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**Plurality of Explanatory Strategies in Biology: Mechanisms and Networks**

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**Abstract:**

Recent research in philosophy of science has shown that scientists rely on a plurality of strategies to develop successful explanations of different types of phenomena. In the case of biology, most of these strategies go far beyond the traditional and reductionistic models of scientific explanation that have proven so successful in the fundamental sciences. Concretely, in the last two decades, philosophers of science have discovered the existence of at least two different types of scientific explanation at work in the biological sciences, namely: mechanistic and structural explanations. Despite the growing evidence about the radically different nature of these two types of explanation, no inquiry has been conducted to date to determine the ontological reasons that might underlie these differences, nor the way in which these types of explanations can be systematically related with each other. Here, we aim to cover this gap by connecting this plurality of research strategies with the existence of emergent levels of reality. We argue that the existence of these different—and apparently incompatible—explanatory strategies to account for biological phenomena derives from the existence of “ontological jumps” in nature, which generate different regimes of causation that in turn demand the development of different explanatory frameworks. We identify two of these strategies—mechanistic modelling and network modelling—and connect them to the existence of two ontological regimes of causation. Finally, we relate them with each other in a systematic way. In this vein, our paper provides an ontological justification for the plurality of explanatory strategies that we see in the life sciences.

**Keywords:** Scientific explanation; Mechanism; Structural explanation; Networks; Emergence

1. The Ontological Basis of Explanatory Plurality

In his book *Mind and Cosmos. Why the Materialist Neo-Darwinian Conception of Nature is Almost Certainly False* (2012), the American philosopher T. Nagel argues that contemporary biological sciences are unable to explain neither the origin of life, nor the origin of mind. More fundamentally, Nagel claims that no scientific theory can provide a satisfactory account—which for him means a reductionistic explanation in physicalist terms—of how these two complex phenomena could have appeared from the evolution of the physico-chemical world. In his book, Nagel tends to identify the epistemological or explanatory sense of the term “reductionism” with the ontological one, i.e. he conceives “reductionism” as equivalent to “reductive materialism”, as he does not consider that emergentist theories could offer an alternative explanation of the origin of these types of complex systems (and their related properties) in ways compatible with materialism. As he says (Nagel 2012, 55-56): “That such purely physical elements, when combined in a certain way, should necessarily produce a state of the whole that is not constituted out of the properties and relations of the physical parts still seems like magic even if the higher-order psychological dependencies are quite systematic.”

We take Nagel’s example to introduce here why a correct understanding of “the ontological jumps” in nature is so important, and why it is fundamental to properly characterize and conceive the different explanatory strategies that are currently being employed in the life sciences. As it is well known, emergentism—the theory that aims to account for the existence of these ontological “jumps”—appeared in the 1920s as an attempt to find a compromise between two theses: on the one hand, the fidelity towards a basic materialism; on the other, the assumption of the appearance of novel levels of reality (chemical bonding, living systems, the mind) endowed with specific causal powers (cf. Mill 1843; Alexander 1920; Lloyd Morgan 1923; Broad 1925). Of course, the crux of emergentist theories has always been the difficulty to provide a scientifically satisfactory account of how certain complex arrangements of matter can bring forth new interesting properties, and why the appearance of these new properties cannot be reduced to—i.e. why they cannot be logically deduced, at least in principle, from—the theory that works successfully for the explanation of the properties of the lower-level arrangements of matter. In other words, why certain complex relations suddenly generate what are conventionally called “systemic” properties, and why these systemic properties should be qualified as ontologically “genuine” and different from the properties of the lower levels of reality (i.e. emergent), rather than “subjectively surprising”.

Emergentism experienced an important decline since the 1930s, as it remained suspicious both for most scientists and philosophers, especially due to the influence of logical positivism (Kim 1989, 1999, 2006; McLaughlin 1992, 1997; Humphreys 1997; Wilson 2013, 2016; Suárez and Triviño 2019). There are many reasons that justified this suspicion—if not open rejection. Firstly, in agreement with the main claims defended by logical positivism, reductionism was perceived as the only possible way to scientifically account for the properties of “higher” or more complex levels of the reality. Secondly, if—as overwhelmingly new discoveries were showing—higher levels of reality (like biological systems) were made *but of* physical entities, their properties should, at least “in principle”, be explained in the very same terms of the physical sciences. Finally, the possibility of reducing Classical Thermodynamics to Statistical Mechanics constituted an important ontological victory for the reductionists. It showed how a set of laws that had been previously considered emergent could in the end be reduced to the laws of physics, and thus their alleged ontologically distinct explanatory framework finally converged into the explanatory form of the so-called “fundamental” (namely, the physical) sciences.

Nonetheless, the decline of the influence of logical positivism among philosophers of science, together with the development of the so-called “Sciences of Complexity”, have generated a resurgence of emergentism since the last decade of the 20th Century, both among philosophers and scientists (Witherington 2011; Mitchell 2012). In parallel with this resurgence of emergentism—and partially as a consequence of the growth of the Sciences of Complexity as well—philosophers of science have started to admit the existence of a plurality of forms of scientific explanation which go far beyond the type of reductionism that Nagel argues to be necessary in his book (e.g. Dupré 2013; Díez, Khalifa and Leuridan 2013; Rice 2015; Green and Jones 2016; Green 2017; Woodward 2017). In the specific case of the life sciences, two alternative forms of scientific explanation have gained special recognition in the last two decades: mechanistic and structural explanations (Huneman 2010, 2018a, 2018b; Brigandt, Green and O’Malley 2017; Suárez and Deulofeu 2019). The acknowledgment of this plurality of explanatory strategies has given rise to a blossoming of research that is raising very interesting questions, and that is questioning some of the most traditional assumptions about the nature of scientific explanation, as we will show later.

Despite the complementary aspects of these debates, these two dimensions of our current philosophical theorizing have not been connected in a consistent manner yet. Philosophers of science have simply confirmed—by providing several elaborated examples to that end—the existence of a plurality of explanatory strategies which seem to have a radically different nature from each other, but they have not conducted any inquiry about the ontological reasons that are behind this plurality. This chapter aims to contribute to this growing literature by covering this specific gap. Here, we raise the question about how the ontological and the epistemological debates can be systematically related by showing that the different explanatory forms that we observe in the life sciences are a consequence of the existence of “ontological jumps” in nature. These “jumps”, we argue, generate emergent regimes of causation that, first, constrain the application of the laws of nature in a particular domain of reality and, second, justify the appearance of these apparently incompatible explanatory frameworks for each of these domains. Importantly, our study will be focused on the biological sciences. We will inquiry first about the nature of the type of explanations that work well in this domain; second, we will ask about how and why successful explanations in the biological sciences are related to successful explanations in more fundamental sciences.

