Newtonian physics, but a commitment to look for scientific explanations of the autopoietic organization, given that Darwinism does not explain them. (The discipline of artificial life is one of the possible domains for this task).

Yet, the primacy of the organization may pose difficulties, not completely clarified in the autopoietic literature, especially in relation to materiality. The independence of material components may have different consequences depending on whether the organization is peculiar to an individual or follows from a universal definition of life. In the first case, referring to a particular individual, it means that the identity of the system resides in the whole and not in the components; these can change without altering the basic organization. For example, from this perspective the human manipulation of

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some authors (see for example Wicken [67]), the evolutionary theory needs to be provided with full mechanistic explanations.

<sup>8</sup> Similar views appear in the philosophy of Hans Jonas. See [63].

<sup>9</sup> This has sometimes been criticized; see, for example, [49]. However, I think that autopoiesis may be considered to be an organicist theory [9, 15, 22, 44, 54]. In this respect Varela and his coauthors differ with Kant, who believed that living organization cannot be explained scientifically: “Our immodest conclusion is that Kant, although foreseeing the impossibility of a purely mechanical, Newtonian account of life, nonetheless was wrong in denying the possibility of a coherent explanation of the organism. But this ‘Newton of the Grassblade’ was surely not Darwin. . . .” [63, pp. 120–121]. For a deeper account of Kantian views in contemporary philosophy of biology, see [52].

a living being does not produce artificial life, because it is not the organization that was artificially altered, only some constituents. Similarly, we would not consider that a living being with a transplanted organ has changed its identity. Although this is the way life is understood by organicist theories, there is no consensus on the philosophical issue; famous examples like the classical one of Theseus's ship have motivated endless metaphysical discussions about whether the change of one component changes the identity of the system.

However, autopoiesis is also a universal definition of life [29, p. 114]. In this respect, autopoiesis is independent of matter, because its characteristic organization could be realized with different material components and still be considered a living being (for example, in the case of artificial systems or of living systems in different places of the universe). According to the distinction between organization and structure [55], the first denotes the logic or formal account of the system, and the second, its (contingent) material realization. The justification of this definition by which autopoiesis is independent of materiality is probably that it intends to explain identity, and leave diversity as a secondary problem in the definition of life. But, as a consequence of this, the idea of diverse kinds of organizations underlying different levels of life or different taxa was not pursued further.

The second feature of autopoiesis is the aim to account for living organization as a state previous to (and necessary for) reproduction or evolution, that is, to separate processes that are history independent from those that are history dependent:

[P]roceses that are history dependent (evolution, ontogenesis) and history independent (individual organization) have been confused in the attempt to provide a single mechanistic explanation for phenomena that although related are fundamentally distinct [59, p. 187].

History dependent processes do not influence living organization, which relies on processes that are history independent.<sup>10</sup> The aim is to provide a "necessary and sufficient organization for a given system to be a living unity" [59, p. 187], and this organization, in the view of the authors, does not derive from historical processes such as reproduction and evolution.

According to this, living organization does not depend on history; only material structures change in the historical course of reproductions with variations. A consequence of this is that the theory has problems in explaining higher levels of living organization. Sometimes multicellular organisms are considered second-order autopoietic systems, but Varela has often stated that he would like to avoid the extrapolation of intuitions from the basic level to other levels.<sup>11</sup> In order to say that autopoiesis appears in different organizations at different levels it would be necessary to take into account material evolutionary changes leading to evolutionary transitions [34].

In sum, the theory of autopoiesis suggests that history can account for the transformation of autopoietic individuals, but it cannot explain their generation or origins. This poses the question of the role of evolution in explaining life. For the modern synthesis all biological subdisciplines have evolution as a common referent that yields a unified perspective. What would a biology that takes into account both organization and evo-

<sup>10</sup> Sometimes the distinction between historical and ahistorical explanations or perspectives in biology counts evolutionary explanations as the historical ones (ultimate) and developmental and metabolic ones as the ahistorical ones (proximate). Development is also a historical process for autopoiesis, and the difference from evolution is that the former, development, is the history of (structural) transformations of a single unit, whereas the latter, evolution, consists in the replacement of individuals. Thus, the notion of autopoiesis is previous to development (as it is to evolution). Both historical processes, however different they are, emphasize change, whereas autopoiesis tries to characterize what is stable and identical of an individual.

