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## Reconceptualizing the Organism From Complex Machine to Flowing Stream

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*The machine analogy has put us on a wrong scent . . . How long are we to persist in refusing to look sheer hard facts in the face, merely in the interests of a seventeenth-century analogy which by now may well have outgrown its usefulness? Sooner or later biology will have to take account of them if there is to be any theoretical biology.*

—Joseph Henry Woodger (1930: 15–16)

### 1. Introduction

The greatest intellectual revolutions are those that lead to such a profound reorientation in our habits of thought that following their occurrence it becomes almost impossible to comprehend what it was like to think about things in any other way. They transform our understanding so fundamentally that they come to ground and guide our inquiries without themselves ever being directly subject to them. A paradigmatic example is the *mechanization of the world picture* that took place during the scientific revolution (Dijksterhuis 1961). Although there is nothing inevitable about seeing the world as a vast, finely tuned machine (indeed, to Aristotle as to most other ancient thinkers, such a view would have seemed alien and artificial), after the seventeenth century it became difficult to think about nature in any other way. Thereafter, the natural was mechanical and the mechanical was natural.

This radical conceptual transformation, which in many ways precipitated the rise of modern science, is a testament to the power of metaphors. The critical role that metaphors play in the conceptualization of phenomena has not always been appreciated by philosophers. In fact, for much of the twentieth century, metaphors were dismissed as decorative literary devices, of little relevance to scientific understanding. The verifiability principle of logical empiricism rendered any appeals to metaphors meaningless and pushed metaphorical language in general beyond the realm of cognitive significance.<sup>1</sup> Ironically, the idea that metaphors are irrelevant to the

<sup>1</sup> Max Black, probably the first analytic philosopher to take metaphors seriously, bitterly complained about his peers' reaction to the use of metaphors: "To draw attention to a philosopher's metaphors is to

pursuit of generating scientific knowledge emerged during the very same period that witnessed the reorganization of all of natural philosophy around a single metaphor: that of the *clockwork universe* (Collingwood 1945; Dear 2006). Many of the pivotal figures of early modern science and philosophy displayed a dismissive—if not downright hostile—attitude toward metaphors, denouncing them as illegitimate rhetorical devices that compromise the clarity and objectivity of rational discourse.<sup>2</sup> Today such views are rare, as there is widespread recognition of the indispensable roles that metaphors play in scientific theory and practice (e.g. Keller 1995; Maasen et al. 1995; Brown 2003). But out of the endless array of metaphors used in science, it is difficult to think of one that has been more dominant and has exerted a greater influence than the *machine metaphor*, which provided the basic theoretical foundation for mechanistic natural philosophy in both physics and biology.

Although the mechanistic worldview, with its emphasis on reductionism and determinism, collapsed in physics following the quantum revolution of the early decades of the twentieth century, it somehow managed to survive in biology. For a time—especially during the interwar years—it seemed as if biology too would abandon mechanicism, as a collective of biological thinkers known as the *organicists* began to articulate a post-mechanicist philosophical foundation for biology that explicitly rejected the ontological assimilation of organisms to machines (see Nicholson and Gawne 2015). The organicists were inspired by Alfred North Whitehead, who had written in 1925 that '[t]he appeal to mechanism on behalf of biology was in its origin an appeal to the well-attested self-consistent physical concepts as expressing the basis of all natural phenomena. But at present there is no such system of concepts' (Whitehead 1925: 129). Nevertheless, in the end mechanicism not only prevailed but was actually reinvigorated by the meteoric rise of molecular biology (see e.g. Monod 1971). The neo-Darwinian view of evolution that became established during the same period also contributed to the consolidation of mechanicism in biology (see e.g. Williams 1966).

Elsewhere (Nicholson 2013, 2014) I have referred to the central tenet of biological mechanicism—the metaphorical redescription of the organism as a machine—as the *machine conception of the organism* (MCO). The MCO is one of the most pervasive metaphors in modern biology. Part of its success lies in its remarkable plasticity, as it is able to take a variety of different forms, depending on the context. To mention only a few of its contemporary manifestations, in developmental biology it equates the embryo with a computer that executes a predetermined set of operations in accordance with a program encoded in its genes (e.g. Jacob 1973); in evolutionary biology it assimilates organisms to optimally designed artefacts, blindly engineered by natural

belittle him—like praising a logician for his beautiful handwriting. Addiction to metaphor is held to be illicit, on the principle that whereof one can speak only metaphorically, thereof one ought not to speak at all ... [Let us] not accept the commandment, "Thou shalt not commit metaphor", or assume that metaphor is incompatible with serious thought' (Black 1962: 25).

<sup>2</sup> Thomas Hobbes, for instance, declared that '[m]etaphors, and senseless and ambiguous words, are like *ignes fatui*; and reasoning upon them, is wandering amongst innumerable absurdities; and their end, contention, and sedition, or contempt' (Hobbes 1996: 36). One cannot help but wonder how Hobbes saw no inconsistency in decrying the usefulness of metaphors by using one to make his point.

selection (e.g. Dawkins 1986); and in molecular biology it identifies the cell as a factory of highly specialized molecular machines (e.g. Alberts 1998).

In recent years, however, there have been growing voices of dissent from the mechanist orthodoxy, as more biologists and philosophers have begun to question the theoretical legitimacy of the MCO (e.g. Rosen 1991; Lewontin 2000; Kirschner et al. 2000; Henning and Scarfe 2013). It is becoming clear that the MCO offers only a partial and rather distorted view of living systems. Most significantly for the purposes of the present volume, the uncritical—and often tacit—acceptance of the MCO is one of the major reasons for the persistence of substance metaphysics in biology. This should not be surprising, as mechanismism has always served as the main vehicle for substance thinking in science. After all, what are machines if not persistent material things with determinate sets of properties and which exist independently of the activities they engage in? Demonstrating the ontological inadequacy of the MCO is a necessary first step if we are to come to terms with the processual nature of life and lay the foundations for a processual philosophy of biology.