To do so, the chapter is structured as follows. In **section 2**, we introduce three different types of explanatory strategies that have been used in different sciences—concretely, in different parts of the biological sciences—and show why they are epistemologically incompatible. In **section 3**, we investigate the ontological reasons that underlie the validity of mechanistic explanations, and we explain their relation to successful explanations in the fundamental sciences. In **section 4**, we conduct the same type of investigation for structural explanations. In **section 5**, we argue that, in view of the analysis conducted in the previous sections, biology requires complex explanations, and thus both the mechanistic and the structural explanatory strategies are necessary and need to be sometimes combined. Finally, in **section 6** we present our conclusions.

1. Three Types of Explanatory Strategies: Deductive-nomological, Mechanistic, and Structural

As we said before, in his book, Nagel (2012) presumes that the only way of providing a satisfactory scientific explanation of a phenomenon is to do so in physico-chemical terms, as these are the terms employed in the so-called fundamental sciences. Admittedly, the type of scientific explanation that the fundamental sciences have so successfully developed implicitly requires three elements: First, the identification of the relevant observables (state variables); second, the determination of the general laws governing their change (expressed as differential equations, state transition rules, maximization/minimization principles, etc.); and third, the determination of the initial (or boundary) conditions for each particular case. Once these three elements are given, it is possible to provide an explanation of why several physico-chemical phenomena happen, as well as why they occur in the way they do, rather than differently. For example, it is possible to explain why an ice cube melts into water by appealing to observables such as the temperature, pressure, or internal energy of the ice cube, plus a law of nature that says that ice melts whenever it is left at a temperature about 0ºC, plus a set of initial conditions of the case—e.g. that the ice cube is originally at a temperature of -15ºC. This type of explanation has been called *deductive-nomological* (DN, hereafter) insofar as in this type of explanation the phenomenon to be explained is the conclusion of a logical argument whose premises must necessarily include—explicitly or elliptically—*a law of nature* (Hempel 1965; Díez 2014; Deulofeu and Suárez 2018). The law of nature describes the regularity at the fundamental level of reality whose existence serves to predict the phenomena that will be observed and, thus, explains their occurrence. In this vein, the DN approach to scientific explanation conceives explanations in analogy with predictions: a prediction tells you what will happen in the future by appealing to the regularity imposed by the laws of nature, whereas an explanation tells you what has occurred in one particular instance in the past by appealing to the very same regularity.

DN strategies, despite their application in some parts of the physico-chemical sciences, cannot work for explaining the global properties of systems made of an enormous number of parts or elements, though. This difficulty has been however overcome in some cases, such as Statistical Mechanics, where it is possible to average the huge amount of observables and thus reduce the explanations in a different field—Classical Thermodynamics—to explanations in terms of the more fundamental science. However, there are many other systems in which the interacting units cannot be averaged out and, in some cases, they even interact in non-linear and highly selective ways. Actually, this is what happens in those systems that are conventionally called “complex” (such as living systems), and that are the object of study of the Sciences of Complexity.

Some philosophers of science have argued that the complexity of this type of systems makes impossible that any fundamental law of nature could capture their properties and behavior to make them compatible with the strict requirements that DN explanatory strategies pose (Mitchell 1997, 2003; Giere 1999; Woodward 2000). Yet, despite this huge complexity, complex systems often exhibit global (or “emergent”) simplified properties. And the causal connection between the messy set of interactions of the components and the “emergent” global properties remained unexplained. These systems have challenged scientific understanding because their behavior could not be predicted, and their properties were never fully explained through available mathematical models, based on the fundamental laws of nature (Moreno, Ruiz-Mirazo and Barandiaran 2011).

And yet, despite their overwhelming complexity, living systems have been successfully studied for centuries, following a very different explanatory strategy than that of the physical sciences that inspired DN models of scientific explanation. Rather than looking for universally applicable laws or predictive models, biologists have tried to understand the behavior of living organisms by decomposing them into various parts (“structures”), analyzing them separately, and, then, investigating how these parts interrelate and affect one another within the whole system. Note that the point here is epistemological: the point is not denying that the laws of physics do not apply to these systems, but rather that these systems have a structure that makes these laws useless to explain the behavior of these systems. This explanatory strategy—called “mechanistic”—has provided fundamental knowledge about the basic structure and about the integration of many functional parts of living systems.

The mechanistic strategy to study living systems has a long history (cf. Nicholson 2012, 2018), although it has only become popular in analytic philosophy of science in the last two decades, where it is usually characterized as “new-mechanism”. New-mechanism was originally introduced in Bechtel and Richardson (1993) and Glennan (1996), and it acquired popularity after the publication of Machamer, Darden and Craver (2000). New-mechanists share a basic commitment to the two following theses. First, the rejection to the claim that scientific explanations are arguments, as it was widely assumed among defenders of the DN approach; second, the belief that the analytic decomposition of a complex system into their more simple components permits that relatively few parts could be methodologically isolated from the rest such that causal mappings between specific functional operations and their distinguishable structural components could be drawn.[[2]](#footnote-2) Combining these two theses, new-mechanists argue that to explain why a phenomenon occurs consists in providing a mechanism whose action is causally responsible for the production of the phenomenon to be explained. For instance, to explain why nervous signals travel from one neuron to another, it is necessary to explain how the mechanism of synapsis works, specifying how an electric signal can be transformed into a chemical signal (neurotransmitter), and then back into an electrical signal. What plays the explanatory role in this case, new-mechanists argue, is the specification of the mechanism itself, rather than a set of physico-chemical laws of nature, as defenders of the DN approach assumed.

