The Fourth Perspective: Evolution and Organismal Agency

Johannes Jaeger

Complexity Science Hub (CSH), Vienna, Josefstädter Straße 39, 1080 Vienna

Abstract

This chapter examines the deep connections between biological organization, agency, and evolution by natural selection. Using Griesemer's account of the reproducer, I argue that the basic unit of evolution is not a genetic replicator, but a complex hierarchical life cycle. Understanding the self-maintaining and self-proliferating properties of evolvable reproducers requires an organizational account of ontogenesis and reproduction. This leads us to an extended and disambiguated set of minimal conditions for evolution by natural selection—including revised or new principles of heredity, variation, and ontogenesis. More importantly, the continuous maintenance of biological organization within and across generations implies that all evolvable systems are agents, or contain agents among their parts. This means that we ought to take agency seriously—to better understand the concept and its role in explaining biological phenomena—if we aim to obtain an organismic theory of evolution in the original spirit of Darwin's struggle for existence. This kind of understanding must rely on an agential perspective on evolution, complementing and succeeding existing structural, functional, and processual approaches. I sketch a tentative outline of such an agential perspective, and present a survey of methodological and conceptual challenges that will have to be overcome if we are to properly implement it.

1. Introduction

There are two fundamentally different ways to interpret Darwinian evolutionary theory. Charles Darwin's original framework grounds the process of evolution on

the individual's struggle for existence (Darwin, 1859). It is a theory centered around the organism. The neo-darwinian interpretation of the Modern Synthesis, in contrast, sees evolution grounded in the shift of allele frequencies in populations. It completely brackets out the organism, focussing on the lower level of the gene and the higher level of the population instead (see, for example, Walsh 2015; or Amundson, 2005, for a historical perspective). This reductionist approach provided much needed clarity for the study of evolutionary phenomena in the early 20th century. But it hardly does justice to *the complexity of causes underlying evolutionary change* which—through Darwin's struggle for existence—may involve non-trivial contributions of organismic behavior.

Many researchers in the field are aware of this limitation and are trying to move beyond it. The principal aim of evolutionary developmental biology (evo-devo), for example, can be construed as providing causal-mechanistic explanations for the evolution of the complex regulatory processes involved in development (Wagner *et al.* 2000; Calcott, 2009; Brigandt, 2015; DiFrisco & Jaeger, 2019; DiFrisco *et al.,* 2020). The limits of reductionism have also come to the attention of philosophers of biology, and there is much interesting work on the subject (some of which will be discussed here). Unfortunately, progress towards an organismic evolutionary biology remains slow, in part because of the daunting intricacy of the matter, in part because of the lamentable and still widespread identification of "mechanism" with explanations at the molecular level (Nicholson, 2012), but also because many criticisms of reductionism in evolutionary biology remain wide of the mark, failing to properly engage the problem of organismic complexity in a philosophically grounded manner.

One particularly prominent example of this problem is recent talk about understanding the "causal structure of evolution" by addressing the role of "constructive development" and "causal reciprocity" in the context of an "extended evolutionary synthesis" (*e.g.* Laland *et al.,* 2015). *Constructive development*—defined as the ability of the organism to shape its own ontogenetic trajectory—implies some kind of agency, leading to open-ended exploratory evolution, in ways which are never

clearly defined. *Causal reciprocity* emphasizes the mutual influence between ontogeny and phylogeny, or an evolving population and its environment. It is claimed to be widespread and to violate Ernst Mayr's (1961) classical distinction between proximate and ultimate explanations in evolution. One problem is that such claims are hardly original. The constructive role of the organism in evolution goes straight back to Darwin himself (see, for example, Amundson, 2005, or Walsh, 2015), and reciprocal causation is an integral part of many models in classic evolutionary genetics (Svensson, 2018; Buskell, 2019).

However, there is a more serious problem: such shallow theorizing does not even scratch the surface of the causal complexity underlying evolution. It is not wrong. It even goes in the right direction. But it does not go far enough. If we are serious about investigating the complex causes governing evolutionary change, *we must tackle issues such as organismal agency and the fundamentally dialectic nature of evolutionary causation head on*. We must call these problems by their name without avoiding the uncomfortably radical conclusions that might spring from their examination. This is what I am trying to do here.

Tackling the causal complexity underlying the evolutionary struggle for existence is no task for the faint-hearted. The causal structure of evolution is profoundly impenetrable. In fact, I believe that the whole undertaking is completely hopeless, unless it is informed by an adequate ontology and epistemology, specifically developed for the task. Luckily, such a foundation is available in the form of William Wimsatt's *perspectival realism* (Wimsatt, 2007). It properly reckons with the limited nature of our cognitive abilities and the utterly byzantine character of reality. As an added bonus, it takes a differentiated view on the role of reductionism as an epistemic tool in biology, and is antithetical to any quixotic quest for a grand synthesis of evolutionary thought.

At the heart of Wimsatt's ontology lies the recognition that the causal structure of the world resembles a rich and dynamic tropical-rainforest ecosystem rather than the eliminativist desert suggested by traditional ontological reductionism (Wim-

satt, 1994, 2007). In this lush ontological forest, there are areas that exhibit cleanly separated levels of organization, defined as "local maxima of regularity and predictability in the phase space of alternative modes of the organization of matter" (Wimsatt, 2007, p. 209). Examples are the sub-atomic, atomic, and molecular levels studied by physics and chemistry. In other areas of reality, however, this compositional hierarchy breaks down into more localized and less resolved causal structures, captured by *perspectives*—defined as "intriguingly quasi-subjective (or at least observer, technique or technology-relative) cuts on the phenomena characteristic of a system" (Wimsatt, 2007, p. 222). Ultimately, even perspectives break down resulting in *causal thickets*, which are hard to disentangle since they lack any discernible regularity or layering. The causal structure underlying the process of organismic evolution is a perfect example of such an impassable thicket.

Organizational levels and causal thickets require different epistemic strategies. In particular, reductionist methods can be useful, but remain fundamentally limited in the context of *the evolutionary causal thicket* (Wimsatt, 2007). What is needed to assess, complement, and contextualize them is a perspectival approach that aims to cut through the thicket in alternative ways. This refocuses our attention and our limited resources towards important aspects of evolution that are usually neglected in the standard reductionist account of evolutionary genetics.

At first glance, a multiplicity of limited and biased perspectives seems to constitute an insurmountable obstacle for obtaining robust empirical knowledge. There is no way to "step out of one's own head" to gain a truly objective "view from nowhere" (Giere, 2006; Wimsatt, 2007; Massimi, 2016). Upon closer examination, however, an explicitly perspectival approach enriches scientific inquiry into complex causal thickets in two important ways. First, the higher the diversity of perspectives, the wider the range of questions we can ask, and the larger the variety of approaches we can use to answer those questions. Second, comparative analyses of theoretical perspectives yield valuable insights into their respective applicability and limitations, as well as the robustness and consistency of their claims (Giere, 2006; Griesemer, 2006; Wimsatt, 2007; Massimi, 2016). Put sim-

ply, more diverse approaches can lead to broader and more trustworthy insights into complex and entangled processes such as evolution. What we need are more varied and valid perspectives rather than some kind of misguided theoretical synthesis, which is the remnant of an earlier—and by now thoroughly outdated—positivist view of evolutionary biology (Smocovitis, 1996; see also Walsh, 2015).