In an earlier paper (Nicholson 2013), I argued that the MCO fails to provide an appropriate understanding of living systems because organisms and machines differ from one another in a number of crucial respects. Most fundamentally, I claimed, organisms are *intrinsically purposive* (in the sense that their activities and internal operations are ultimately directed towards the maintenance of their own organization), whereas machines are *extrinsically purposive* (given that their workings are geared towards fulfilling the functional ends of external agents).<sup>3</sup>

The present chapter presents a totally different argument against the MCO: one based on thermodynamic considerations. As I will show in the next section, thermodynamics supplies a surprisingly effective means of elucidating the ontological distinction between organisms and machines.<sup>4</sup> The thermodynamic character of life is incompatible with the MCO and calls for the adoption of a processual view of the organism, which is exemplified by the Heraclitean metaphor of the stream of life. In section 3 I will examine the intellectual development of this alternative metaphorical conception and consider the extent to which it captures the nature of living systems. I will follow this in section 4 by discussing three specific ontological lessons that we can draw when we reconceptualize the organism from complex machine to flowing stream. The first relates to questions of normativity and agency, the second concerns the problem of persistence, and the third addresses the nature and origins of order. I will conclude by briefly reflecting on the broader consequences of this shift in perspective.

<sup>3</sup> Another way of expressing this is that organisms act on their own behalf, while machines serve the interests of their makers or users (for the full argument, see Nicholson 2013; for various illustrations, see Nicholson 2014).

<sup>4</sup> It is a pity that thermodynamics has not played a greater role in the philosophy of biology, especially given that the implications of thermodynamics for the field were explicitly recognized by some of its earliest practitioners (see Needham 1928: 81–5). The only major exception was the debate—particularly prominent during the late 1980s—regarding proposals to extend, modify, or even reformulate the neo-Darwinian theory of evolution in accordance with thermodynamic principles (e.g. Brooks and Wiley 1986; Wicken 1987; Weber et al. 1989).

## 2. Organisms $\neq$ Machines: The Argument from Thermodynamics

Ironically, thermodynamics initially served to vindicate, rather than undermine, the MCO (understood here as a heat engine rather than a clock). The science of thermodynamics arose from the desire to understand heat engines, particularly the relationship between heat and work, and the presumed conformance of organisms to the first law of thermodynamics—a version of the principle of the conservation of energy—enabled them to be treated as veritable engines. The pioneer in this respect was Antoine Lavoisier, the father of modern chemistry, who in the late eighteenth century famously characterized respiration as a form of combustion. Along with Pierre-Simon Laplace, Lavoisier conducted the first calorimetry experiments, comparing the heat and carbon dioxide produced by a guinea pig with that produced by the combustion of carbon.<sup>5</sup>

During the nineteenth century, the rise of thermodynamics was so intertwined with concurrent developments in physiology—united as these disciplines were by their common interest in ‘engines’, be they technological or biological—that some of the earliest enunciations of the first law, such as those by Hermann von Helmholtz and Robert von Mayer in the 1840s, were tied to efforts to elucidate the relation between chemical energy and physiological activity. Helmholtz, a physiologist by training, was led to his formulation of the first law of thermodynamics by his demonstration of the equivalence between animal heat and energy, as well as by his discovery that only physico-chemical processes are involved in the generation of animal heat. And Mayer, a practising physician, gave very explicit consideration to the bearing of the first law on organisms:

In the living body carbon and hydrogen are oxidized and heat and motive power thereby produced. Applied directly to physiology... the oxidative process is the physical condition of the organism’s capacity to perform mechanical work and provides as well the numerical relations between [energy] consumption and [physiological] performance.

(Meyer, quoted in Coleman 1977: 123)

At the end of the century, Max Rubner conclusively established that organisms are subject to the first law by showing experimentally that the amount of energy returned to the environment by an organism (for instance, in the form of excretory products and heat) is equivalent to the energy taken in, assuming no change in weight. Although this by itself did not prove that organisms are heat engines—in fact, upon close examination, the original analogy between combustion and respiration turns out to be rather problematic<sup>6</sup>—it appeared to offer little reason to question the MCO.

<sup>5</sup> Lavoisier’s own formulation of the MCO went like this: ‘The animal machine is governed by three main regulators: respiration, which consumes oxygen and carbon and provides heating power; perspiration, which increases or decreases according to whether a great deal of heat has to be transported or not; and finally digestion, which restores to the blood what it loses in breathing and perspiration’ (Lavoisier, quoted in Jacob 1973: 43).

<sup>6</sup> In combustion, the surmounting of the energy of activation—which is necessary for the accomplishment of oxidative reactions—is achieved by raising the temperature considerably, whereas in respiration this is not needed. Instead, respiration relies on the enzymatic lowering of the energy of activation. If the

The second law of thermodynamics is a completely different matter. Indeed, it is when we consider how organisms conform to it that the MCO absolutely breaks down. The second law negates the possibility of a perfectly efficient transformation of heat into work. It stipulates that the amount of free energy (i.e. energy capable of performing work) is constantly decreasing, while the amount of dissipated energy (measured in terms of entropy) is correspondingly increasing. Every natural change, whether physical or chemical, exhibits this utterly irreversible tendency—pithily described by Arthur Eddington as the ‘arrow of time’—which results in a net, ever growing increase in disorder. Such an inexorable trend towards a uniform distribution of heat and the consequent ‘running down’ of the universe into a state of dead inertness is diametrically opposed to what we find in the living world, where there is a clear evolutionary tendency for complexity and organization to increase progressively with time. What are we to make of this paradoxical situation?