<sup>11</sup> When dealing with higher levels, Varela studied specific systems, such as the nervous system or the immune system, although assuming that they are embodied in the context of the organism.

lution be like? Autopoiesis proposes a view of organization that is both independent of materiality (structure) and independent of history. The challenge is to construe a view that can take both of these left-out aspects into account within a theory of life as autonomous organization.

### 3 Information and Organization

In the description of autopoiesis, genes or nucleic acids do not play a role different from that of the other cellular components; rather, they engage in production relations like the rest of the molecules. The argument behind this is that cells are self-organizing and self-producing systems (*self* including the whole network of recursive reactions), not instructed by any component (either internal or external) of the system. The theory rejects the notion that genes carry information, or that semantic information or symbols are required to characterize life,<sup>12</sup> which is considered a preformationist idea. Varela [55] distinguishes between operational and symbolic explanations of phenomena, the second being shortcuts or abbreviations of full explanations, made by an observer for pragmatic reasons. In this way, the role of genes in the cell is not informational (but involved chemically in the network of reactions), and nothing special about genes is needed to account for living organization.<sup>13</sup>

In order to be able to discuss the consequences of this position, it is useful to see a recent defense of information by Maynard Smith [32], as his position makes explicit many assumptions that are widely held but rarely enunciated.

#### 3.1 Genetic Information as a Primitive

In a recent article, Maynard Smith [32] presents arguments to defend the belief that genes contain semantic information, as a response to the parity thesis of DST (see footnote 13 below). He develops two main points for his argument: one based on the arbitrariness of the genetic code, and the other on the functionality of the genome.

The notion of genetic code refers to the matchings between triplets of nucleotides and amino acids performed by tRNA: chemical affinities between the paired elements are not enough to explain that this is done systematically (that is to say, chemistry would allow for different pairings). This is the reason to propose the existence of a code, and, for Maynard Smith, it is also a reason to draw an analogy between language or information at the human level and at the genetic level (though he acknowledges that there are many differences between them). The existence of a code is also an argument for open-ended evolution, because it allows for heredity that is unlimited: that is to say, not confined to the samples transmitted, but relying on a system of “representation” that may potentially refer to any kind of component.

The other point is that natural selection is considered as equivalent to (non-conscious) intentionality. The information transmitted in a message encoded in human languages is intentional, because the agent has the intention to transmit it, and it is

12 “[T]he informational molecule is in no way different from any other molecule, its process of interaction from that of chemical species. The reason the name ‘informational’ comes up at all is that we can change the time scale of our observation, consider the realization of these units through several generations, and observe the continuity and reliability of their process of specification of components in an evolutionary process. In other words, we abstract or parenthesize in our descriptions a number of causal or nomic steps in the actual process of specification, and thus reduce our description to a skeleton that associates a certain part of a nucleic acid with a certain protein segment. Next we observe that this kind of simplified description of an actual dynamic process is useful in following the sequences of reproductive steps from one generation to the next, to the extent that the dynamic process (i.e., the kind responsible for bonding, folding, and so on) stays stable. This seems to be the origin of the idea of genetic material as the central element of study for evolution and historical processes in biology” [56, p. 43].

13 More recently, in a similar view, proponents of the *developmental systems theory* (DST) [20, 39, 40] have enunciated a *parity thesis*, according to which “any sense in which genes code for phenotypic traits or program development or contain developmental information can be equally well applied to other factors required for development” [20, p. 195].

different from the information one could gather from observing some natural phenomenon (a natural meaning). An example used by Maynard Smith to explain this is the difference between inferring that it is going to rain from seeing black clouds in the sky and inferring it from listening to a weather broadcast. Although both events may inform us of the same fact (i.e., that it is going to rain), only the broadcast has the intention to communicate and has been arranged according to that intention. In the same way, genes (or nucleic acids) have the form they have because natural selection has arranged them, and in this way they are different from other resources (environmental or internal) that, although relevant for explaining the phenotype we observe, have not been formed to serve that function. Thus, the function of genomes is to carry information, and their form arises from this function.