In this spirit, James Griesemer (2006) suggests a radical change of philosophical focus for evolutionary theory, from selecting the best among competing approaches and generalizing it, towards a comparative analysis of the strengths, weaknesses, and complementarities of different local perspectives. These perspectives are not right or wrong, better or worse, *per se*, but succeed or fail to achieve their specific purpose. Griesemer (2006) distinguishes three kinds of evolutionary perspectives: structural, functional, and processual. To this, I will add *a fourth perspective* here, which emphasizes the agency of evolving organisms. A truly comprehensive science of evolution will have to include all four. Together, they yield more inclusive explanations of relevant evolutionary phenomena than each one of them on their own. In addition, a comparative approach allows us to reveal and assess the abstractions, idealizations, and simplifications that each approach is bound to make. Finally, the robustness of specific claims "can only be assessed if a scientific community pursues phenomena from a variety of perspectives… It is not enough merely to compete." (Griesemer, 2006, p. 363). Is it really that surprising that a field centered on biological diversity would profit from a more diversified epistemic approach?

Furnished with these epistemological tools, we will now embark on a journey that explores the importance of organismic organization and organismic agency for the basic principles underlying evolution by natural selection. This journey starts with an introduction to the central concepts of organizational closure and organizational continuity in section 2. I then briefly recall Lewontin's (1970) minimal conditions for natural selection in section 3. These conditions by themselves may be simple, but their mapping onto the physical world is incredibly complex. To unravel this complexity, we can take structural, functional, or processual perspectives, as de-

scribed in section 4. In section 5, I will focus on Griesemer's (2006) reproducer perspective, a processual view demonstrating that genetic replicators must be deeply embedded in a complex and hierarchical life cycle to be able to multiply themselves. Section 6 reviews why an organizational account of reproduction is necessary to understand such life cycles and, at the same time, implies organismal agency and self-determination. For this reason, agency itself becomes a fundamental aspect of systems that are evolvable by natural selection. This is why we need a forth perspective on evolution. Section 7 presents a very preliminary exploration of what such an agential perspective would look like in terms of its mathematical and explanatory structure. I conclude with some general thoughts on what this implies, not only for evolutionary theory, but for scientific explanation in general.

2. Organizational Closure and Continuity

In this chapter, I focus on processual and agential perspectives on evolution, which revolve around the distinctive *organization* of living systems and how it is maintained—within and across generations—through *continuous regeneration* (Saborido *et al.* 2011; Mossio & Pontarotti, 2020; DiFrisco & Mossio, 2020). Biological organization, of course, is the unifying topic of this volume, and I refer the reader to its introduction for a general overview (Mossio, this volume; see also Moreno & Mossio, 2015). In this section, I will only briefly revisit those organizational concepts that are particularly relevant to my argument.

The organizational account is founded on the basic insight that the important difference between life and non-life is not a difference of composition (what organisms are made of) but a difference in the way that system components relate to each other (how organisms are organized). The central defining feature of biological organization is *organizational closure*, a concept introduced by Jean Piaget (1967), which means that all essential parts of a living system mutually depend on each other, could therefore not exist without each other, and must maintain each other through their collective interactions. Organizational closure is complemen-

tary to thermodynamic openness; in fact, it can only occur in far-from-equilibrium systems. It leads to a causal circularity that is already reflected in La Mettrie's metaphor of the living body as "a spring that winds itself." Organisms are closed to efficient causation (Rosen, 1991): their organization is maintained *from within,* even though matter and energy constantly flow through the system. It is in this sense that organisms are self-making and self-producing: they are *autopoietic systems* (Maturana & Varela, 1974; Maturana, 1980).

Causal circularity and closure are necessary but not sufficient to account for the organization of autopoietic systems. Biological organization also requires a dialectic relationship between the physico-chemical processes that materially compose an organism, and the system-level constraints that act upon them (Montévil & Mossio, 2015; Mossio *et al.* 2016). *Processes* denote various kinds of transformations (such as chemical reactions or the physical rearrangement of cells and tissues) that involve the generation, constitution, alteration, consumption, and destruction of system components. *Constraints* act on processes but remain unaltered by them (at least at the time scale at which the constrained process occurs). Constraints can be external or internal to the system. They reduce the degrees of freedom of the process on which they act. Their effect is strongly context-dependent. Examples of organismic constraints are enzymes, or the vascular system in vertebrates, which catalyze their metabolic reactions and transport blood without themselves being altered at the time scale of the process they constrain.

Just like any other physico-chemical component of a living system, its constraints need to be constantly replaced, repaired, and maintained. Enzymes, for example, decay and must be replenished through the processes involved in protein synthesis. This means that constraints can depend on each other. They are generated by processes on which other constraints are acting. In turn, they can generate other constraints by regulating the processes that produce them. The synthesis of enzymes, for example, depends on ribosomes whose synthesis, in turn, depends on enzymes. If each constitutive constraint in a living system is both dependent on and generative for at least one other constraint, then there is *closure of constraints*,

which represents a specific kind of organizational closure (Montévil & Mossio, 2015; Mossio *et al.* 2016). It means that the constrained overall dynamics of the system determine the conditions for the continued existence of the constraints. In this way, the processes and constraints of a living system logically and materially entail each other. One is required for the existence of the other.

This raises the question of how living processes and constraints co-emerge through their dialectic dynamic interactions. Kauffman (2000) argues that living organization must be powered by *work-constraint cycles*. Incorporating this into the account of Montévil & Mossio (2015), we can say that the constrained release of energy by the organized system provides the physical work required to maintain its existing constraints and to constantly generate new ones. In this way, work-constraint cycles can explain various kinds of self-organization far from equilibrium, but are not yet specific enough or sufficient to account for the emergence, persistence, and propagation of organizational closure in living systems. For this, we need the additional concept of *organizational continuity* (DiFrisco & Mossio, 2020; Mossio & Pontarotti, 2020). It means that closure at any particular time dynamically presupposes closure of constraints that have operated earlier (see Bickhard, 2000). Organizational continuity represents a specific type of causal continuity. The key point here is that the particular organization of constraints in an organism not only can but *must* continuously change for it to maintain organizational closure and to continue living (Montévil *et al.*, 2016; see also Nicholson, 2018). It must engage in a process of continuous regeneration (Saborido *et al.* 2011). Hans Jonas (1966) calls this *needful freedom*—the capacity of living matter to change its form—and the *thermodynamic predicament*—the irremissible necessity for it to do so.

On this view, the organism can be seen as a continuously changing but persistently closed organization of constraints that "lifts itself" out of the thermodynamic background of all possible physico-chemical processes (see, for example, Hofmeyr, 2000; Kauffman, 2000). It does this through work-constraint cycles that recursively actualize a closure of constraints. What this means is that the organiza-

tion of constraints at any point in time—the channeling of physico-chemical processes in certain directions—arises from *within* the organism itself. Due to the condition of organizational continuity, it is a consequence of previous organismic constraints, of earlier organizational closure. For this reason, we cannot predict its temporal evolution from considerations of far-from-equilibrium thermodynamics (or other physical laws of nature) alone. It is in this sense that the organism has a degree of *autonomy* from its environment (Moreno & Etxeberria, 2005; Moreno & Mossio, 2015). The organism generates its own dynamics of unfolding closed constraints. These constraints not only determine the internal constitution of the system, but also its interactions with the environment. Simply put, all organisms possess at least some minimal kind of agency—they "act on their own behalf" (Kauffman, 2000; Moreno & Mossio, 2015, esp. chapter 4).