The founders of thermodynamics were perfectly aware of this paradox, but instead of dealing with it they simply ignored it. William Thomson (later Lord Kelvin), who coined the term ‘thermodynamics’, explicitly excluded living processes in his formulation of the second law in 1851.<sup>7</sup> Years later, Helmholtz declared that whether or not the second law is violated by ‘the fine structure of living organized tissue appears to me still to be an open question, the importance of which in the economy of nature is very obvious’ (Helmholtz, quoted in Needham 1928: 81). James Clerk Maxwell attempted to confront the problem by suggesting how the second law might be contravened, but his suggestion required postulating a cunning microscopic being—which Thomson dubbed ‘Maxwell’s Demon’—capable of sorting molecules according to their speed without the expenditure of work, thereby reducing the overall level of entropy. Given the total lack of evidence for the existence of such a fanciful creature, by the early twentieth century biologists—with the exception of a few neo-vitalists such as James Johnstone (1921)—assumed that organisms do conform to the second law. The question that remained was how.

The eventual resolution of the paradox came with the realization that the second law requires only that the universe *as a whole* exhibits an increase in entropy. Local eddies of order (or ‘negative entropy’) can be sustained and even propagate, as long as, overall, there is a global entropic increase. This was lucidly pointed out by Erwin Schrödinger in his influential book *What Is Life?* (Schrödinger 1944). Schrödinger explained that an organism stays alive in its highly organized condition by importing matter rich in free energy from outside of itself and degrading it in order to maintain a relatively low entropic state within its boundaries. The organism thus preserves its internal organization—thereby eluding (at least for a time) the inert, time-invariant state of thermodynamic equilibrium we call *death*—at the expense of

transformation of energy were to take place in organisms in the same way that it does in heat engines, then, at temperatures at which living systems can exist, the coefficient of their useful activity would fall to an insignificant fraction of 1 per cent (see Oparin 1961).

<sup>7</sup> Thomson’s original enunciation of the law was this: ‘It is impossible *by means of inanimate material agency*, to derive mechanical effect from any portion of matter by cooling it below the temperature of the coldest of surrounding objects’ (Thomson, quoted in Keller 1995: 49, emphasis added).

increasing the entropy (in the form of heat and other waste products) of its external environment.<sup>8</sup>

Understanding how organisms conform to the second law allows us to see why they are fundamentally different from machines. Organisms have to constantly exchange energy and matter with their surroundings in order to maintain themselves *far from thermodynamic equilibrium*. Machines, on the other hand, exist in equilibrium or near-equilibrium conditions, and consequently do not have to constantly exchange energy and matter with their surroundings. Organisms, in other words, are necessarily *open systems*, whereas machines can be open or closed. As a result, they differ in the kind of stability they exhibit. Machines exhibit a static stability, which they attain when they reach an equilibrium state that reflects the cessation of their activity. Organisms, in contrast, exhibit a *dynamic stability*, which is based on their capacity to actively maintain a low-entropic ‘steady state’ where there is a continuous, perfectly balanced import and export of materials. The stability of machines at equilibrium means that they do not require free energy for their preservation, while the opposite is true for organisms.<sup>9</sup> A further difference is that, whereas the activity of a machine is temporary and its onset is reversible (given that a machine can return to a state of operation after being at rest), the actively maintained steady state of an organism is *fixed and irreversible*. An organism must remain permanently displaced from equilibrium; the moment it yields to it, death inevitably and irrevocably ensues.

The theoretical distinction between equilibrium and non-equilibrium systems is of paramount importance. Classical thermodynamics was only ever equipped to deal with equilibrium systems (which is why the aforementioned paradox concerning life and the second law arose). The recognition of non-equilibrium systems led to the development in the mid-twentieth century of what has come to be known as *non-equilibrium thermodynamics*, which concerns itself with steady states, irreversible processes, and non-linear reactions. The subject matter of this relatively new branch of thermodynamics extends beyond the living realm, as organisms are not the only far-from-equilibrium open systems found in nature. Whirlpools, flames, and tornadoes are familiar examples. Less familiar but well-studied cases include Bénard convection cells and oscillating chemical reactions such as the Belousov–Zhabotinsky reaction. Ilya Prigogine, whose foundational work in establishing non-equilibrium thermodynamics earned him a Nobel Prize in 1977, referred to these open systems as *dissipative structures*. Perhaps the most significant achievement of this new field of physics has been to show how self-organization arises in nature—that is, to explain how the macroscopic patterns of order displayed by dissipative structures spontaneously emerge from non-linear interactions and become stabilized in far-from-equilibrium conditions through an ongoing flux of energy and matter (see Nicolis

<sup>8</sup> Organisms, then, far from disobeying the second law, help to enact it. Life, with its unassailable tendency to proliferate, actively contributes to the dissipation of energy by leaving large amounts of entropic waste in its wake.

<sup>9</sup> The distinction I draw here between static and dynamic forms of stability corresponds to the distinction some authors have made between ‘energy-well’ and ‘far-from-equilibrium’ stability (e.g. Bickhard 2000; Campbell 2009).

and Prigogine 1977). Organisms, from this perspective, are the most stable and complexly differentiated dissipative structures in existence.

In biological theory, the thesis that organisms are dynamically stable open systems was most systematically articulated by Ludwig von Bertalanffy (1932, 1942, 1950, 1952). However, as Evelyn Fox Keller (2008) has shown, its intellectual roots can be traced back to the ideas of a number of nineteenth-century authors, including Herbert Spencer, Gustav Fechner, and especially Claude Bernard, who memorably asserted that organisms persist in time by keeping their internal environment constant in the face of external disturbances. Bernard's conception was the basis for Walter Cannon's famous concept of *homeostasis*, which he coined with the explicit purpose of accounting for the distinctive thermodynamic character of the organism:

The highly developed living being is an *open system* having many relations to its surroundings. . . . The coordinated physiological reactions which maintain most of the *steady states* in the body are so complex, and are so peculiar to the living organism, that it has been suggested. . . . that a specific designation for these states be employed—*homeostasis*. (Cannon 1929: 400, emphasis added)

The above thermodynamic considerations point to *metabolism* as the single most important characteristic of life. Metabolism refers to the balanced coupling of the energy-releasing processes of catabolism (i.e. the breakdown of organic matter by means of cellular respiration) with the energy-consuming processes of anabolism (i.e. the buildup of the macromolecular constituents of cells) that are continuously going on in an organism. Crucially, metabolism is what maintains the organism in a steady state far from equilibrium, liberating large amounts of free energy for the organism to use while simultaneously 'freeing it from all the entropy it cannot help producing while alive' (Schrödinger 1944: 71). It is this emphasis on metabolism, which the non-equilibrium thermodynamics of organisms prescribes, that enables us to understand the ontological inadequacy of the MCO.<sup>10</sup>

### 2.1. Addressing potential objections to the argument

Let us now consider a series of objections that may be raised against the preceding argument. First of all, while some machines (like clocks and computers) are closed systems, others (like heat engines and water pumps) are decidedly open, as they exchange matter, and not just energy, with their surroundings. Although the difference between them and organisms is obvious when they are at rest, do they not display a dynamic form of stability when they are in operation that is akin to that shown by organisms? Can we not say, in the case of engines, for example, that they 'metabolize' their fuel just as organisms metabolize their food?