Maynard Smith suggests that this view is corroborated by experiments in ALife using genetic algorithms. He mentions a case in which different strategies to play a competitive game are evolved in an artificial system, with the result that, starting with randomly generated strings for genotypes, optimal strategies for individuals to play the game appear in the simulation. He understands this example as corroborating the notion that the genome provides an informational system that may be shaped or programmed by natural selection in such a way that, with time, the evolutionary process ends up with the structure required for adapted organisms:

Such a system depends on genetic information, but the way in which that information is responsible for biological form is so different from the way in which a computer program works that the analogy between them has not, I think, been particularly helpful, although it is a lot nearer the truth than the idea that complex dynamic systems will generate biological forms “for free” [32, p. 192].

In the view of Maynard Smith, the focus on genes (and the notion of information to describe their properties and function in the organism) makes it possible to grasp what is peculiar to living systems in contrast with complex nonliving dynamic systems. Although self-organization, or order “for free,” is an important aspect, his position involves a certain skepticism about its real importance to understand life, provided that all self-organizing processes in organisms are controlled by genes. In this approach, then, information is taken to be some sort of *primitive* from which all the relevant aspects of organisms unfold. However, there are other modes to conceive the role of information.

### 3.2 Genetic Information as a Derived Property

One problem with the view of information as a primitive is how to understand the origin of life or of autonomous systems.<sup>14</sup> In evolution, first, self-maintaining and self-producing autonomous systems must have appeared, and only later would they have been endowed by a genetic system that ensured the reliable production of the necessary proteins. From this perspective, information is not the starting point; the most likely picture is that the genetic system has been able to follow or to go behind the already existing proteins and that the primitive cells have evolved into more sophisticated ones, endowed with genetic mechanisms [13].

An organization endowed with a genetic system must derive from an already autonomous one. The derived character of information is not only temporal precedence,

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<sup>14</sup> The origins-of-life field is divided between those who study the properties of certain molecules, specifically nucleic acids, and those who study the formation of whole organizations or cells.

but also that it has a causal role within a dynamical system.<sup>15</sup> This requires a physical account of the role of genes in an autonomous system. For example, for Pattee nucleic acids carry information in the form of records or templates used by dynamic processes to construct proteins [42]. Proteins are understood as *constraints*, that is to say, as physical devices that direct or catalyze metabolic physicochemical paths. Thus, within the context of the cell, the constraining action of proteins acts as a way to ensure the stability and functionality of the metabolic network, and the minimal organization for a living cell should be characterized as a *semantic closure* between two types of components: informational (or symbolic) and dynamic [43]. If autopoiesis and semantic closure are to be compared,<sup>16</sup> one possibility is that the two of them refer to two different organizations, the first earlier in evolutionary time and the second more complex or more evolved. We can imagine that the transition could have been generated after many structural couplings of the minimal autopoietic systems with the environment in such a way that they led to a major change in the organization, namely, one that went from forms of autonomy without genes (autopoiesis)<sup>17</sup> to forms with a genetic system (semantic closure) [51]. Another possibility is to consider that they propose alternative models to characterize minimal life.

On the multicellular level the notion of information as a primitive becomes less adequate, if possible, than at the single-cell level [47]. The biological literature has often embraced the notion of *genetic program* to explain the development of multicellular organisms, but implicit here is a conception of genes as primitives, so that the morphological phenotype is determined by its genotype. This view changes rather radically if we consider, as many authors do, that the genetic stabilization of phenotypic production in evolution is a process that goes behind the establishment of morphology, and not before or as a trigger of it [38]. Thinking this way, many phenomena, such as phenotypic polymorphism (organisms that have different forms in different settings or in different phases of their life cycle) and morphological plasticity, are easier to explain. The genotype-phenotype correlation is a derived property produced by the stabilization of morphologies via genetic mechanisms [48, 61].

In the early stages of the origin of multicellularity the morphology of the first organisms was mainly produced by physical properties characteristic of “soft matter” [37]. Morphological variation in response to the environment is a primitive, and the role of genetic systems is to constrain this variation, that is to say, to make the system less dependent on environmental conditions. This theory is based on the fact that self-organizing properties of cell aggregations are important in shaping the form of multicellular organisms. Development is an interplay between *generic* processes (dynamic physicochemical processes, such as gravity, adhesion, diffusion, and interfacial tension, underlying the organization of both living and nonliving systems) and *genetic* processes (dependent on highly organized interactions between specific macromolecules, formed via coevolution of macromolecules, whose properties are coordinated so as to achieve certain very specific functions).