In general, a mechanism can be defined as a set of entities—also called “parts”—and activities—also called “operations”—organized in such a way that the activities between the entities are causally productive of regular changes from start or set-up to finish or termination conditions (cf. Machamer, Darden and Craver 2000; Glennan 2002; Bechtel and Abrahamsen 2005; Craver 2007; Craver and Darden 2013). In other words, a mechanism is an arrangement of parts (a structure) that performs a function because of the activities that the set of parts engages in as a consequence of the way they are organized. In this vein, a mechanistic explanation must always include two necessary and sufficient components to be satisfactory: first, the *model of the mechanism* (entities, activities, organization); second, a *causal story* which connects the orchestrated functioning of the model of the mechanism to the phenomena that are produced and that are required to be explained (Issad and Malaterre 2015, p. 270).

Given this characterization of mechanistic explanations, it becomes necessary to specify the criteria to single out the parts of the mechanism whose interaction causally produces the phenomena to be explained. In other words, as mechanisms are arrangements of parts (“structures”) whose causal interactions perform a *function*—understood as a set of selected (see **section 5** and **footnotes 4 and 5**) terminations conditions—it is necessary to provide a criterion to distinguish the arrangement of parts that the mechanism comprises from other arrangements of parts. One possible way of solving this problem has been adopted by Craver (2007, p. 144), who appeals to Woodward’s (2000, 2003) “difference-making” account of causation to single out the arrangements of parts that constitute the mechanism, *vis à vis* those elements that are considered external. In this account, to determine the arrangements of parts that constitute the “boundaries” of the mechanism, one must intervene in the parts of the mechanism, altering their behavior, and observing whether the alteration has any effect on the production of the phenomenon. This results in a view according to which “a part is causally relevant to the phenomenon produced by a causal mechanism if one can modify the production of this phenomenon by manipulating the behavior of the part, and one can modify the behavior of the part by manipulating the production of the phenomenon by the causal mechanism” (Nicholson 2012, p. 160).

New-mechanism has been the mainstream theory of scientific explanation at least since the publication of Machamer, Darden and Craver (2000). However, in recent years, things have changed in philosophy of science. On the one hand, some philosophers have pointed out that the new-mechanistic explanatory strategy is not suitable to deal with several aspects of the biology of organisms, including several aspects of development, reproduction, or many other biological processes (cf. McManus 2012; Dupré 2013, 2017; Nicholson 2013, 2018; Isaad and Malaterre 2015; Alleva, Díez and Federico 2017). On the other hand, the new-mechanistic strategy seems simply not suitable to deal with many of the properties of “complex” systems that are explained by making use of the tools provided by the Sciences of Complexity (cf. Huneman 2010, 2018a, 2018b; Jones 2014; Green and Jones 2016; Brigandt, Green and O’Malley 2017; Deulofeu, Suárez and Pérez Cervera 2019). Concerning the later point, the application of the new-mechanistic strategy to account for the properties of complex systems would consist in assuming that complex systems result from the sum of several mechanisms working in a coordinated manner, so that the final outcome is the result of this combination, in the same way as it occurs in a classical mechanism. This type of explanatory strategy, new-mechanist argue, can be considered mechanistic as well, provided that the concept of “mechanism” is redefined accordingly (cf. Bechtel and Abrahamsen 2005; Bechtel 2015a, 2015b). But, as we will argue, this explanatory strategy does not seem to fit well with the requirements of the new-mechanistic conception of explanation, and thus we are left with another explanatory strategy that following Huneman we call “structural strategies”.

Structural explanatory strategies rely on the use of new techniques—such as cellular automata, genetic algorithms, Boolean networks, chaos and dynamical systems theory—derived from graph theory. These strategies, which we will globally call “network modelling”, provide rigorous ways to study the emergent properties of a great variety of “complex” biological systems in a way that contrasts sharply with the new-mechanist strategy. While the key element that defines mechanistic explanations is the fact that the mechanism *produces* the phenomenon that is being explained, bringing a set of entities and activities from certain set up conditions to a termination condition, *no phenomenon is produced by any mechanism* in structural explanations. Rather, structural explanations work because the empirical system whose properties require explanation is identified with a mathematical structure whose properties can be mathematically studied. Structural explanation obtains in virtue of the relations of identity between the empirical system and the mathematical system, irrespectively of the causal mechanisms that bring about the properties in the empirical system. Thus, according to this view, structural explanations could be considered explanatory in Kitcher’s (1989) sense of providing a “unification”, because they (in a certain sense) connect a diversity of empirical systems subsuming them under a set of basic patterns and principles that are mathematical. Notice that the point here is merely epistemological, as no one would in principle deny that the final outcome that is produced in these systems results from the action of causes (see **section 5**). The point that defenders of structural explanation have raised is that, whatever these causes are, they are not structured in a mechanistic way, and knowing them is irrelevant to explain the properties of the complex system—as the techniques used in the Sciences of Complexity demonstrate.

Take the example of the stability behavior of the microbiome, which has been systematically studied in Deulofeu, Suárez and Pérez-Cervera (2019). The stability behavior of the microbiome refers to the well-documented empirical observation that establishes that the species that compose the human microbiome keep their relative densities constant during the human’s lifetime.[[3]](#footnote-3) The stability behavior of the microbiome is counter-intuitive because the microbiome is affected by constant perturbations that, in principle, should alter this stability. Therefore, the fact that the microbiome shows this type of robustness requires an explanation. Deulofeu et al. demonstrate that the stability behavior of the microbiome is not explained in virtue of any mechanism that regulates the microbial species’ densities, but in virtue of the network-like structure that is attributed to the system. They argue that the reason why the explanation of the stability behavior of the microbiome cannot be mechanistic is that, even though there seems to be a model of the mechanism defined in terms of the entities, activities, and their organization, all the details of the causal story that brings about the termination condition—stability behavior—are lost in the complexity of the mathematical analysis. As a mechanistic explanation necessarily requires the existence of a causal story, Deulofeu et al. argue that this explanation is non-mechanistic, but structural. If defenders of the view that all explanations—including structural explanations—are mechanistic want to redefine the concept of mechanism to fit these examples (e.g. Bechtel 2015a, 2015b), they would have to renounce to the requirement of a causal story. But doing so seems to entail renouncing to the most basic ontological commitments of the concept of “mechanism”, as we will explain in **section 4** (see also Issad and Malaterre 2015; Deulofeu, Suárez and Pérez-Cervera 2019).