The problem of equating fuel with food is that it drastically underestimates the physiological pervasiveness of metabolism. No matter how dynamic a functioning

<sup>10</sup> Metabolism, incidentally, is also the basis for Humberto Maturana and Francisco Varela's (1980) seminal theory of autopoiesis (literally self-production), which has been fruitfully elaborated in recent decades by a number of philosophers and theoreticians of biology interested in the idea of autonomy (see, e.g., Moreno and Mossio 2015 and chapter 10 here).

machine may be, it is always possible to distinguish the machine's physical frame—which remains fixed—from the materials that flow through it. The actual structure of the machine does not itself take part in the chemical transformations that the fuel undergoes as it passes through it. Instead, it serves as a channel that facilitates the exchange of materials as fuel is converted into waste. An organism, in contrast, changes wholly and continuously as a result of its metabolizing activity. Organisms are constantly being reconstituted from the matter they import from their surroundings, and consequently it is impossible to maintain the distinction between food materials and bodily constituents. As Hans Jonas phrased it, in an organism '[t]he exchange of matter with the environment is not a peripheral activity engaged by a persistent core: it is the total mode of continuity (self-continuation) of the subject of life itself' (Jonas 1966: 76, n. 13).<sup>11</sup> This is why the fuel–food analogy is so misleading, and why the stability of a machine—despite its apparent dynamicity—ultimately resides in an unchanging material structure. In machines there is a specific 'inflow' and a specific 'outflow'. In organisms *everything flows*.<sup>12</sup>

Even after accepting this, a critic might wish to insist that it is still inappropriate to characterize the form of machines as fixed. Although machines do not exchange their material constitution externally in the way organisms do, many do modify their structure *internally* to suit their purpose. Windmills, catapults, bicycles, and typewriters all change their physical configuration in order to accomplish their function. Why, then, should we not regard these internal structural rearrangements as comparable to the ones that organisms undergo?

The trouble with this (more restricted) comparison is that it overlooks the fact that the physical displacements that the parts of a machine undergo conform rigidly to a precise, predetermined cycle of operations. The successful execution of a function by a machine implies a periodic restoration of the spatial relations among its parts—a 'resetting' of its internal configuration that enables it to perform its function again. So, although a machine may contain parts that move about, this does not mean that it goes through a genuine process of transformation. Its physical architecture is still very much fixed; it is just that this fixity is reflected in a recurrent spatio-temporal pattern rather than in a totally static structure. The only real change that machines experience is the gradual wearing down of their parts, which eventually leads to their irrevocable entropic degradation (unless, of course, an external agent intervenes).

The situation with organisms is completely different. Organisms autonomously modify their structure in response to cues from their environment. When injured, they are usually able to heal themselves and repair the damage—and this is as true for bacteria as it is for complex multicellular organisms like trees and vertebrates. Some organisms (e.g. salamanders) can even regenerate entire body parts, often following the self-amputation of limbs, in order to avoid predation. The astonishing plasticity

<sup>11</sup> Jonas' insightful analysis of metabolism is also discussed in chapters 8 and 18.

<sup>12</sup> It is rather striking that the organicists were already aware of this fact. For example, John Scott Haldane, who was heavily influenced by Claude Bernard, wrote in 1917 that '[t]he organs and tissues which regulate the internal environment . . . are constantly taking up and giving off material of many sorts, and their "structure" is nothing but the appearance taken by this flow of material through them' (Haldane 1917: 90; see also Russell 1924 and Woodger 1929).



of organisms contrasts with the brittleness of machines, which tend to stop working when their parts break or are damaged. Of course, redundancy and self-repair can be built into the design of machines to some extent. Nevertheless, although this can make their operation more robust and more reliable, the inherent limitations of their fixed architecture remain.

Not only do organisms modify themselves, but they do so *adaptively*, in a way that optimizes their physiological performance. Now a critic could still argue that servomechanisms—machines controlled by negative feedback with a certain capacity to self-regulate (e.g. thermostats) or to self-steer (e.g. homing missiles)—also modify their operation adaptively in response to external inputs; in fact, they are often described as ‘homeostatic machines’. However, this argument misleadingly conflates the thermodynamic meaning of Cannon’s original use of the word ‘homeostasis’ with the cybernetic meaning the term acquired after the Second World War. The adaptability of servomechanisms (measured in terms of input–output adjustments) is of a very limited kind, its mode and range being defined in advance in accordance to a set design. Servomechanisms are closed, near-equilibrium systems, and consequently they are not capable of truly adaptive self-maintenance.<sup>13</sup>

At this point, the most doggedly persistent of critics may take all of the above considerations on board and simply resort to stretching the concept of machine sufficiently for it to encompass everything that is distinctive about organisms. But in the end this does not really help the critic’s defense of the MCO, as it undermines the very properties of machines that make the MCO a heuristically useful idealization in the first place. An instructive illustration of this can be found in a curious paper titled ‘Living and Lifeless Machines’, in which the distinctive properties of organisms are forcefully shoehorned into the framework of the MCO. This leads the author to make a number of exceptionally strange assertions. For example, he notes that ‘[t]he living body is analogous to a motor car in which the chassis, brakes, cylinders, pistons, connecting rods, valves and bearings all contained combustible material, some of which was burnt whenever the driver placed his foot on the accelerator’ (Kapp 1954: 101). The question we must ask is this: how is such a bizarre imaginary motor car still analogous to an *actual* motor car? Can the causal operation of the latter really be used to shed light on the causal operation of the former? If not, then what is the point of clinging on to the MCO, if the price to be paid is that our understanding of machines has to become completely distorted in order to accommodate the characteristic attributes of organisms?<sup>14</sup>

The far more sensible option is to simply accept the fact that machines are not good models for coming to terms with the ontology of organisms. The MCO, despite its obvious heuristic value in biological research, does not provide an adequate

<sup>13</sup> For more detailed critiques of the cyberneticists’ efforts to assimilate servomechanisms to organisms, see Taylor 1950, Jonas 1953, Oparin 1961, and Nicholson 2013.