In sum, information as a primitive and information as a derived property are two views that, although very different, share the belief that genes play a distinctive role in living organization. The theory of autopoiesis accepts neither of them in principle, although its criticisms are mostly directed against the first one. The second one is more easily made compatible with autopoiesis, which states that because organisms construct their own identities, these identities cannot preexist in the form of inherited

<sup>15</sup> Other approaches have tried to account for a causal and dynamic notion of information—for example, [6, 67].

<sup>16</sup> Yet, the two approaches also adopt different epistemological perspectives. See [11] for more on this.

<sup>17</sup> Luisi reports that “self-reproducing micelles and vesicles can be considered as the simplest autopoietic systems, but hardly as living ones. Interestingly, Varela did not object to the tagging as ‘living’ of this micellar or vesicular systems (F. Varela, personal communication)” [28, p. 58].

components. But, if genes are embedded in a self-constructing network of dynamical components, and it is this network that interprets and uses the information of genes, then it is not genes but the autonomous network that defines the identity. In the use of the concept of information to explain the role of genes in the cellular organization one must be very careful. Yet an account of autonomy in which genes play no special role has the problem that it is not possible to explain certain material relations made possible because of the role of genes.

#### 4 Reproduction, Development, and Sameness

Imagine a world in which creatures generate and die, but do not reproduce. There, new beings would come into existence whenever the required conditions were present (reactive materials, food, temperature, etc.), and they would end when energy or certain capacities extinguish or disappear. Perhaps from the remains of the extinguished creatures new ones would appear. In this scenario there is no transmission of an *organizing agent* to the offspring; all organization depends only on generative properties of the emergent self-organized system. It is a true paradise of “order for free.” Now suppose that these beings start to multiply somehow, producing offspring of the same kind. How would these creatures achieve sameness in kind? For autopoiesis, the way living systems achieve this goal can also be considered to be a consequence of their autonomy. This view of reproduction requires a more encompassing notion of inheritance than the one implicit in the replicator.<sup>18</sup>

The phenomenon of reproduction requires a unity and a process to generate a new unity of the same kind. M&V distinguish three different modes of reproduction to get this sameness: via replication, copy, and reproduction [30, pp. 100–102; 31, Chap. 3]. In replication there is a mechanism that can produce many unities of the same kind. One example is a factory: the productive mechanism and the produced unity are operationally different systems, and the productive mechanism produces elements that are different from itself, and independent of each other, such as cars or pencils. Copying is the process in which we have a model and a projection procedure to transfer the model into another unity. If the result of the copy is used as a model for the next copy, subsequent copies will be historically connected. Reproduction is the case in which a unity is broken so as to produce two unities of the same kind. The resulting unities are not identical to each other or to the original, yet they pertain to the same kind as the original; they have the same organization.<sup>19</sup> For the reproducing unity to

<sup>18</sup> We may compare this view with the more radical gene centered view of neo-Darwinism, in which, precisely because reliable reproduction is seen as the main property of living systems, the gene, understood as a replicator, is situated at the center of biological ontology. In this view [7], coming from a perspective in which evolution, and not individual organization, is the main living phenomenon, the relevant units of evolution are not organisms (or genotypes), but single genes or replicators. Dawkins coined the terms “replicator” and “vehicle” to refer to the source of evolutionary variability and the target of selection, respectively. But in his view, organisms are only vehicles for gene propagation. Hull [23] challenged this dichotomy in that it failed to grasp the real importance of the two processes involved, by making the entities on which selection acts (i.e., vehicles) be direct consequences of genes. Instead, he proposes to analyze biological phenomenology by considering two kinds of categories with independent status. These categories were called “replicators” and “interactors.” A replicator is “an entity that passes on its structure directly in replication,” whereas an interactor is “an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential” [23, p. 318]. Whereas the first distinction places genes at the center of all phenomenology, the second opens the way to a hierarchical vision of individuals, in which we may distinguish both replicators (not every inheritance is genetic in Dawkins’ sense) and interactors (different cohesive individuals) at various levels.