In this way, the organizational account grounds the teleological notions of *biological function,* as well as *self-determination* and *agency* on naturalistic principles that lie perfectly within the scope of scientific explanation (see also section 7 below). Functional constraints in living systems are defined as those that contribute to organizational closure and continuity (Mossio *et al.,* 2009a; Moreno & Mossio, 2015; Mossio & Pontarotti, 2020). Self-determination arises from the recursive and reflexive diachronic emergence of functional constraints from previous realizations of organizational closure (Mossio & Bich, 2017). Agency is defined as the capacity to internally generate causal effects (actions) that involve interactive functions—those constraints subject to closure which mediate the organism's boundaries and exchanges with its environment (Moreno & Etxeberria, 2005; Barandiaran & Moreno, 2008; Barandiaran *et al.,* 2009; Moreno & Mossio, 2015). Put more simply, the organism selects and initiates the kind of interactions it has with its surroundings. This kind of agency is an observable property of an organism—its ability to cope with a particular situation, to pursue its goals in response to opportunities or obstacles present in its perceived environment (Walsh, 2015).

What is most important to point out here, is that *all these teleological properties are a direct and necessary consequence of the fundamental self-maintaining orga-*

nization of living systems. Anything that is alive can be legitimately described from the perspective of organismic agency and goal-orientedness (Walsh, 2015).

But if such teleological aspects are fundamental—and unproblematic from the point of naturalistic explanation—why do we constantly attempt to explain them away? Why do we ignore them? Why do we not take them at face value, even though they imply profound and radical challenges for our thinking about biological systems and their evolution? What does this mean for what we consider a scientific explanation? These are the kind of questions that will keep us busy throughout this chapter.

3. Minimal Conditions for Darwinian Evolution by Natural Selection

To better understand the close and intricate relationship between organismal organization, agency, and the process of evolution by natural election, we must briefly review the prerequisites for this type of evolution to occur. Ever since Darwin, biologists and philosophers of biology have sought to stipulate the most concise formulation of necessary and sufficient conditions for evolution by natural selection (reviewed in Godfrey-Smith, 2007, 2009). The shortest one I could find is Sober's "Darwinian general principle:" "*if* there is heritable variation in fitness, *then* there will be evolution" (Sober, 1984, p. 28, original emphasis).

The most cited core requirements are those first published in Lewontin (1970) and, slightly revised, in Lewontin (1978), which state that the process of evolution by natural selection is based on three fundamental principles or propositions: (1) *the principle of variation*: there is variation in physiological, ontogenetic, morphological, and behavioral traits between individuals in a population; (2) *the principle of heredity:* this variation is (at least in part) inherited such that offspring resemble their parents; (3) *the principle of differential fitness*: different phenotypic variants vary in their influence on the rate of survival and reproduction of their bearers in different environments, leading to different numbers of offspring in ei-

ther immediate or remote generations. While these principles hold, a population will undergo evolution by natural selection.

There are many more elaborate formulations of these conditions, and it has been pointed out that any simple enumeration of core requirements provides more of *a recipe for evolutionary change*, rather than a true summary that encapsulates all cases of evolution by natural selection (Godfrey-Smith, 2007). For the purposes of my argument, a recipe will suffice. It is absolutely not my intention to defend any kind of adaptationism stating that evolution occurs by natural selection only. Quite the contrary, my interest here is to explore a new perspective on what makes such evolution possible in the first place. In this spirit, I will continue my argument by reviewing three existing perspectives on evolution by natural selection before adding a new one to the canon.

4. Three Different Perspectives on the Evolutionary Causal Thicket

The minimal conditions for evolution by natural selection appear deceptively simple. However, the path to understanding how they map onto physical reality is complex and full of conceptual pitfalls. One particularly important aspect of this problem concerns the connection between population-level descriptions of evolution and the underlying causal structure of the process, which is ultimately rooted in Darwin's famous struggle of individual organisms for their survival (Walsh, 2015; see section 1). It seems unlikely that population-level statistical averages (*e.g.* mean and relative fitness measures) and emergent properties (arising from interactions of individuals and their environment) will suffice to explain all aspects of these highly complex and heterogeneous underlying causal dynamics at the organismic level. But what kind of understanding *can* be gained at this underlying level? Considering the immensity, diversity, and complexity of individual-level causal interactions, is it possible to gain any foothold at all? This question not only remains unresolved, but mostly also unasked in current evolutionary biology.

One way to unravel the evolutionary causal thicket is to distinguish different perspectives that can validly be adopted to tackle the central problems related to evolution by natural selection. As already mentioned, we can distinguish three kinds of perspectives on evolution by natural selection (Griesemer, 2006). Each of these perspectives focuses on a different set of questions, and has different advantages and limitations. I will briefly review each of them (with examples) and show how they relate to one another.

1. *Structural perspectives* focus on *what* evolves. The most famous debate in this domain is concerned with the units of selection (Lewontin, 1970). Approaches within this perspective consider evolving lineages as organizational hierarchies of compositional levels (molecules, organelles, cells, tissues, organs, organisms, populations, and species). They ask at which level (or levels) selection applies and attempt to identify the pertinent structural units on which it acts. Such units must meet the minimal conditions for evolution by natural selection through completing the circle of development, reproduction, and selection (Brandon, 1990). Evolutionary change is treated as change in unit structure. Structural approaches are indispensable for the investigation of multilevel selection. They are powerful tools for the formalization of selection and inheritance. Their main weaknesses are that they leave unexamined the evolutionary origin of the multilevel hierarchy they presuppose, and that they have difficulties accommodating inter-level processes such as development (which maps changes at the genetic level to phenotypic ones; see Griesemer, 2000a,b, 2006, for details).

2. *Functional perspectives* focus on *why* things evolve. A well known example is the replicator-interactor perspective developed by Dawkins (1976, 1983) and refined by Hull (1980, 1981, 1988). Replicators are entities able to transmit their structure directly and (relatively) intact through a copying process that produces more entities like themselves. Interactors, in contrast, are entities that engage with their immediate environment in ways that lead to differential replication. The focus here is not on the exact structure of either repli-

cators or interactors (even though the former are generally assumed to be genes, and the latter organisms), but on the functional roles they play in generating the minimal conditions for evolution by natural selection. Dawkins and Hull differ on this matter. While Hull acknowledges selection of interactors at multiple compositional levels, Dawkins only recognizes replicators as true units of selection, since they alone are stably and faithfully copied and transmitted through the germ-line from generation to generation (see Griesemer, 2005). Apart from being the cause of inheritance, replicators also determine the development of the interactor's phenotypic traits, and even the construction of environmental features such as beavers' dams and human megacities, as proposed by Dawkins' (1982) perspective of the "extended phenotype." The environment then acts as a filter on populations of interactors, allowing some to survive and reproduce better or worse than others, depending on what kind of (extended) phenotypes are encoded by their replicator genes. This leads to a clean separation of development and inheritance. These processes do not interact directly, even though they share replicators as their common cause. Its conceptual simplicity is the main advantage of this perspective. At the same time, its failure to accommodate causal interactions between the processes of development, selection, and inheritance is also its biggest shortcoming. It leaves the functional separation of these processes unexamined, presupposing an excessive form of genetic determinism instead, which leads to an extremely oversimplified replicator/gene-centered view of evolution. Another problematic aspect is that both replicators and interactors are defined in circular ways that implicitly depend on goal-oriented processes (*i.e.* replication and the interaction of the organism with its environment), which are simply taken for granted (see Griesemer, 2006, for details).