 In view of the previous example we can assume that a key element of structural explanation is that, rather than relying on the mechanism that causally produces a phenomenon, they rely on the mathematical (network-like) properties of the system. This is a fundamental element of the explanatory strategy that dominates the study of complex systems. Instead of trying to figure out how a phenomenon is causally produced, the structural strategy consists in uncovering the organizational features that generate an emergent property in a system, despite all the possible range of activities that can alter its mechanistic details. In that vein, structural explanations are non-causal—in the mechanistic sense of causality—but are still explanatory of some properties of complex systems, in virtue of the form of organization that these systems realize (Huneman 2018c). In other words, structural explanations rely on some sorts of mathematical properties of the empirical system—its topology, its tendency towards reaching a point of equilibrium, etc.—and abstract away from the causal details that the components of the system engage in and that lead to the realization of the property. The explanation is thus possible in virtue of this abstraction, plus the tendency of the system to realize the property in virtue of its mathematical structure alone.

This overview leaves us with three different and non-compatible types of explanatory strategies. Firstly, *DN strategies*, overwhelmingly used in the physical sciences and that rely on the existence of laws of nature to explain the phenomena in that realm. Secondly, *mechanistic strategies*, commonly used in many parts of the biological sciences—i.e., molecular biology—and that rely on the existence of arrangements of parts whose interaction causally produces a concrete outcome. Thirdly, *structural strategies*, employed in the sciences of complexity and that are based on the existence of a robust tendency in the system whose particular conditions are very hard to change.

1. The Ontology of Mechanistic Explanations in Biology: From Physico-chemical Laws to Mechanisms

As we have pointed out, mechanistic explanations have been—and still are—extremely successful in many parts of biology. But we have not explained the ontological reasons why this is so. To answer this question, we have to deal with two different problems. On the one hand, we should explain how systems that are ultimately governed by physico-chemical laws can coherently be explained by a form of mechanisms, which implies a form of explanation radically different from that of the DN explanatory strategy. On the other hand, the question is how these mechanistic explanations, which are typically reductionist and analytic, could be coherently related with the recent holistic structural approaches. We will try to answer the first question in this section, and we will develop the others in **section 4**.

So, the question we are now asking is how a highly complex domain of lawful physico-chemical relations can give raise to another domain of relations where the units that interact are physico-chemical structures such that their interrelations are neither determined by physico-chemical laws, nor by systemic properties. For, as we explained, to talk about mechanisms it must be implicitly assumed the existence of a world of units—mechanisms—capable of adopting a diverse and potentially indefinite number of relationships with one another in virtue of the nature of the entities that conform the unit, the type of activities they can engage in, and the way in which these entities are organized (cf. Machamer, Darden and Craver 2000; Glennan 2002; Bechtel and Abrahamsen 2005; Craver and Darden 2013; Craver 2007; Arnellos and Moreno 2012). There are three key ideas underlying this conception of mechanisms (cf. Nicholson 2012; Militello and Moreno 2018).

* Firstly, the idea of a stable organization of sets of *constraints* harnessing the action of physical (or chemical) laws. In fact, *what characterizes a mechanism are not the physico-chemical laws, but how the particular arrangement of selective constraints that the mechanism poses harness these laws* in such a way that the phenomena under study are systematically produced (Polanyi 1968). Or, to express it differently, how the model of the mechanism determines the causal story that in turn produces the phenomena that scientists aim to explain, in a way that does not directly depend on the action of the physico-chemical laws that ground the existence of the mechanism.
* Secondly, the notion this set of constraints (the “structure” of the mechanism, or the model of the mechanism) serves a function or purpose. As the Webster dictionary defines it, a mechanism is “a process, technique, or system *for achieving a result*” (italic is ours). Namely, a mechanism is a set of constraints performing an “engineering-like” process.[[4]](#footnote-4) For example, nobody would consider that a random set of rocks, which in a river speed up the flow of water by narrowing the bed, constitutes a mechanism because this effect is not functional. As we said in the definition of mechanism that we introduced in **section 2**, the mechanism needs to produce the phenomenon, that is, it needs to lead the process from a set of initial conditions to the termination conditions.
* Thirdly, the implicit assumption that through processes of arrangement of parts, an open[[5]](#footnote-5) world of functions can be achieved. In other words, the idea is that mechanisms are the result of *compositional* processes of arrangement of parts, namely, the idea of construction.[[6]](#footnote-6)

Interestingly, and connected to these three assumptions, we argue that what is behind the existence of a *mechanistic explanatory strategy* is a system constituted by a set of ontologically mechanistic relations. And behind a mechanistic relation what we find is *a set of* *constraints* operating on statistical thermodynamic flows. By constraint we mean a material structure that, in a given system, harnesses the (lawful) microscopic process (cf. Pattee 1972; Umerez and Mossio 2013) (**Figure 1**). Suppose, for example, a set of chemical reactions. Chemical processes consist of molecular transformations (through chemical reactions) from a set of molecules to another different set. Chemical reactions encompass changes that only involve the positions of electrons, explained in terms of physical (quantum) laws. In addition to these laws, chemical processes are also governed by the second law of thermodynamics, which means that the final products of these chemical processes must be a set of highly stable equilibrium compounds. Thus, we argue that it is precisely the existence of this set of constrains one of the elements that makes mechanistic explanations possible, and ontologically—and epistemologically—distinct from DN explanations.



**Figure 1**. Exemplification of the immune cascade triggered by the process of scratching in patients with dermatitis. The initial trigger, exemplified as a *mechanical disruption*, generates a reaction in different types of cells, which is partially caused by the allergens that bypass the epidermis during initial disruption. The mechanism is complex, involves several entities, and includes cases of loops, but it is mechanistic for it shows how the parts interact after an initial stimuli (scratch) triggers the reaction of the system. The final state is the inflammation of the epidermis. From Cevikbas and Steinhoff (2012).