<sup>14</sup> Kapp is by no means the only author to stretch the MCO beyond breaking point. The history of biology is littered with memorable examples, including Julien Offray de La Mettrie’s *clock that winds itself* or Karl Ernst von Baer’s *machine that constructs itself*, to paraphrase their respective formulations of the MCO. A more recent example is Richard Dawkins’ (1998: 17) ‘machine that work[s] to keep itself in being, and to reproduce its kind’.

theoretical understanding of the nature of living systems. As we have seen, the thermodynamic character of life demands a *processual* conception of the organism. Whatever else they may be, living systems are highly stabilized flows of energy and matter. Machines may take part in various processes, but organisms are *themselves* processes. This inescapable fact must constitute the starting point for any theory of the organism. In the next section we will examine the history of attempts to develop an alternative conception of living systems that successfully reflects their processual nature.

### 3. The Stream of Life: A Processual Conception of the Organism

The MCO has been the most pervasive view of living systems since the seventeenth century, but it is certainly not the only conception one finds when surveying the history of biological thought. In fact, many of those who criticized the MCO in the past sought alternative metaphors that could highlight the very features of organisms that the MCO conveniently ignores or inadvertently distorts. A good place to start is the work of Bertalanffy, who—as we have already mentioned—was responsible for popularizing the idea that organisms are open systems that maintain themselves in a steady state far from equilibrium.

In his organicist treatise *Problems of Life*, Bertalanffy (1952) illustrated the processual nature of the organism by appealing to the famous aphorism of the Presocratic philosopher Heraclitus that it is impossible to step into the same river twice because fresh water is forever flowing through it. A stream is never the same at two successive temporal points; it is permanently changing. This image encapsulates the Heraclitean worldview, which emphasized the endless movement and change of all things. Bertalanffy argued that '[w]ith this Heraclitean thought we put our finger on a profound characteristic of the living world' (ibid., 124). Like the river, ever changing in its waves yet persisting in its flow, an organism only *appears* to be constant and invariable, but in reality it is the manifestation of a ceaseless current. As Bertalanffy put it, 'living forms are not *in being*, they are *happening*; they are the expression of a perpetual stream of matter and energy which passes the organism and at the same time constitutes it'. He referred to this processual view of the organism as the *stream of life conception* (SLC) and counted it 'among the most important principles of modern biology' (ibid.).

The SLC allows us to grasp, in simple and evocative terms, many of the key characteristics of organisms that were highlighted in the previous section. The external form of a stream is stable only because of the constant flow of water molecules that enter into it and emerge out of it. The moment this flow is interrupted, the stream itself disappears, as its very existence depends on the steady movement of water passing through it. In the same way, the physical form of an organism is merely the visible expression of the constancy of catabolic and anabolic processes going on within it. Its persistence through time is entirely dependent on the extremely intricate balancing of these two opposing kinds of reactions. As metabolism proceeds, with the steady import of nutrients and export of wastes, not much remains at a later time of

the matter that once composed the organism. The SLC thus embodies two essential and complementary aspects of organismic dynamics: the continuous exchange of matter that lies at the very heart of the concept of metabolism on the one hand,<sup>15</sup> and the surprising stability of form that is maintained in spite of this material exchange on the other.<sup>16</sup>

Bertalanffy deserves credit for being the first to explicitly recognize that the thermodynamic openness of organisms requires the adoption of a processual perspective. However, he was by no means the first biologist to propose that processual metaphors offer a more accurate portrayal of the ontology of living systems. Throughout the nineteenth and the first half of the twentieth centuries, a wide range of authors independently arrived at the conclusion that organisms are best served by metaphorical conceptions that stress their dynamic, non-equilibrium qualities. We can explore the versatility of the SLC by considering some of its most notable historical formulations.

As early as 1817, Georges Cuvier felt compelled to define life as a *vortex*—that most paradigmatic of dissipative structures—using language that clearly prefigures the thermodynamic observations that Schrödinger and others would make more than a century later:

Life then is a vortex, more or less rapid, more or less complicated, the direction of which is invariable, and which always carries along molecules of similar kinds, but into which individual molecules are continually entering, and from which they are continually departing; so that the *form* of a living body is more essential to it than its *matter*. As long as this motion subsists, the body in which it takes place is living—*it lives*. When it finally ceases, *it dies*.

(Cuvier 1833: 14)

The vortex metaphor enabled Cuvier to make conceptual sense of the persistence of organismic form coupled with the transience of its constituent materials. This idea was picked up some years later by William Whewell, who—in the section of *The Philosophy of the Inductive Sciences* that dealt with what he was the first to call ‘the philosophy of biology’—paraphrased Cuvier by asserting that ‘life is a constant form of circulating matter’ (Whewell 1840: 46). Thomas Henry Huxley identified life more specifically with a vortex of water—a *whirlpool*—remarking that the constituents of an organism ‘stand to it in the relation of particles of water to a cascade, or a whirlpool’. Moreover, just as ‘the stoppage of a whirlpool destroys nothing but a form, and leaves the molecules of the water, with all their inherent activities intact, so what we call the death . . . of an animal, or of a plant, is merely the breaking up of the form, or manner of association, of its constituent organic molecules’ (Huxley 1870: 402).