3. *Process perspectives* focus on *how* evolutionary change occurs. As their name indicates, these perspectives focus on processes as the basic units of evolution. One example of such a perspective is process structuralism, which aims to understand the law-like behavior of developmental processes that generate

biological form (Goodwin, 1982a,b; Webster & Goodwin, 1982, 1996). It describes these generative processes as morphogenetic fields, whose underlying causal structure determines their dynamic behavior and the kind of phenotypic transitions they can produce. A methodical exploration of these structures through dynamical modeling and simulation would result in a rational system of related forms and the transformations between them. This provides an ahistorical "space of the possible," which the historical process of evolution explores. In this sense, process structuralism provides an understanding of the structured variability that provides the substrate for natural selection to act on. This is something neither structural nor functional perspectives can provide. But there are two main drawbacks. First, the rules behind the processes that generate variability are assumed to be universal and time-invariant, an assumption that is no longer tenable (see section 6). Second, process structuralism only deals with regular phenomena in evolution. However, the generic forms that are actually realized in evolution are probably only a tiny fraction of all possible forms, which means that contingency probably still plays a dominant role in evolutionary dynamics (Griffiths, 1996).

Developmental systems theory (DST) is another example of a process perspective, which addresses this problem of contingency (Oyama, 1986; Oyama *et al.* 2001). Its basic unit is a developmental system, a process which is organized through the interactions of a variety of developmental resources in ways that lead to the completion of the life cycle. The precise structure of these interactions is not the focus here, since it is assumed to be a contingent product of evolution by natural selection. Instead, DST emphasizes the distributed and decentralized nature of control in evolving developmental systems. On this view, the transformation of biological form not only requires genetic resources, but also epigenetic and environmental factors that are treated as equally important. In other words, the entire developmental system, rather than the gene, is the replicator (Griffiths & Gray, 1994). The main weakness of the approach is, however, that the boundaries of a developmental system

are extremely difficult to define. This makes it hard to represent different modes of inheritance or to delimit life cycles between parents and offspring (see Griesemer, 2000a, 2006, for more details).

Traditionally, all of these perspectives are seen as competing with each other. DST, for example, explicitly positions itself as an alternative and a replacement for process structuralism (Griffiths, 1996). However, the existence of generic forms and more or less plausible evolutionary transformations does not deny the importance of historical contingency. Both can be seen as complementary aspects of the evolution of form. Similarly, functional approaches—in their unbridled ambition to provide a complete and unified account of evolutionary change—often treat structural or process perspectives as superfluous. However, we have seen how these perspectives can cooperate in a debate about the nature of the replicator. Griesemer (2006) expands on this topic by introducing his own process perspective, which sheds light on the nature of biological multiplication. This *reproducer perspective*—originally developed as a tool to investigate major transitions in evolution (Griesemer, 2000c)—powerfully illustrates how we can identify and transcend the limitations of specific approaches through an inclusive and comparative perspectival framework.

5. Reproducers, Evolvability, and the Completion of the Life Cycle

The reproducer perspective takes a closer look at the process of biological replication (Griesemer, 2006). In the previous section, we have seen that Dawkins' ultra-reductionist functional approach considers replicators as the only valid units of evolution. They alone are transmitted stably and faithfully through the kind of template-based copying process—exemplified by semi-conservative DNA replication—that is presumed to form the basis for heritable variability. We have also noticed the circularity of their definition: replicators are essentially defined as structures able to replicate, which takes the seemingly goal-oriented process of replica-

tion itself for granted, leaving its underlying principles (and its origins) unexamined.

Can this circularity be avoided? To find an answer to this question, we have to examine the rules underlying the copying process. Specifically, to be a proper unit of evolution, an entity must adhere to the following three principles (Szathmary & Maynard-Smith, 1993): (1) *the principle of multiplication:* entity *A* must give rise to more entities of type *A*; (2) *the principle of heredity:* entity *A* must produce entities of type *A* (not *B*); (3) *the principle of variability:* the copying process is not perfect such that, every so often, entity *A* will give rise to an entity *A'* (which, in fact, may be identical to entity *B*). If we add different copying rates for different entities, we arrive back at Lewontin's minimal conditions for the process of evolution by natural selection as described in section 2. What is new in this approach centered on the unit of evolution is an explicit focus on the notion of biological "multiplication."

What does it mean for an entity *A* to give rise to more entities of type *A* in an evolutionary context? And which conditions must be met for this process of biological multiplication to result in principles of heredity and variability that enable evolution by natural selection? There are several reasons to suspect that simple template-based replicators fail to meet these conditions. They are all connected to the problem of *evolvability:* the capacity of a system to generate (at least potentially) adaptive variability (Wagner & Altenberg, 1996).

The first of these reasons is that template-based copying by itself is too fragile and imprecise to support the kind of stability that is needed for the evolution of complex living systems. This argument is rooted in Eigen's paradox (Eigen & Schuster, 1977, 1979). In its original formulation, it states that the production of complex enzymes requires a large and complex genome, while the replication of a large and complex genome requires complex enzymes (necessitating a complex and precisely regulated cellular environment). More specifically, the enzymes required for genome replication must be able to proof-read, *i.e.*, to correct errors in

the copying process. Without proof-reading, complex genomes would be too unstable to evolve: copying mistakes would rapidly accumulate over time, inducing an *error catastrophe* that causes the collapse of the organization of a living system. This sets a very narrow upper limit on the size and complexity of evolvable genomes. But even if most mutants would be viable and able to reproduce (as may be the case in viral evolution), the original genome would quickly be lost in a sea of different variants, leading to the inevitable dilution and disappearance of any evolutionary lineage.

How could this fundamental limitation on the evolvability of complex living systems be overcome? One way is through compartmentalization and the hierarchical organization of living systems. Szathmary and colleagues have formulated a *stochastic corrector* model, which shows how compartmentalized probabilistic replicators can overcome Eigen's error catastrophe by constantly being selected at the higher level of the compartment population (Szathmary, 1986; Szathmary & Demeter, 1987; Grey *et al.* 1995; Zintzaras *et al.*, 2002). This indicates that multilevel composition may be required to render an evolutionary unit evolvable.

Alternatively, it has been proposed that autocatalytic processes could lead to stable self-maintenance without complex genomes or hierarchical organization. Based on this general idea, Eigen & Schuster (1979) developed their own minimal autocatalytic model, the *hypercycle*, as a proof of concept. Unfortunately, hypercycles were shown to be extremely vulnerable to "selfish" replicators within them. In the meantime, Stuart Kauffman (1971, 1986, 1993) was proposing more general and robust models for autocatalytic sets. Kauffman's models consist of networks of chemical reactions that are capable of self-maintenance through catalytic closure: every reaction within the set is catalyzed by at least one product of the network itself. Even though this avoids error catastrophes, it is difficult for autocatalytic sets to generate the kind of variability that evolution requires. In stark contrast to the fragility of template-based replication, these sets are too rigid, since any reaction that does not contribute to the self-maintenance of the network is quickly outcompeted. Because of this, the system strongly converges to one particular optimal and

invariant set of autocatalytic reactions (an attractor in the sense of being a strongly self-maintaining organization), which leaves very little heritable variability for selection to act upon (Fontana & Buss, 1996).