<sup>19</sup> An anonymous reviewer of this article posed the following question about this passage: “Does this mean that a significant mutation, perhaps changing the organization, makes the process something other than reproduction?” The answer to this question depends on how we understand organization. According to the way M&V use the term in most of their writings, it is not the organization but the structure that would be changed in this case, because if the novelty does not destroy the system, that is to say, if the offspring is viable, then the organization that underlies all living systems, autopoiesis, is conserved under a different structure. The intuitive notion of distinctive organizations underlying taxa at levels higher than the organism (species, family, kingdom, etc.) is not explicitly considered by M&V, who do not address diversity as a difference in organization.

produce two similar copies and not to be destroyed itself, it must realize its organization in a distributed, not compartmentalized, way. Some systems cannot be reproduced, as they cannot get to this distributed stage.

Thus, M&V characterize a general relation consisting in producing similar items, one that includes self-reproduction as a subset, according to the properties of similarity, historicity, and evolvability [12]. Similarity refers to the degree of resemblance between original and copy, whatever the causal link responsible for the relation. In fact, this causal link might not reside in the terms themselves: for example, the serial copies produced by factory machinery or a photocopying device resemble each other exactly, but this resemblance is due to an external factor. Historicity, however, will cause resemblance due to the fact that each of the members of a series is the “model” of the subsequent copy. This property is retained in evolvability, but in this case the historical relation between model and copy includes the introduction of variations that can be amplified or not, depending on their viability. This classification states that the way in which living systems reproduce is such that the offspring does not inherit only genetic material duplicated via replication, but also many other components.

Griesemer [19] has further elaborated the notion of reproduction in work that brings to mind M&V’s intuitions.<sup>20</sup> He also considers that the notion of reproduction must be able to explain the *biological autonomy of reproducers* [19, p. 280]. In his view, reproduction is a process with two aspects: progeneration and development. Progeneration is multiplication of unities with material overlap, that is to say, some of the parts of the offspring were previously parts of the parents (similar to what M&V call reproduction). Examples for this are the division of a bunch of grapes (M&V) and the cutting of a loaf of bread (Griesemer). Cell reproduction by fission is a living example. Progenerating organisms must be agents of reproduction, not merely material or efficient causes (self-reproducing in M&V’s terms). For Griesemer, genealogy must be understood as a flow of matter; material overlap is important because the kinds of materials specify relevant sameness. In multicellular organisms it must be completed with development, the process by which sameness of kind is realized, often despite substantial variation-producing forces. In this sense DNA replication is only part of the cell reproduction, and RNA viruses are not considered to progenerate, as there is no material overlap (unless by accident): they do not reproduce; they replicate by virtue of the development of their hosts (which is the productive mechanism). Thus, the distinction between replication and reproduction is assigned to the role of development in their respective processes. Replication is a process abstracted from development,<sup>21</sup> while reproduction involves development, unless it is mistakenly identified with copying. The requisite of development has the consequence that in order to represent reproduction, the offspring must have the capacity to reproduce. The production of offspring that cannot reproduce would be only progeneration.

M&V consider that autopoiesis is previous to reproduction both in evolutionary time and in theoretical preeminence. Yet, it is clear that terrestrial life at least has developed very sophisticated forms of reproduction of its different forms of organization at the different phylogenetic levels. One of the important points of Griesemer’s work on reproduction is to stress that genealogy cannot be understood only as the transmission of genes in replication; in order to understand reproduction itself as a process occurring in autonomous systems, it must take into account all sorts of material overlapping.

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20 It is not clear whether his work has been influenced by M&V; they are not among his references.

21 Griesemer thinks that evolutionary theory has proceeded by abstraction of informational genes from the substantial body.

## 5 Evolution of Organized Wholes

M&V [31, 60] defend a view of evolution that they call *natural drift* and that is fundamentally a criticism of the so-called *received view* [50] related to the modern synthesis in evolutionary biology. The term “natural drift” is, as far as I know, a neologism, perhaps deriving from two much more used terms in evolutionary biology: “natural selection” and “random genetic drift” (Sewall Wright, Kimura). M&V obviously mean to distinguish it from them so as to characterize evolution in a way that may be compatible with the general view of autopoiesis as an account of the organization of the living state.