By the early twentieth century, advances in the study of biochemical energetics—driven by research into the thermodynamics of living systems—had become difficult

<sup>15</sup> The term ‘metabolism’, we should not forget, derives from the Greek word for change. More explicitly still, the German word for metabolism is *Stoffwechsel*—literally, ‘material exchange’.

<sup>16</sup> An interesting implication of the dynamic stability of form is that, as Nicholas Rescher (1996: 52–3) has acutely observed, Heraclitus was only half-right when he declared that we cannot step into the same river twice. We may not be able to step twice into the same *waters*, but we can certainly step twice into the same *river* (that is, of course, assuming we also stayed the same!).

to ignore, and this is reflected in the SLC formulations of the time (cf. Gilbert 1982). Lawrence Henderson (1913: 23–4), for instance, argued that ‘[l]iving things preserve, or tend to preserve, an ideal form, while through them flows a steady stream of energy and matter which is ever changing’. John Scott Haldane (1919: 49) also stressed the energetic and material flux taking place in the organism, declaring that ‘organic structure is nothing but a molecular stream’. Charles Sherrington (1940: 82), for his part, described the cell as ‘an eddy in a stream of energy’ and as ‘a stream of movement which has to fulfil a particular pattern in order to maintain itself’ (ibid., 83).

While some of those who adopted the SLC drew quite generically on dissipative structures like vortices in the way that Cuvier had done—such as Ralph Stayner Lillie (1945: 28), who emphasized ‘the “vortex-life” feature of the vital constitution’—the majority were captivated specifically by the fluidity of *water*, finding in streams, waterfalls, and rivers the most suitable analogues for the organism. Edward Stuart Russell (1924: 6) observed that, ‘[j]ust as in a stream a ripple of constant shape and position is formed by the water flowing over a pebble, so the apparently static form and composition of organic substance are merely the expression of continuous... activity’. A similar assertion was made by Edmund Sinnott (1955: 117), who wrote that ‘[a]n organism has a sort of fluid form like a waterfall, through which water ceaselessly is pouring but which keeps in its descent a definite pattern’. Conrad Hal Waddington pointed out in *The Strategy of the Genes* (Waddington 1957: 2) that organismic form ‘is more nearly comparable to a river than to a mass of solid rock’, and Alexander Oparin (1961: 9) stated—echoing Bertalanffy and alluding to Heraclitus—that ‘[o]ur bodies flow like rivulets, their material is renewed like water in a stream. This is what the ancient Greek dialectician Heraclitus taught’.

Water, however, was not the only resource available to those wanting to underscore the dynamic stability of living systems. Some biologists resorted to fire in their articulation of the SLC, identifying the organism with a *flame*. John Burdon Sanderson Haldane (son of John Scott Haldane) claimed that ‘a man is as much more complicated than a flame as a grand opera is more complicated than a blast on a whistle. Nevertheless, the analogy is real’ (Haldane 1940: 57). This is not such a far-fetched analogy as it may seem. When a candle is lit, the flame flares up but almost immediately settles into a stable dynamic form that represents the attainment of a steady state. As long as it is continuously supplied with wax and oxygen, the flame is able to maintain itself far from equilibrium. It achieves this by keeping its temperature above the combustion threshold and vaporizing the wax, which induces convection that pulls in oxygen and removes combustion products. For Haldane, the flame analogy depicted the inherent dynamicity of life in ways that accentuated the inadequacy of the MCO. He indicated, among other things, that ‘a flame is like an animal in that you cannot stop it, examine the parts, and start it again, like a machine. Change is part of its very being’ (ibid.).<sup>17</sup>

Nevertheless, by the mid-twentieth century the SLC was rapidly losing ground to the MCO. This was partly a consequence of the shift in the biological agenda that took place during this period. The focus on metabolism and energetics that had

<sup>17</sup> For additional flame-based formulations of the SLC, see Brillouin 1949 and Bertalanffy 1967. The thermodynamic character of flames and its relevance for understanding organisms is also examined in chapter 10.

shaped physiological and biochemical research in earlier decades gave way to molecular biology's intense preoccupation with the structure and specificity of macromolecules, especially nucleic acids and proteins. As interests shifted from the plasticity and adaptability of biological form to the coding, replication, and expression of genetic information, so did the metaphorical conceptions used to characterize living systems. In the last third of the twentieth century, the MCO regained its place at the centre of biological theory and the SLC almost completely disappeared from the biological discourse.

Only in recent years—as the explanatory limits of molecular biology have become apparent—have we begun to witness the first signs of a revival of the SLC. In an influential article titled 'A New Biology for a New Century', Carl Woese specifically singled out the MCO as one of the major obstacles impeding further progress in biology. In place of the MCO, Woese invoked the SLC as a more appropriate metaphor with which to think about organisms:

If they are not machines, then what are organisms? A metaphor far more to my liking is this. Imagine a child playing in a woodland stream, poking a stick into an eddy in the flowing current, thereby disrupting it. But the eddy quickly reforms. The child disperses it again. Again it reforms, and the fascinating game goes on. There you have it! Organisms are resilient patterns in a turbulent flow—patterns in an energy flow. A simple flow metaphor, of course, fails to capture much of what the organism is. None of our representations of [the] organism capture [*sic*] it in its entirety. But the flow metaphor does begin to show us the organism's (and biology's) essence. And it is becoming increasingly clear that to understand living systems in any deep sense, we must come to see them not materialistically, as machines, but as (stable) complex, dynamic organization[s]. (Woese 2004: 176)

Woese is, of course, right to point out that the SLC does not capture every aspect of living systems. Even different versions of the SLC vary in their capacity to portray particular features of organisms. For example, a flame depicts metabolism more accurately than a whirlpool in that metabolism is essentially a series of chemical reactions; and, while the steady state of a flame is similarly sustained by continuous chemical changes, the steady state of a whirlpool is not.