All of this suggests that Lewontin's minimal conditions on their own are not quite sufficient. They remain ambiguous. Evolution by natural selection not only needs heritable variability, it needs *the right amount of heritable variability in the right context*. Neither systems that are too stable, nor systems that are too unstable can evolve. Stuart Kauffman famously illustrated this by his metaphor that evolvable systems must be poised "at the edge of chaos," a dynamic regime including "islands of chaos" among a "percolating network or order" (Kauffman, 1993). Whatever we make of this metaphor, it is certainly true that the principle of variability imposes more specific and stringent conditions on evolution than is evident at first sight, and that some sort of self-organization within the context of a hierarchical organization is required for natural selection to occur.

Based on the argument so far, let us take a closer look at the self-organizing processes able to generate the kind of heritable variability required for evolution. There is another reason why biological multiplication must be more complex than a simple template-based copying process. Copying does not require any material continuity between generations. Copies must resemble their template in form (*e.g.* similar genetic sequences), but can be made of different material components (the bases that are incorporated into the newly synthesized strand of DNA come from outside the original double helix). In this case, there is a clear separation between copying cycles: we can precisely determine when one cycle ends and another one begins. In contrast, biological multiplication always involves some *material overlap* between parents and offspring, between reproducer and reproduced. Organisms arise from material components of other organisms, and they do this in a gradual manner.

This implies some kind of *development,* which can be defined in a broad and minimal sense as "acquiring the capacity to reproduce" (Griesemer, 2006). Unlike the

common (and narrower) definition of development as "embryogenesis" or "morphogenesis," this more general concept applies to unicellular and multicellular life forms alike. To come back to Eigen's example: a mitotic cell must first replicate its genome before it can divide again. This qualifies as "development" *sensu* Griesemer. To avoid confusion, I will use the term *ontogenesis* to describe the totality of regulatory processes—metabolic, physiological, developmental, and behavioral—that are involved in acquiring the capacity to reproduce.

This brings us to a central point of the argument: it is the process of ontogenesis which must provide the error-correcting capabilities that are needed to produce the kind of heritable variability required for evolution by natural selection. Both template-based replicators and auto-catalytic networks lack ontogenesis, which is why they are not properly evolvable. In Eigen's example, a complex genome cannot be faithfully replicated unless it is embedded in the kind of complex and precisely regulated cellular environment which provides the necessary proof-reading enzymes. Genome replication only ever happens if it is embedded within the more complex context of a cell cycle (even in those cases where the resulting cells do not separate completely). This illustrates the fundamentally dialectical relationship between ontogenesis and reproduction in evolution. They logically and materially entail each other. This relationship goes beyond mere causal reciprocity (see section 1). Ontogenesis and reproduction do not only influence each other, *but cannot exist independently*—they *must* co-emerge for organisms to be evolvable. They dynamically presuppose each other (Bickhard, 2000). The resulting system is a true unit of evolution called *a reproducer* (Griesemer, 2006).

Reproducers are more complex than replicators, since they include ontogenesis and material overlap between generations. Ontogenesis and reproduction together form the *life cycle* of the reproducer. *This life cycle must be completed* for biological multiplication to continue from generation to generation. Variability cannot disrupt life-cycle completion without disrupting evolution. In other words, freshly multiplied entities *a* must be *organized* in a way that enables them to mature into entities *A*, which have the capacity to reproduce. Otherwise, they are not evolv-

able. This constitutes a *principle of ontogenesis* (or *development*), which we must add to the principles of multiplication, heredity, and variability to define a proper unit of evolution (Griesemer, 2006).

One additional point requires our attention. In principle, ontogenesis could be based exclusively on some robust but spontaneous process of self-organization. However, this alone does not allow for natural selection to occur: in such systems, there is no true heredity of organization (beyond parents and offspring sharing the physical context that enables self-organization) and thus no selectable heritable variability. Moreover, it is quite probable that, even if they could evolve, purely self-organizing reproducers would easily be outcompeted by those possessing some kind of inherent hereditary processes, which lead to a much more efficient and stable propagation of organization across generations. Thus, heritable variability must be reliably re-generated and re-established through ontogenesis during each generation. For reproducers to meet the minimal conditions for evolution by natural selection, they not only require ontogenesis and material overlap between parents and offspring, but also some kind of inter-generational *continuity of organization* that allows for heritable variability to be re-generated. The precise nature of this kind of organizational continuity will be the focus of section 6.

In the reductionist framework of Dawkins, the source of organizational continuity is located entirely within the replicators themselves: it is the genes alone that are transmitted across generations, and genes alone determine the phenotypic traits of the interactor. This presupposes, however, that replicators are able to reproduce (complete a life cycle) all by themselves. Unfortunately, we have just shown that this is not the case: the simple template-based copying process on which replication is based fails to provide proper principles of heredity and variability for evolution by natural selection. To put it more simply: *replicators can only evolve if they are embedded in the more complex dynamics of a reproducer process* (Griesemer, 2006). The reproducer perspective therefore absorbs and replaces functional perspectives based on replicators as the fundamental units of evolution. The latter may still be useful to study the evolutionary role of genetic replication

—but they can no longer serve as the foundation for a comprehensive theory of evolution. What the reproducer perspective offers is no extended synthesis, but rather evolutionary theory put back on its original Darwinian footing (see Walsh, 2015). A couple of examples will serve to illustrate this fundamental point.

The simplest reproducer systems that we currently know of are infective prions and virus particles. Because of their self-assembling structure, they are the closest we have to a "naked" replicator in nature. The mature, infectious forms of these entities self-aggregate from their macromolecular components according to simple thermodynamic principles. Thus, at first glance, they appear to lack proper ontogenesis or organizational continuity as defined above. However, this appearance is misleading. To generate their macromolecular components, prions and viruses rely on the pathways for biosynthesis and the homeostatic maintenance of the cellular milieu in a living host. These cellular processes are necessary to provide the substrates and the appropriate conditions for self-aggregation to occur. Moreover, both biosynthetic pathways and homeostatic mechanisms are central features of the host's self-maintaining organization (Hofmeyr, 2017). They provide the organizational principles required for prions and viruses to acquire the capacity to reproduce. Therefore, prions and viruses are not evolvable at all, if considered as isolated replicators apart from their hosts. In order to evolve, they *must* be embedded within a reproducer—the complex ontogenetic processes that constitute their host's life cycle (see Moreno & Mossio, 2015, chapter 4, for a more detailed discussion).

As a second example, let us look at multicellular animals, which are vastly more complex than prions and viruses. They are particularly interesting in our context, because of their exceptionally well-defined separation between germ-line and soma. As we have seen in section 4, the strict separation of reproduction (germline) and development (soma) is a central postulate of replicator-inheritor theory. But even in this case, replicators must be embedded in the larger context of a reproducer process in order to propagate and evolve. In fact, there are replicator processes at multiple levels of organization. We have already seen that the replication

of a genome only ever occurs in the context of a cell cycle. At the tissue level, the maintenance and proliferation of germ cells requires a specific niche within the context of the larger multicellular body. Finally, at the organismic level, animal reproduction relies (at least to some extent) on the behavior of the organism, its complex and goal-oriented interactions with the environment and other members of its species. We'll revisit this important point in section 6.