The notion of natural drift defends an ahistorical notion of adaptation: instead of considering that adaptations are traits evolved by natural selection, all existing organisms are well adapted to their environments in that they constitute viable ways of living and interacting with their environments. It amounts, thus, to a critique of adaptationism in evolutionary biology [17], in view of the evidence of molecular neutral changes without effects in morphology or selection [26] and the need to integrate developmental aspects in evolutionary accounts, as well as a perspective that views organisms as active agents of their evolutionary change (and not passive effects of natural selection) [27]. M&V do not deny the existence of selection and its role in evolution, only that it has generative properties. Thus, they say that it must be seen as a result of the different conservation of lineages of autopoietic forms, not as a mechanism to generate them. In evolution the viable organisms satisfy certain conditions; they do not optimize them.

In biological thought, the movement that started to propose changes in this direction in the 1980s (see, for example, [4, 18]) has grown considerably. With some differences in approach, the already mentioned DST [20, 39, 40], the emerging discipline of developmental evolutionary biology (or evo-devo) [21, 35], and the thermodynamic [8] and complexity based [24, 46] approaches to evolution are pushing toward a broader understanding of evolution that implies a new place for the integrated organism. Probably the main point on which they agree is that developmental processes play a crucial role, and although the proponents have different views on the role of genes, there is wide consensus in the supposition that evolution cannot be successfully understood and modeled by attending only to the genetic level. As Alberch wrote: “In evolution selection may decide the winner of a given game but development non-randomly selects the players” [1, p. 665].

The first way in which the idea that elements other than genes have to be considered as eligible players appeared was with the notion of *developmental constraints*. Its proponents tried to show that the evolutionary game was not played only at a genetic level and that processes at other levels, especially at the morphological one, determine the possible forms, independent of function. This notion was probably the first inroad of contemporary developmentalism into evolutionary biology, and it was integrated without much difficulty as the idea that development limits (perfect) adaptation [33], and therefore the morphospace is not filled with all the a priori conceivable forms, but has some empty spaces corresponding to impossible morphologies [2]. Yet this notion of limitations seen as a counterpart of selection itself cannot be considered completely satisfactory for grasping the actual positive role of development. If we analyze the work of the people who proposed the concept, such as Alberch, we realize that the notion was intended in a more positive way,<sup>22</sup> that is to say, as the assertion that morphogenesis is the process in which novelty and innovations appear in evolution, and the realization that variation at the genetic level is to a certain degree unimportant

22 Gould [16] also noted that the dictionary definition of constraint provided both a positive and a negative sense. In the context of a hierarchical thinking, Pattee [41] considered that constraints limit degrees of freedom at one level whereas they open a whole range of them at a higher one; in this respect, they are *enabling*.

in the production of this novelty. Yet, if these internal factors (as opposed to the externalism implied by their being shaped by natural selection) have to be studied, one must complement the approach of population genetics with another one rooted in self-organizing properties of pattern formation [3].

Aside from discussions about the role of genes, the developmental approach considers that the level of morphology formation is largely independent of the genetic one, as variability does not correspond with genetic variability. This has brought the concept of homology back into the center of evolutionary thinking and debate [36, 62]. The identity and sameness of some organic forms across close or even distant taxa is again a matter of inquiry after so long a period of concentration on variability and diversity. This has been a consequence of shifting the focus from genes to development: to cell assemblages organized as morphological units or modules. The other grand change has been the inclusion of environmental factors causing phenotypic plasticity [53]. All of these have produced a changed framework for understanding evolvability as a property of developmental systems [10].

## 6 Conclusion

The theory of autopoiesis intends a radical transformation of biological thought to focus on the individual organism and, more concretely, on the organization that provides its identity. Its emphasis on the unity and identity of organisms appears to create a difficulty in understanding change and diversity, especially because of its separation of organization and materiality. However, standard evolutionary thinking itself has a similar problem with materiality, in that changes are perceived as changes in the abstract domain of genes. In addition, it lacks understanding of organization and organized individuals.

Some recent developments of evolutionary thinking that try to bring development and self-organizing proximate causes to the nucleus of evolutionary explanations seem to be closer to autopoiesis. They lead to a perspective less focused on genes as the locus of evolutionary change, and more aware of the importance of morphological form. Reproduction is not confined to a hereditary system reduced to genes (replicators), but involves the need for other factors (epigenetic) and for considering material flow. Evolution is constrained by bauplans constructed according to self-organizing properties of matter. These developments construct an adequate domain in which to think about the evolution of autopoiesis, but for that purpose material arrangements have to be brought in.

A biology that takes into account both organization and evolution recognizes the primacy of the organism as a key ontological unit.

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