At a more general level, however, it is obvious that organisms differ from flames, whirlpools, and other dissipative structures in a number of ways. For a start, organisms exhibit a far greater degree of stability, being able to maintain themselves for much longer periods of time. The key to their extraordinary stability lies in their ability to store energy, which enables them to manage their metabolic needs without having to rely on a constant supply of external energy, like other dissipative structures. In addition, organisms are distinctive in that they are demarcated by a physical boundary—a semi-permeable membrane—which helps regulate the intake and out-take of materials flowing through them. It is also evident that organisms display much higher levels of internal complexity, as they are functionally differentiated and hierarchically organized. Most dissipative structures lack these features because they spontaneously self-organize under appropriate conditions—a phenomenon that Stuart Kauffman (1995) memorably called 'order for free'—and this results in a single ordered macroscopic structure within which it is difficult to differentiate distinct functional contributions to the maintenance of the overall system.

Organisms, on the other hand, do not arise spontaneously but instead derive from previous organisms, and their structure reflects the gradual consolidation, through the eons of evolution, of an intricate ‘higher-order self-organizing dynamic among component self-organizing processes’ (Haag et al. 2011: 329).

Some authors have seen in these differences an unbridgeable gap separating organisms from all other dissipative structures—a gap that undermines any attempts to elucidate the former by examining the latter. For instance, Alvaro Moreno and Matteo Mossio have recently argued in their book-length treatment of autonomy (which they regard as the defining characteristic of living systems) that non-living dissipative structures ‘are not relevant for understanding autonomy, not only because they are “too simple” . . . but also because they cannot be taken as a “starting point” for the emergence of closure and autonomy’ (Moreno and Mossio 2015: 18). This seems a rather excessive (not to mention premature) conclusion. Inanimate self-organizing systems are undoubtedly simpler than animate ones, but there is a clear continuity between the two, as the latter must have emerged from the former at some point in the distant past. So, if there is anything that non-living dissipative structures offer biology, it is precisely a starting point from which one may investigate life’s origins.

But, even more importantly, organisms and other dissipative structures are fundamentally isomorphic from a purely physical point of view. As we saw in the previous section, they can be understood by means of the same thermodynamic principles. Even Moreno and Mossio admit that autonomy ‘is essentially grounded in thermodynamics’ (ibid., 6) and that many of the autonomous features of organisms ‘in fact *derive* from the fact that they are thermodynamically open systems, in far-from-equilibrium conditions’ (ibid., xxviii). It is therefore difficult to see what exactly the problem is, if there really is one, with invoking the SLC and drawing on simple dissipative structures to shed light on aspects of more complex ones—provided, of course, that one recognizes that knowledge of the former cannot by itself suffice to explain the latter.

#### 4. Organisms as Streams: Three Lessons for Biological Ontology

The SLC constitutes a promising point of departure for thinking about the ontology of organisms. In direct contrast to the MCO, it correctly identifies and accurately portrays the specific thermodynamic character of living systems. It supplies a firm physical foundation upon which we can begin to articulate a theory of the organism that does justice to its thoroughly processual nature. Although undoubtedly not sufficient, the SLC does show us a path through which we can ultimately *arrive* at a fully fledged biological understanding of organisms that is simply beyond the reach of the MCO. In this respect, the SLC can act as a ladder that can eventually be kicked away after it has served its purpose. After centuries of dominance of the MCO, the question in front of us is simple: what does biological ontology look like when we reject the mechanical and adopt the processual? In this section I will examine three concrete ontological lessons that we can draw from reconceptualizing the

organism from complex machine to flowing stream. The first relates to questions of normativity and agency, the second concerns the problem of persistence, and the third addresses the nature and origins of order.

#### 4.1. *First ontological lesson: 'Activity is a necessary condition for existence'*

Perhaps most evidently, using the SLC to shed light on the ontology of organisms allows us to make sense of their peculiar existential predicament. Owing to their thermodynamic condition, organisms—like all other dissipative structures—can only exist insofar as they are able to maintain themselves in a steady state far from equilibrium, and this requires a constant expenditure of free energy. The existence of a whirlpool, for instance, is a direct consequence of its own unremitting activity, which is what enables it to maintain itself through time. In the same way, if an organism is to stay alive, it has to keep acting ('working', in the thermodynamic sense) to avoid the ever present threat of equilibrium. To stop acting is to stop existing. As far as any living system is concerned, to be *is* to act. We can draw from this our first ontological lesson, which is that, for an organism, *activity is a necessary condition for existence*.

This assertion constitutes a radical departure from the conventional ontological stance of the western philosophical tradition, which is firmly rooted in substance metaphysics. A great deal of philosophical thought throughout history has been tacitly committed to the scholastic principle *operari sequitur esse* (Rescher 1996)—that is, activity is subordinated to being and thus follows from it; there can be no activity if there is no being to begin with. The processual nature of organisms requires that we relinquish this principle, given that—in the biological world, at least—activity and being necessarily presuppose one another. Being is neither ontologically nor temporally prior to activity, as the very existence of a living being is only possible by means of continuous activity.

Unsurprisingly, the MCO perfectly encapsulates the traditional substance-ontological position. The existence of a machine is totally independent of whether or not the machine happens to be performing its function. Machines have two modes of being: they can be active ('on') or they can be at rest ('off'). They can move back and forth between these two states without jeopardizing their structural integrity, and this is due to the fact that they exist in reversible, near-equilibrium conditions. The problem is that organisms, much like waterfalls or tornadoes, do not have an 'off' switch.<sup>18</sup> Metabolic processes can be slowed down, for example during sleep or hibernation, but they cannot be stopped completely. Even organisms in extremely dormant states, such as seeds or spores, exhibit basal levels of metabolic activity. Absolute stasis

<sup>18</sup> It should not escape anyone's attention that the ability to study machines successfully when they are turned off is the key to the enormous methodological appeal of the MCO. If organisms are machines, then we are justified in believing that they can be fruitfully investigated in abstraction from time. It is only when we adopt the SLC and are confronted with their processual nature that we realize that studying organisms atemporally is not to study them as they actually exist. It becomes apparent that using methods that strip organisms of their temporal extension (methods such as anatomical techniques that involve the desiccation, pickling, fixing, or freezing of biological samples) means resigning ourselves to characterizing static snapshots of an inherently dynamic reality.

signifies death, not inactivity, as it implies the irreversible attainment of thermodynamic equilibrium.