Let me emphasize the main point of the argument once again: replicators cannot be the fundamental units of evolution unless they are embedded in a reproducer system, which necessarily includes a process of ontogenesis that generates the kind of heritable variability needed for evolution by natural selection. With this in mind, we can now reexamine the nature of a replicator. The ontogenetic process underlying replication must have the specific character of a *coding system* (Griesemer, 2006). To complete the replication cycle, ontogeny must produce an interactor. The traits of this interactor must somehow be *encoded* in the genome. For this to work, the number of possible states in such a coding system must vastly outnumber the actual states that occur in an evolving population. This kind of coding process is what allows for a separation of genotype and phenotype. Without the cell to interpret and replicate it, however, there is no sense in which the genome carries a code (see Waddington, 1957). Therefore, replication must be seen as a highly specialized and context-dependent ontogenetic process, embedded in a hierarchy of reproductive organizations. As stated in no uncertain terms by Griesemer (2006, p. 359): "Far from being master molecules, genes are prisoners of development, locked in the deepest recesses of a hierarchy of prisons" (see also DiFrisco & Jaeger, 2020).

6. Organization, Reproduction, Agency, and Minimal Evolution

The reproducer account blurs the distinction between structural, functional, and processual perspectives. It shifts our focus from replicators to the more general category of reproducers as the fundamental (processual) units of evolution. Con-

sidered from a functional point of view, the central question about biological multiplication shifts from a simple template-based copying process (replication) to the propagation of complex *biological organization* across generations (reproduction). What are the heritable organizational principles that enable the reproduced system to acquire the capacity to reproduce? What are the heritable organizational principles that govern its ontogenesis and the completion of its life cycle through reproduction? Griesemer (2006) argues that these principles have to be based on some kind of organized *material propagules*, not mere informational programs as in a replicator perspective. These propagules must not only account for ontogenesis to explain self-maintenance, self-production, and self-regeneration within a life cycle, but must also form the basis for *an organizational account of reproduction.*

There are several such accounts in the literature. The ones I will focus on here extend the notions of organizational closure and organizational continuity (see section 2) across generations, beyond the temporal boundaries of the individual organism (Christensen & Bickhard, 2002; Saborido *et al.* 2011; Mossio & Pontarotti, 2020; DiFrisco & Mossio, 2020). One option, from a functional point of view, is to treat entire reproductive lineages as organized systems (Christensen & Bickhard, 2002). However, such higher-order organization remains difficult to delineate precisely. Instead, we can take a more focused approach and consider the reproducer-reproduced dyad as a continuously organized system (Saborido *et al.* 2011). The important point here is to distinguish the boundaries of self-maintaining organization from the boundaries of the individual (DiFrisco & Mossio, 2020).

On the one hand, reproducer and reproduced can be considered the same organized system since there is organizational continuity between the two: closure of constraints must be maintained throughout the process of reproduction. An egg cell, for example, is both the product of the organization of the reproducer as well as the source of the organization of the reproduced. It exerts its function within the context of a cross-generational organization (Saborido *et al.* 2011; Mossio & Pontarotti, 2020). On the other hand, the reproduced system is not the same individual as the reproducer. In fact, reproducer and reproduced often continue to co-exist,

more or less independently of each other. In this context, they must be treated as different organized systems. But there is no contradiction here, just a simple distinction: what sets apart reproduction from ontogeny is not a break in organizational continuity, but a difference in the number of organized systems that are present at a given moment (DiFrisco & Mossio, 2020). Discontinuities between generations are characterized by fission (*e.g.* nuclear or cellular division, budding, or birth), or fusion (*e.g.* gametic, in case of sexual reproduction) of organized systems. A fertilized egg cell is the product of the functional organization of two different reproducer systems. It is dynamically presupposed by both of them (Bickhard, 2000).

On this view, the reproductive process is seen as the means of an organism to maintain its organization beyond the boundaries of its individual life cycle despite the discontinuities that characterize reproduction, and reproductive functions are those that contribute to inter-generational closure. But what exactly is meant by organizational continuity across generations? This concept clearly goes beyond mere material overlap through propagules (Griesemer, 2006), and it is more specific than the general notion of shared developmental resources (Griffiths & Gray, 1994). We have already seen in section 2 that organizational continuity is a special case of causal continuity. Now that we have extended it to organizational closure across generations, it enables a new principle of heredity as *continuous self-maintenance of cross-generational functional organization* (Mossio & Pontarotti, 2020). Remember that this does *not* imply that any specific physical structures or components of the system must persist unchanged through reproduction. Structure and material composition are in constant flux. What persists is the organization required to acquire the capacity to reproduce a specific kind of biological entity, a disposition for recurrent ontogenesis where similar functional constraints reoccur at the time scale of each generation (Mossio & Pontarotti, 2020).

This organizational account of the reproducer affects several of the principles that underlie the minimal conditions for evolution by natural selection. Most important of all, it renders the replicator obsolete, and replaces it with reproducers as the

proper units of evolution. Furthermore, it suggests a new organizational principle of heredity: conservation of cross-generational functional organization, which requires organizational continuity. This kind of heredity enables and at the same time also depends on a new principle of ontogeny: the capacity to reproduce must be re-acquired during each generation in order to complete the life cycle (Griesemer, 2006). The flip-side of both principles of ontogeny and heredity is a revised principle of variability (Montévil *et al.*, 2016): variation can only occur under the general constraint of maintaining organizational closure within and across generations. Without this kind of cross-generational organizational continuity, life cannot go on and evolution cannot occur. In summary, we end up with the following set of tightly interlocked principles: *a new principle of ontogeny, radically revised and refined principles of heredity and variation (plus Lewontin's unchanged original principle of differential fitness)*. Together, they comprise an extended and disambiguated set of minimal conditions for *an organizational theory of evolution by natural selection, which has the organism (and its struggle for existence) back at its core,* as it was in Darwin's original theory (Walsh, 2015).

But this is not all. Behind this revision of the minimal conditions for evolution by natural selection lies an even more significant implication for evolutionary theory. It is rooted in the simple fact that organizational closure must be retained throughout ontogeny and reproduction for a life cycle to be completed. And the life cycle must be completed for evolution to occur. In other words, *without organizational continuity and the functional conservation it enables, there is no reproducer, and thus no proper unit of evolution. Without organizational continuity, there are no evolvable systems.*

If we accept this general conclusion, we must face another profound consequence: any proper unit of evolution, any evolvable system, must involve some kind of agency. It must be based on an autonomous system with some degree of self-determination, since self-determination and autonomy are fundamental properties of organized systems (see section 2). This is even true for the example of prions and viruses from section 5: they require a host with organizational continuity (and thus

agency) to reproduce and evolve. It may come as a surprise, but *evolution by natural selection is always the evolution of autonomous self-determining agents*, or occurs in higher-level organized systems—such as eco-systems, cultures, or economies—that involve autonomous self-determining agents. This basic insight has important implications for the theory of evolution. But what are these exactly? What does it mean to look at evolution from an *agential perspective*?

7. The Fourth Perspective: an Agential Theory of Evolution

Before I outline the possible shape of an agential theory of evolution, it is important to reiterate what agency is, and what it is not. Most importantly, *agency is the capacity of an organism to originate causal effects from within its own boundaries* (Barandiaran *et al.,* 2009), particularly those that define its interactions with its external environment (see section 2). These effects are observable as goal-oriented actions—selected from a more or less ample behavioral repertoire—which enable the organism to attain its ends by taking advantage of opportunities or avoiding obstacles in its experienced environment (Walsh, 2015). Biological organization and continuity provide the self-determination and autonomy necessary for true goal-oriented agency (*cf.* sections 2 & 6). Shadlen and Gold (2004) call this kind of relative autonomy "freedom from immediacy." While the organism's actions arise from its interactions with its environment, they are not directly imposed or determined by it.