However, the existence of a set of constraints is still not enough to ontologically distinguish the peculiarity of mechanistic explanations—as they are applied in biology—either from DN explanations, or from structural explanation. In a biological system, what biologists care about are not the chemical laws, but how these chemical laws are harnessed so as to generate a set of biological functions (metabolism, growth, agency, reproduction, etc.). And of course, from the thermodynamic perspective, this implies that these chemical reactions are maintained in far-from-equilibrium (FFE, hereafter) conditions. In a similar way as the engineer explains how a steam machine works by mentioning how the pressure of the steam is harnessed through the specific organization created by the material constraints (pipes, valves, cylinders, pistons, rods, etc.)—rather than by appealing to the fact that chemical laws say that heat produces expansive pressure in steam—a biologist will explain the behavior of living systems by appealing to the organizational structure of their internal constraints (organs, tissues, cells and ultimately, enzymes) that functionally drive the chemical flows. In other words, living systems behave as they do thanks to the organization of their material constraints—mechanisms—and not as a consequence of the laws of chemistry. In that vein, what provides explanatory force—and ontological distinctness—to mechanistic explanations is not only the existence of a set of constraints (this also happens in structural explanations), but *the way in which these constraints are specifically organized in living systems* such that wide repertoires of functional diversity and high levels of structural complexity appear, and generate an open world of functions through processes of arrangement of parts (cf. Arnellos and Moreno 2012, 15-18).

The existence of this specific kind of systems raises a question, though. How can basic chemical processes generate structures that constrain their own dynamics, and that we argue to be what makes the existence of mechanisms possible? The answer is complex, and its understanding is precisely one of the keys to properly conceptualize the origin of life. (Cf. Ruiz-Mirazo and Moreno 2016; Ruiz-Mirazo, Briones and de la Escosura 2017.) This is, roughly speaking, what according to the current scientific knowledge, we can hypothesize. Because of very specific boundary conditions (those of certain parts of the terrestrial surface 3.500MYA), many autocatalytic closed organizations had appeared in which certain compounds and/or aggregated of compounds exerted an action on the neighboring processes such that these processes contribute to the maintenance of the whole set of reactions. In the primitive Earth, driven by the energy of the Sun or by geo-thermal energy, many chemical reaction cycles would have appeared. For instance, a constant flow of energy and micro-porous surfaces would have favored the appearance of FFE chemical cycles leading to the formation of relatively complex organic compounds (Martin and Russell, 2003). The idea of reaction cycle implies gathering together different reactions, i.e., embedding the processes of synthesis—and degradation—of new structures in a SM organization. The “core” of a chemical SM organization is the idea of *autocatalytic cycle*. Autocatalytic cycles are minimal forms of FFE chemical organizations. These systems are not only driven by external boundary conditions: a component—a catalyst—drives the network kinetically, keeping these systems in FFE conditions. A catalyst acts thus as a constraint: a material structure that selectively biases the microscopic lawful processes (in this case, a molecule which, because of its shape, selectively modifies the rates of certain reactions). The crucial point here is that an autocatalytic cycle generates a constraint, since the outcome of the action of the catalyst (the constraint) leads to its own re-production. The cycle therefore is not only maintained by the external set of boundary conditions, but also by the action of the constraint harnessing the underlying chemical interactions so that the process closes itself recursively. In more complex autocatalytic SM systems, it is possible to detect several constraints (catalysts, a membrane, etc.) in action. These diverse constraints should mutually enable their continuous regeneration, generating a cyclic causal regime called “closure of constraints” (cf. Mossio and Moreno 2010; Arnellos and Moreno 2012; Moreno and Mossio 2015). All this shows that the causal regime of biological systems is radically different from that of physico-chemical ones, in the sense that they create a set of material structures that constrain the underlying thermodynamic processes in a recursive way.

Importantly, we must highlight at this point that the initial appearance of constraints does not immediately lead to the origin of mechanisms, as the ontological conditions required for mechanisms are more demanding than the mere existence of a closure of constraints. As argued in Arnellos and Moreno (2012), the first protocells must have been able to exhibit minimal functional differentiation, realized by a system under a closure of constraints with the capacity of self-maintaining its organization. For this to happen, the protocell needs to start generating the basic components of its membrane, so as to keep it separate from its surrounding environment, and to guarantee that the processes that allow its self-maintenance to occur within its boundaries. However, this is still not enough to talk about mechanisms, for mechanisms demand further ontological requirements to be met. Concretely, they demand that some of the primitive set of constraints are organized to produce new functions based on combinatorial processes. That is to say, it is necessary that a very specific type of macromolecular components appear, so that they can play the role of constraints across different and potentially indefinite systems. Only once this happens, the kind of structural complexity that is achieved is such that it can trigger new structural changes and new combinatorial possibilities. And for this to happen, it is necessary that a modular organization emerges, i.e. *a type of organization in which different functional components may be separated and recombined allowing this wide arrange of combinational processes* (cf. Keller 2009). This is the basis for the generation of composite devices able to perform highly specific types of work, namely, *machines* (cf. Militello and Moreno 2018). Recall that, as it has been defined, a mechanism is a structure that performs a function in virtue of its entities, the activities they engage in, and their organization. The orchestrated functioning of the mechanism is responsible for one or more phenomena. Now, it is easy to see that many macromolecular aggregates in the cell fulfill this definition. For example, many proteins are constituted by secondary structures which are organized in rigid parts, whose relative movements can generate different effects, leading to the amplification of small displacements, or other mechanical effects described by a list of words borrowed from the description of machines: lever and spring, ratchet and clamp, etc. (Morange, personal communication). Of course, these material structures could be seen as machines performing a function only within the global organization of the cell.

In sum, though the appearance of systems whose global behavior can be explained through mechanisms requires a relatively high level of underlying complexity, the mechanistic description may ignore a lot of this underlying complexity to provide a successful form of explanation *at the relevant level*. This form of explanation is possible due to the existence of constraints that harness the physico-chemical laws, and to the existence of a global organization of constraints that performs a specific function and allows the regeneration of the set of constraints.

1. The ontology of Structural Explanations: From Mechanisms to Networks and Back

Despite the importance of mechanistic explanations in biology, they cannot fully account for the biological phenomenology. As we said in **section 2**, biological systems are constituted by an enormous amount of interacting entities. Everywhere and at every level of the biological organization, one can observe large sets of entities interacting in parallel (molecules in metabolisms, genes interacting in regulatory genetic networks, neurons connecting each other in neural networks, organisms exchanging chemicals with their neighbors in swarms, species interacting through food webs in ecosystems, etc.). These locally relatively simple interactions, however, often bring forth complex emergent behaviors. And in all these cases, what happens globally cannot be explained through functional decomposition, as we showed for the case of the microbiome, where the emergent stability behavior is not explained because of the causal relationships between the species that compose it, but as a result of the topological structure of the system. Indeed, the set of interacting species generates the global behavior, and thus the emergent property; but it is not possible to explain this behavior by attributing specific functions to each bacterium, or to each species, for many of them can be eliminated (perturbing the system) and the microbiome will keep exhibiting the same behavior.