This kind of *agential emergentism* (Walsh, 2015) stands in strong opposition to the more traditional approach to "agency" in evolution, which was first introduced by Ernst Mayr, and is still widely shared by biologists today. Mayr (1961) popularized the notion of *teleonomy* to denote preprogrammed behavioral routines that *appear* goal-seeking because they are adapted to their environment through evolution by natural selection. On this view, there are no causal effects (no actions) that are generated within the organism. Organisms have no intrinsic goals. There is only automated processing of external stimuli into responses adapted to a given

environment. In other words, *there is no true organismic agency*. Adapted behaviors are explained entirely by factors in the external environment. The environment poses problems that organisms solve through evolution by natural selection (Lewontin, 1978; Levins & Lewontin, 1985). While denying true agency to organisms, this view can lead to the strange result that information-processing becomes interpreted as cognitive ability in simple organisms without a nervous system (*e.g.* bacteria; see Fulda, 2017, for an excellent critique). Such paradoxical consequences arise because the conventional view does not take agency quite serious enough—as it does not even include true agency in its ontology.

What happens to evolutionary theory if we *do* take agency at face value? Walsh (2015) provides a very thorough philosophical analysis of this question, and concludes that a number of implications follow from agential emergentism. First, evolution must be treated as a fundamentally *ecological* or *relational phenomenon* arising from the purposive engagement of the organism with its experienced environment (Darwin's struggle for existence). Second, it is not possible to causally separate the processes of inheritance, reproduction, and development: "fragmented" evolutionary theory is an idealization. Third, there is no privileged control by replicator genes: genetic causation always has to be interpreted in its organismic context (see also DiFrisco & Jaeger, 2020). These insights do not fundamentally differ from claims made by other movements towards a more organismic evolutionary biology, such as the extended evolutionary synthesis (Laland *et al.,* 2015). However, there is a central question that an agential theory of evolution raises, which remains largely unexplored by other approaches: *how does true organismic agency impact evolutionary change?* Timid first steps towards an exploration of this question have been made in studies of phenotypic plasticity (*e.g.,* West-Eberhard, 2003; Moczek *et al.,* 2011; Levis & Pfennig, 2016; Uller *et al.* 2019) and niche construction (*e.g.,* Odling-Smee *et al.,* 2003; Scott-Phillipps *et al.,* 2014; Uller & Helanterä, 2019). But so far, none of these efforts incorporate the dialectic multilevel dynamics underlying biological organization and the goal-oriented behavior of the organism. They remain anchored in a flattened and shal-

low cybernetic view of "agency" as information-processing and feedback-driven goal-seeking.

Why is that so? The problem is as simple as it is fundamental: because of the widespread mechanistic distrust concerning the notion of purposiveness, we do not possess the conceptual and mathematical tools required to appropriately incorporate true organismic agency into models of evolutionary dynamics. This is why we'd rather pretend the phenomenon does not exist, rather than taking it seriously. In fact, there are three related epistemological and methodological issues that need to be considered here.

The first issue concerns the general nature of our scientific theories, which predominantly fall under what Lee Smolin (2013) has called the Newtonian paradigm, or "physics in a box," and which Rosen (1991) identifies with mechanistic reductionism. Theories that adhere to this paradigm are *object theories*: they describe and explain the dynamics of a set of objects in a predefined space of possibilities (the bounded "box" or *configuration space* of the system). There is *transcendence*: the behavior of the objects is determined entirely by principles (forces, laws, etc.) that are outside and beyond themselves. There is an *explanatory asymmetry*: these principles determine the properties of the objects, but the objects do not explain the principles. The traditional teleonomic account of "agency" outlined above corresponds to an object theory. It must avoid invoking actions generated from within the organism at all cost, otherwise it would no longer comply with the rules that define an object theory. This is why it fundamentally fails to capture the nature of true agency in the first place.

An *agential or agent theory* of evolution is a fundamentally different kind of theory (Walsh, 2015). It does not conform to the Newtonian paradigm. Organisms become both the subject and the object of evolution (Levins & Lewontin, 1985). There is *immanence:* agents themselves cause changes in their own state and organization, through interactions with their perceived environments (see also Fontana & Buss 1994, 1996). There is *explanatory reciprocity*: agents both generate and

respond to the conditions of their existence. There is no predefined "box" or configuration space. There is no list of prestatable possibilities. Agents generate their own rules internally, which is what enables their autonomy and, ultimately, their open-ended evolution (Kauffman, 2000, 2014; Ruiz-Mirazo *et al.,* 2004; Longo *et al.,* 2012). Some things in evolution happen *because organisms make them happen* (Walsh, 2015). This is the central conclusion we have to draw once we accept autonomous reproducers as the fundamental units of evolution.

The second issue concerns what we accept as a scientific explanation. Aristotle distinguished four ways of answering the question 'why'. His four causes—material, formal, efficient, and final—are not really causes in the modern sense, but rather *aitia,* denoting something (or someone) responsible for a given phenomenon. For simplicity, I will use the less technical (but also less precise) notion of *(be)causes* here. (Be)causes correspond to different categories of determinants that complement each other to yield a full understanding of a phenomenon. This does not imply that Aristotle had a non-factive notion of causation, even though our modern scientific notion of "cause" is much more restricted: it roughly corresponds to efficient (be)causes only. In addition, modern science implicitly takes the material (be)cause for granted, although it no longer considers it a proper cause.

This is illustrated by current accounts of mechanistic explanation (*e.g.* Nicholson, 2012; Craver & Tabery, 2019). Evo-devo, for instance, relies on dynamic mechanisms as explanations, which are formulated in terms of structures "that perform a function in virtue of [their] component parts, component operations, and their organization," and whose "orchestrated functioning" is "manifested in patterns of change over time in properties of its parts and operations" (Bechtel & Abrahamsen, 2010, p. 323). Developmental evolution is characterized by plausible transformation sequences for such dynamic mechanisms (DiFrisco & Jaeger, 2019). Such explanations (called *lineage explanations*; Calcott, 2009) rely entirely on material and efficient (be)causes, that is, on changes in the components of the mechanism and the operations between them.

Robert Rosen, in "Life Itself" (1991), formalizes Aristotelian (be)causation, explicitly distinguishing between material and efficient causes in his relational characterization of organizational closure. Formal (be)causes can also be integrated into his account. Very roughly speaking, formal (be)cause relates to the *kind of causal organization* that implements closure—for instance, the specification of particular functional relationships within the system (Hofmeyr, 2018). Similarly, process structuralism distinguishes between different kinds of morphogenetic fields based on the functional relations that determine their structure (Webster & Goodwin, 1982, 1996). In both cases, different systems (organisms or morphogenetic fields) are categorized by the relational properties that characterize their organization. Such *relational explanations* are perfectly scientific; but they are not mechanistic. They do not explain the behavior of a system in terms of cause and effect, but rather tell us what kind of a system it is in terms of its relational properties.

The organizational account of organismic agency relies on material, efficient, *and* formal (be)causes—mechanistic *and* relational explanations—which complement each other. Organizational closure, achieved through the closure of constraints, is the defining relational property of living systems. It is a formal (be)cause. However, it is not simply imposed on the material flows constituting the organism. Instead, it is continually regenerated, constantly (re)emerging over time through the dialectic dynamic interactions of material processes and the constraints they generate (DiFrisco, 2014; DiFrisco & Mossio, 2020). These processes represent the material and efficient (be)causes of the organism.

In contrast to all the above, population-level evolutionary genetics relies on *statistical explanations* that are neither structural nor mechanistic, accounting for their phenomena in terms of statistical relevance or conditional dependence instead (see Woodward, 2019). The agential perspective adds *a fourth kind of explanation* to evolutionary theory—*naturalistic teleological explanation* (Walsh, 2015)—thus completing the Aristotelian repertoire of (be)causes.

Natural teleological explanation does not describe any large-scale trends or tendencies in evolution. It applies exclusively at the level of the evolutionary individual. While mechanistic explanations show how specific causes *produce* their effects (answering the question 'how' something happens), teleological explanations account for the means that are *conducive to* the attainment of the organism's goals (answering the question 'why' something happens). The latter kind of questions are often the most relevant in evolutionary biology, but have been considered philosophically troublesome for a very long time. This does not have to be case (Walsh, 2015). Goal-oriented behavior is empirically observable. The goals of an organism do not exert any pull on it from the future, but naturally emerge from its interactions with its experienced environment (the individual's struggle for existence).

For these reasons, naturalistic teleological explanation does not suffer from any of the problems that usually render teleological explanations problematic. First, it does not imply non-actual (*e.g.* future) causes of present effects. Second, it does not imply any intentionality (or even cognitive abilities). Third, it is based on a naturalized notion of normativity (see section 2 and Mossio *et al.* 2009a). Goal-oriented behaviors arise because the organism strives to maintain organizational closure and continuity in order to continue living, to reproduce, and to evolve. It does this by autonomously selecting actions from its behavioral repertoire in response to opportunities and obstacles in its experienced environment (see section 6). Put simply, naturalistic teleological explanation is a necessary part of any agential theory of evolution, because of the immanence of *rules which are generated by the agents themselves* (Walsh, 2015).

This leads us to the third and last issue, which consists of a number of methodological challenges concerning the mathematical and conceptual tools we use to study evolving systems. These tools are often borrowed from physics (as discussed, for example, in Fontana & Buss, 1996, or Knuuttila & Loettgers, 2016), and most of them were originally developed within a strictly Newtonian paradigm. Let us take dynamical systems theory as an example, which is used to support dy-

namic mechanistic explanations in evo-devo (see Brigandt, 2015; DiFrisco & Jaeger, 2019). In this framework, we first prestate the space of possible trajectories of a system (its configuration space) before homing in on those that are actually realized in specific circumstances through validation of the model with empirical data (see, for example, Jaeger & Crombach, 2012; Jaeger *et al.,* 2012; Jaeger & Monk, 2014; Crombach & Jaeger, 2021). This is classical "physics in a box." It is a very powerful approach for simulating developmental processes, but breaks down at the level of whole-cell or whole-organism models, since traditional dynamical systems models cannot deal with systems based on organizational closure. In fact, it cannot deal with self-constructing systems in general (Fontana & Buss, 1994, 1996).

Organizational closure, considered in a dynamic context, leads to the continuous (re)generation of the rules and constraints that determine the behavior of the system. Therefore, systems with organizational closure require models that rewrite their own equations and boundary conditions based on principles generated from *within* themselves. This recursiveness lies at the heart of Rosen's (1991) conjecture that organisms cannot be completely captured by any finite algorithm. Although, recursive formalisms (such as Lambda-calculus), which allow for operations on operators, can be used for simulating organized systems with closure (Fontana & Buss, 1994, 1996; Mossio *et al.,* 2009b), this still falls short of capturing the full potential of an evolvable living system. The reason for this is because the different processes and constraints that constitute an organism not only recursively influence, but mutually depend on each other for their very existence (see section 2). Organisms *embody* their self-generated rules in a way which is impossible to fully implement within any predefined computational environment with its externally specified hardware and syntactic rules (Rosen, 1991). It may be the case that to fully capture an organism with its capabilities of survival, reproduction, and open-ended evolution, we'd have to actualize a synthetic, evolvable reproducer with a complete life cycle in the laboratory.

8. Conclusion

What I have presented here remains a very tentative outline of an agential approach to evolution (*cf.* Walsh, 2015). It rests on the organizational account of reproduction and organismal agency (Moreno & Mossio, 2015; Mossio & Pontarotti, 2020; Mossio, this volume), as well as the perspective of the reproducer and its life cycle as the fundamental unit of evolution by natural selection (Griesemer, 2006). The major implication of the theory is that all evolving systems are agents (or involve agents among their parts), which implies that understanding organismic agency is absolutely fundamental for understanding evolution. These are strong claims that must be supported by strong evidence. Unfortunately, we have barely begun to study agency and its role in evolution, and many obstacles remain on the road to a more mature, robust, and empirically supported theory.

Some of these challenges are philosophical: they concern the nature of the new account, its mathematical methodology, and the kind of explanations we need to understand the role of organismic agency in evolution. What should be clear by now is that an agential theory will look very different from what we are used to calling a scientific theory within the traditional Newtonian paradigm. Instead of providing a mechanistic explanation of agency and its evolution in terms of efficient causation only, this new theory will rely on all Aristotelian aitia or (be)causes: material, efficient, formal, and final. Final (be)causes will be incorporated in the form of naturalistic teleological explanations for the behavior of individual evolutionary units (reproducers) engaged in their struggle for existence. I must emphasize again: this kind of teleology does *not* imply any large-scale goal-directedness in evolution. Whether macroevolutionary trends exist or not is not at issue here. Naturalistic teleological explanation strictly only applies to the goal-directedness of an individual's behavior.

Some of the challenges are empirical. These apply at two different levels. To fully understand Darwinian evolution—and its underlying struggle for existence—we need a naturalistic account of organismic agency. Organizational closure through

the closure of constraints, and organizational continuity enabling the continual (re)emergence of organization and the completion of the life cycle, provide the most detailed and convincing explanation for agency and its role in evolution that we have today. Yet, they still remain largely disconnected from the empirical study of regulatory processes in systems and synthetic biology. The first challenge will be to cross this divide in order to test the organizational account empirically. The second challenge resides at the level of the organism's goal-oriented behavior, which is itself an empirical observable (Walsh, 2015). Now that we have a philosophical justification to do so, we can apply naturalistic teleological explanations to account for the means that are conducive to the pursuit of an organism's goals. In a way, this is already common practice in ecological research. What remains to be done is to embed this existing practice as a research program within the agential perspective on evolution.

Despite all the remaining challenges—and the speculative nature of the argument—I hope to have convinced the reader that it is worthwhile to take process and agency more seriously in the study of evolution. Most current research remains restricted to traditional structural and functional approaches, with genetic replicators as their focus. Processual and even more so agential perspectives remain severely understudied, mainly because of theoretical objections and prejudices that do not hold up under closer scrutiny. This unnecessarily limits the scope and depth of evolutionary research today. Efforts to provide extended synthetic accounts do not really solve this issue, because the problem is the attempt at synthesis itself. Evolution is a process that generates diversity. Why not embrace an equally diverse approach to evolutionary explanation? An agential theory properly contextualizes and enriches existing structural, functional, and processual approaches. It provides *a fourth perspective on evolution, a truly organismic angle*. All four illuminate each other's limitations and domains of applicability, and each provides its own epistemic approach (Griesemer, 2006; Wimsatt, 2007). Together, they address a much greater range of evolutionary phenomena than any single perspective could ever cover on its own.

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