We refer to these systems as “networks”. By the concept of network is meant a system constituted by a set of units that interact locally in a simple way, where each unit is altered by interactions with its neighbors, and conversely, such that ultimately all units receive influences from all the other units of the system (**Figure 2**). The defining characteristic of a network is the existence of recursion, which implies a closure of the paths of interaction on themselves. For example, a social network is a way of representing a social structure, assigning a graph: if two elements of the set of actors (such as individuals or social organizations) are related according to some criterion (professional relationship, friendship, kinship, etc.), then a line connecting the nodes representing these elements is constructed. Another example is metabolism, which can be viewed as a network. Metabolism could be represented by a system of units (nodes) interconnected (reactions) where nodes are metabolites and reactions are arcs with associated functions. A characteristic of the networks is the emergence of global patterns. These global regularities arise when the entire network is stabilized (a "dynamic attractor"), and in turn the emergence of these global phenomena may affect the behavior of the components of the network.



**Figure 2**. Graphical representation of a random network. The dots represent the *nodes*, and the blue lines that join them represent the *edges*. Different networks have different structure but can be equally used to represent different complex systems. From Javaheripi (2019).

One of the main features of networks is their holism or systematicity, namely, that their global behavior cannot be explained through the detailed knowledge of the behavior of each unit (Jones 2014; Issad and Malaterre 2015; Green and Jones 2016; Deulofeu, Suárez and Pérez-Cervera 2019). Though authors like Bertalanffy had emphasized the importance of holistic processes in biological systems, the mechanistic atomistic strategy was predominant, because until recently no quantitative methods to deal with complex holistic systems were available. Fortunately, as we pointed out in **section 2**, the study of the networks has been developed in the last decades thanks to the tools provided by computer simulation, as well as other mathematical developments. As a result, we have nowadays a new scientific domain called “graph theory” that studies the relation between network architectures and dynamics. This new scientific domain has allowed scientists to study complex holistic systems with strongly and recurrently interacting components showing that, despite their variety, they share certain generic properties (Moreno, Ruiz-Mirazo and Barandiaran 2011).

The scientific approach of complex holistic systems consists essentially in the quantitative study of the conditions under which certain sets of components, once they overcome a point or critical mass of interconnections, lead to the emergence of new global properties. This phenomenon happens in a wide variety of (physical, chemical, biological, neural, ecological, social, computer, etc.) systems, which can be said to be almost universal. But what is of particular interest is that, though the complexity of the dynamics leading to the global behavior of the network is not analytically tractable, there are ways to predict that behavior that rely solely on the level of interconnectedness among the parts of the system. In fact, thanks to the use of computer simulators and numerical methods consisting in a fine-grained step-by-step update and recording of the state of all the interrelated variables of the system, it is nowadays possible to draw the state space of these networks. As Moreno et al. (2011, 318) explain, “the evolution of the system is “synthetically” reproduced in the course of the simulation, rather than deduced for a given time value. Under these conditions, the prediction of the global property requires an enormous amount of parallel computation, where the complexity of the computational simulation is almost equivalent to that of the simulated system. Since sensitivity to initial conditions might be critical, the process is repeated for a wide range of initial conditions and the behavior of the system recorded. A full record of different simulations allows drawing the state space of the system (given certain boundary conditions and specific parameters) so that regular and reproducible patterns of behavior can be observed. Under different network configuration parameters, the rules governing components or boundary conditions can be systematically studied through simulation, and a deeper understanding of the structure-function mapping is gained without a strict decomposition or a one-to-one localization.”

As we said in **section 2**, the explanatory strategy that relies on the network structure of the systems is called “structural explanation” (after Huneman 2018a). Epistemologically, and in contrast with mechanistic explanations, structural explanations do not gain their explanatory force from unveiling the causal (mechanistic) structure of a given phenomenon (or rather, a set of similar phenomena). Rather, structural explanations rely solely on the mathematical organization of the system and presume that the entities and activities will behave in such a way that the phenomenon to explain will obtain, provided that their specific organization is not altered. Ontologically, systems that realize a network-structure *constrain* the behavior of the entities that compose them so that the emergent properties that the system realizes are maintained because the recursive/cyclic action of these constraints, as we explained in **section 3** (see also Arnellos and Moreno 2012, 15-18). The nature of the entities in the system, the type of activities they perform, or the causal paths that they follow are largely irrelevant and, importantly, can be very different across empirical systems that share the same structural explanation, while the final outcome—an emergent and systemic property—does not get altered provided that the organization (or “architecture”) of the system is the same across systems. In that vein, a structural explanation results from the identification of an empirical system with a mathematical structure, and from the ascription of the properties of the mathematical structure to every empirical system that can be ascribed the same mathematical structure (Huneman 2010, 2018a, 2018b; Jones 2014; Deulofeu, Suárez and Pérez-Cervera 2019).

Structural explanatory strategies, in their specific application to network models, can also be considered in a different way, namely, as a tool for predicting the behavior of complex dynamic systems. In this sense, and again in sharp contrast with mechanistic explanations, *network models provide a prediction* of the global behavior of a complex holistic system, rather than an understanding of the relations and functions of their parts—entities, activities. Of course, this second sense is not completely different from the first one, since the behavior of the network is a consequence of its mathematical properties. The difference lies in the fact that whereas the former sense looks for the establishment of similitudes between different empirical systems that have the same mathematical structure (e.g. computers, socials networks, genetic networks, and metabolic networks), the second is more focused on the study of the specific dynamical properties of an empirical complex system (e.g. the microbiome, or the immune system).

This immediately raises a question. What is the ontological reason that makes networks suitable systems for structural explanations? In a sense, the functioning of complex holistic networks can be more easily related to a traditional law-based physical system than to a mechanistic organization. Of course, in a network we have a huge number of observables and, rather than a universal law, we can have different local rules, depending on the type of network we are dealing with—random, small-world, scale-free, etc. The behavior of a complex network cannot be described in a simple set of differential equations, but, as Fox Keller has pointed out, “in a messy complex of algorithms, vast systems of differential equations, statistical analyses, and simulations. Such models can only be successfully formulated in the most intimate back and forth relation with experiment”, (Keller 2005a, 7-8). Despite these mathematical difficulties, a peculiarity of network analysis is that the behavior of the whole system can be calculated, and therefore predicted. This prediction is possible because the level of interconnectedness of the elements within the network, and the way in which they are globally related, generates a structure whose behavior becomes expectable irrespectively of the nature of the entities that interact, or the specific causal paths that they follow. In other words, structural explanations that rely on the network-structure of the system work in virtue of the role of the system in constraining the behavior of the entities that constitute them in a recursive way.[[7]](#footnote-7)

Concerning this last point, William Bechtel and some of his collaborators have recently argued that network explanations are not, in the end, different from mechanistic explanations, provided that the concept of mechanism, and the heuristics dictated by the mechanistic explanatory strategy are understood correctly (Bechtel and Abrahamsen 2005; Bechtel 2015a, 2015b). Bechtel argues that, if we recognize that the boundaries of the mechanism are always imposed by the researcher, we can see that network explanations are not but ways of expanding the boundaries of the mechanism in the search of additional mechanistic components at any level. To quote: “In such cases, [scientists] can relax these boundaries and search for additional entities outside the mechanism as initially construed with which its parts interact or consider longer timescales during which the operations have effects. There is no guarantee that this strategy will always be successful, but when it is, the pursuit of mechanistic explanation is still a useful research strategy. It is important, though, to keep in mind that *it is a heuristic strategy of scientists who delineate mechanism boundaries*” (Bechtel 2015b, 93, emphasis ours).

We agree with Bechtel that the mechanistic heuristic can be applied to the study of systems that operate over longer timescales than those of simple, standard mechanisms. Furthermore, we can concede that part of this is what happens in some cases of network analysis (e.g. prediction of the behavior of specific empirical complex systems) insofar as the model of the mechanism seems to be always included in at least some of these explanations, as argued in Deulofeu, Suárez and Pérez-Cabrera (2019). However, there is a substantial difference that Bechtel does not mention, and that generates a clear difference between the appeal to mechanisms and the appeal to networks in scientific explanation. While in the case of the former, the existence of a specific causal story that brings the mechanisms from a set of initial conditions to a termination condition is necessary, or there is not mechanistic explanation, the same is not true in the case of structural explanations that appeal to the network structure of the system. In the case of the latter, the causal details are irrelevant to provide a successful explanation, and the reason why this is so, we argue, is ontological: in a network system, the set of constraints that is created by the global architecture—conceived in terms of interconnectedness—is such that the global property that emerges can be realized by a set of different causal configurations. This means that even when a network contains mechanisms, their role could be ignored, since the same type of properties could correspond to a variety of underlying mechanisms, as these are individuated according to the specific causal stories that define them.

In that vein, however, network-based analysis does not allow specific interventions in the systems that it explain, for they remain neutral with respect to the causes that bring the phenomena about. It is for this reason that the discovery of the specific type of mechanism becomes necessary to understand how and why a given biological system behaves, as well as to discover specific interventions in the system. But also, notice that despite this, there are ontological reasons to consider these systems different from mechanistic systems. As Fox Keller has argued, “Biological systems are, as we know, extraordinarily complex, but again because of evolution, they are complex in somewhat different ways than systems in physics are understood to be complex: for one, they are always and inevitably hierarchical. Accordingly, familiar notions of emergence, rooted in the non-linear dynamics of uniform systems (gases, fluids, or lattices), are not adequate to the task (…) The central point is that the inhomogeneities and ordered particularities of biological systems are essential to their functioning and hence cannot be ignored; indeed, to ignore them is to risk exactly the kind of biological irrelevance that has historically been the fate of so many mathematical models in biology” (Keller 2005a, 7). And, referring explicitly to the explanatory scope of structural explanations, she argues that “first, power law distributions are neither new nor rare; second, fitting available data to such distributions is suspiciously easy; third, even when the fit is robust, it adds little if anything to our knowledge either of the actual architecture of the network, or of the processes giving rise to a given architecture (many different architectures can give rise to the same power laws, and many different processes can give rise to the same architecture” (Keller 2005b, 1066). In the same line, Huneman admits that structural explanations are incomplete and need to be complemented by mechanistic explanations—and the other way around. To quote:

“So a first kind of relation between mechanistic and topological explanations is that they can be two stages of a complete explanation of the same phenomenon, related in a diachronic way: why does phenomenon X exists? Because of some topological properties Ti of the system X; and why does S have Ti? Because of some mechanism proper to S, its surroundings and parts, etc.” [[8]](#footnote-8) (Huneman 2010, 226)

Accordingly, there are good reasons to look both for mechanisms and for network structures if we try to fully understand biological phenomena.

1. Biological Systems do Require Complex Explanations: How Mechanistic and Structural Explanations Relate

In fact, neither mechanistic nor structural explanations, taken separately, are sufficient to fully understand why biological systems behave the way they do. Let us take the example of robustness. Robustness refers to the ability of a system to keep its properties—e.g. its organization—despite the perturbations it experiences. Very often, network-like models are provided to explain the degree of robustness of a great variety of biological systems (ecosystems, metabolic networks, developmental processes, the microbiome, etc.). On the other hand, at the same type, more local analyses tend to focus on the set of specific mechanisms that causally try to explain why a given type of organization is more robust against perturbations than another one.

But how are these two approaches related in biological systems? In other words, how both of them—being radically different—could notwithstanding provide a valid explanation of some of the properties of these systems? Ultimately, network like models explain robustness by redundancy (cf. Kitano 2004) and/or by “distributed robustness” (cf. Wagner 2005), namely, because the network is such that it contains different and alternative pathways which buffer the outcome despite possible change in one of the nodes. Yet, behind this level of description, a regulatory mechanism could be in place. For example, in the development of full-fledged multicellular organisms, a gene regulatory subsystem exerts a fine-tuned control on how and when early-undifferentiated cells become differentiated and spatially allocated. Notice that there are many examples of multicellular systems genetically homogeneous presenting a certain degree of cellular differentiation without the existence of any (developmental) regulatory subsystem. The problem, however, is that functional coordination is achieved only if the functional diversity is poor, and these multicellular organizations cannot achieve significant degrees of functional integration.[[9]](#footnote-9) Now, although a regulatory mechanism is (as any other mechanism) obviously based on localized functional parts, it could happen that certain parts of the mechanism constitute themselves a network. This is the case of the regulatory genetic networks. To understand why they constitute a mechanism, we have to understand that this epigenetic molecular network constrains functionally the intercellular relations. And it can do this task because it is organized in a special way, namely, operating in a dynamically decoupled way from the level of the processes they constrain according to a higher-level norm (the epigenetic program) (cf. Bich, Mossio, Ruiz-Mirazo and Moreno 2016). But considering the epigenetic domain, these regulatory genes interact with each other recurrently, bringing forth certain topological (structural) properties which, substituting localized action, become the relevant level of control. Thus, in this example, we see that it is the articulation between a functionally distinguishable organization of constraints—the regulatory mechanism—and a distributed recurrent network of (part of) these constraints that, all together, constitute the explanation of how functionally diversified development happens.

This shows that the higher degree of complexity achieved by biological systems requires an organization structured in different (sub)systems interconnected at different levels and time scales. In other words, it requires the creation, within the system, of subsystems that can modify the parameters of other subsystem parts. Since these subsystems work at different rates and with different operational rules, the system has an increased potential to explore new alternative forms of global self-maintenance that are not accessible to ‘flat’ systems without any hierarchy or modularity in their organization. In this way, the higher-level subsystem creates a set of functional constraints on the lower-level dynamics. At the same time, the controlled level plays a fundamental role in the constitution and maintenance of the controller level (and hence, of the whole system).

Therefore, biological systems convey specific forms of complexity that, through holistic-emergent processes (which are continuously taking place), produce both network holistic patterns and new, more complex structures which, in turn, are bound to become selective functional constraints acting on the dynamic processes that underlie those holistic processes. The reason why those functional constraints can be described as mechanisms is that they act as distinguishable parts (or collections of parts) related to particular tasks (e.g., catalytic regulation) performed in the system. So, both aspects are, thus, complementary: the holism of the global network of processes and the local control devices/actions that are required for the system to increase its complexity. Moreover, the newly created and functionally diverse constraints may give rise (once a certain degree of variety is reached) to new self-organizing holistic processes, which, in turn, may be functionally re-organized (cf. Moreno, Ruiz-Mirazo and Barandiaran 2011). In this way, an increase in organizational complexity can take the paradoxical form of an apparent “simplification” of the underlying complicatedness, giving rise to levels of organization in which a mechanistic de-compositional strategy might be locally applicable. The idea, taken originally from Pattee (1973), would be that new hierarchical levels are created through a functional loss of details of the previous ones, thus generating systems where both mechanisms *and* networks are simultaneously realized and co-existent.

1. Conclusions

The organization of biological systems combines holistic processes described in terms of networks and others with distinguishable parts that can be described as mechanisms. What is characteristic of the biological complexity is precisely the entanglement of processes that require locally mechanistic explanations, with others, more global, massively parallel and holistic, whose behavior tends to generate "emerging patterns" and phenomena of "self-organization".This combination can occur at various levels, and can generate new forms of holism, because interactions between functionally distinct parts in a lower level can generate global emerging phenomena in a higher level, and conversely.Therefore, the study of biological systems requires a deep reconsideration of the approaches and methodologies developed so far, aiming at an integration of the mechanistic methodology, based on the analysis of functional parts and the reconstruction of behaviors, with the new network-modeling, based on the discovery of forms of regularity in massively parallel non-linear systems.

It is time to come back to Nagel’s challenge: if, as modern science argues, the grounding of complex level phenomena are but physical systems, science has to explain the relevance of specific forms of explanations for higher level phenomena, namely, why these specific forms of explanations work, and how they are related with the DN type of explanations that are still at work successfully in the “fundamental” sciences. After all, we could not respond to the question of why purely physical elements, when combined in a certain way, can give raise to biological (or mental and social) properties in a “non-magic” way (as Nagel says) only by showing that we have specific ways of explanation for biological, mental or social phenomena that work successfully. It is necessary also to explain how and why these explanations are connected with each other and, above all, to explain how and why they could be connected with the basic explanations of the physical sciences. In this chapter, we have started this task by exploring: first, how the ontology that grounds the validity of mechanistic vs. structural explanations differs, and how this results from the evolution of living systems (**section 3**, **section 4**); second, by arguing how and why these two modes of explanations relate to each other, and explaining why they are sometimes complementary (**section 5**); finally, by connecting all this to the way in which living systems harness the laws of nature to create their own constraints, thus generating their own regime of causation.

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2. It is important to note, although in passing, that the new-mechanist’s commitment to the existence of *causal mappings* between a functional operation and the components that bring those operations about does not necessarily commit all new-mechanists to either to a physical reductionism (e.g., Salmon 1984), or to an “ontic” (e.g., Craver 2014) interpretation of mechanistic explanation. Rather, new-mechanists often assume a hierarchical structure of the world and believe that different mechanisms can be found out at different levels, realized by different entities, activities and forms of organization (cf. Krickel 2018). [↑](#footnote-ref-2)
3. Notice that “species density” is an emergent property of the system, i.e., it only exists in so far as there is a microbiome. We will say more about this in the rest of the paper. [↑](#footnote-ref-3)
4. However, this “engineering-like” process could also be achieved by a non-intelligent agent, like natural selection in non-human made systems. [↑](#footnote-ref-4)
5. “Open” does not mean unlimited. The idea is that parts should be amenable to combinatorial processes, namely, that the combination of parts is not determined by intrinsic, lawful interactions. [↑](#footnote-ref-5)
6. By this we mean a scenario where components can act as building blocks in constructive operations, namely, that parts can be combined in different ways instead of being driven deterministically towards unique aggregates. [↑](#footnote-ref-6)
7. Notice that this requirement is less strict than the ontological requirements to speak about mechanisms, as we said in **section 3**. [↑](#footnote-ref-7)
8. Notice that Huneman uses “topological” to refer to a specific subclass of structural explanations, as he makes clear in Huneman (2018a). [↑](#footnote-ref-8)
9. For a discussion on this point, see Arnellos, Moreno and Ruiz-Mirazo (2014). For a general discussion on regulation and complex functional integration, see Christensen (2007) and Bich, Mossio, Ruiz-Mirazo and Moreno (2016). [↑](#footnote-ref-9)