The indissoluble bond linking existence to activity in organisms and other dissipative structures obtains because their operation is directed *inwardly*, towards the generation and maintenance of their own organization. The operation of machines, by contrast, is directed outwardly, towards the production of something external to themselves. Organisms, unlike machines, are *autopoietic*; they persist as a result of their own activity. This ongoing self-producing activity is not optional—not undergoing constant metabolic regeneration is not a possibility. The thermodynamically grounded fact that organisms *need* to keep acting in order to keep existing helps to account for the emergence of a rudimentary form of *normativity* in nature (cf. Mossio et al. 2009; Christensen 2012). It is because its existence depends on its own activity that an organism *must* act in accordance to the operational norms that enable it to persist through time. If the organism stops following these norms, it ceases to exist. What this means is that it is in principle possible to objectively specify what is intrinsically ‘good’ or ‘bad’ for an organism (that is to say, what is and what is not in an organism’s ‘interest’) by evaluating its activities according to the contribution they make towards the preservation of its organization in far-from-equilibrium conditions.<sup>19</sup>

Attributing intrinsic normativity to the behaviour of organisms implies ascribing *agency* to them in some minimal (i.e. non-intentional) sense. Fortunately, the ontological interdependence of activity and existence also helps us come to terms with this elusive notion (cf. Barandiaran et al. 2009; Barham 2012). It is generally assumed that, in order to be an agent, an entity must be able to distinguish itself from its surroundings and, in doing so, delineate an external world with which it can maintain causal interactions. Organisms demarcate themselves from their surroundings through their metabolic activities, by taking in and pumping out energy and matter from outside of themselves. Importantly, the capacity of organisms to individuate themselves and interact with their environment is a direct consequence of their thermodynamic exigency to regulate their exchanges with it in order to ensure their continued viability.

As agents, organisms are inherently *active*, as opposed to machines, which are typically reactive. The former are primary sources of activity, whereas the latter must be activated by external means. A clock has to be wound up, a computer has to be turned on, a car has to be started, the keys of an organ have to be pressed, and so on. This crucial difference—already highlighted by Bertalanffy (1952), among others—reflects yet another respect in which the MCO distorts biological ontology. According to the MCO, the organism is essentially a passive system, being set into action through outside influences. Just as a vending machine, by virtue of an internal mechanism, delivers an article after a coin is inserted, so an organism performs a

<sup>19</sup> Of course, it is also possible to make normative claims about the operation of machines, but there is an essential difference. Whereas in the organism the norms of its operation are endogenously generated and are intrinsically relevant to its own continued existence, in the machine they are imposed by an external agent (usually the machine’s maker or user), who monitors the machine’s operation and evaluates its performance according to his or her own needs or interests.



preset operation upon receiving a stimulus from its environment.<sup>20</sup> In actual fact, because activity is a necessary condition for existence, a stimulus never really triggers the onset of activity in a hitherto inactive organism, but rather modifies the preexisting network of processes that are already occurring within it.<sup>21</sup>

This leads to the important conclusion that, more often than not, it is not so much the nature of the external stimuli as the organism's internal physiological state that determines its reactions and behaviour. And as an organism's current physiological state is a product of the sequence of past events that led to it, it follows that the *history* of an organism fundamentally shapes its behaviour. Again, the contrast with machines is instructive. The operation of a machine is not significantly influenced by its history. After a machine executes its function, its configuration is reset to its default inactive state, and every time this happens the particular historical record of its operation—beyond the gradual wearing down of its parts—is erased. However, because an organism never stops functioning during its lifetime (as we have seen, it *cannot* do so), it never returns to the same exact state. The upshot of all of this is that organisms cannot be fully accounted for without affording careful consideration to their individual historical (i.e. developmental) trajectories.

One last implication of this first lesson is that it explains why organisms are inextricably intertwined with their environment. After all, the incessant activity of organisms that guarantees their continued existence is an activity of exchange *with* their environment. Organisms are totally dependent on their environment for the energy they need to maintain themselves far from equilibrium. In addition, they are quite literally composed of the materials they import from it. It is therefore misleading to presume that an organism can be understood in isolation from the environment in which it is always embedded. This assumption, like so much of what we have discussed, has its basis in the MCO. Although a machine requires energy from outside of itself to carry out its function, its existence does not rely on the fact that it has permanent access to environmental resources. A machine is placed in an environment and reacts to the stimuli it receives from it. An organism, by comparison, is *made* from its environment, and at the same time helps to *construct* it through its activities (which include its metabolic exchanges with it). This process is known as *niche construction*, and it has recently been recognized to have profound consequences for evolution (see Odling-Smee et al. 2003).

#### 4.2. *Second ontological lesson: 'Persistence is grounded in the continuous self-maintenance of form'*

Our second lesson concerns the conundrum of diachronic identity, often referred to as 'the problem of persistence'. As we will see in what follows, taking the SLC as the

<sup>20</sup> This problematic conception has found its way not only into the study of physiology and animal behaviour but also into molecular biology. As Robert Rosen wryly remarked, '[g]enetic engineers, who are the molecular biologists turned technologists, habitually regard their favorite organism, *E. coli*, as a simple vending machine; insert the right token, press the right button, and the desired product is automatically delivered, neatly packaged and ready for harvest' (Rosen 1991: 21).

<sup>21</sup> Chapter 17 illustrates this claim in the context of olfaction.

starting point for our biological ontology forces us to rethink how we individuate and reidentify a particular organism over time. Ordinary physical objects are usually reidentifiable by means of their material constitution, which tends to remain invariant. The problem with streams, flames, and hurricanes is that their identity over time does not coincide with the identity of the materials that compose them. In the same way, the material content of an organism is in constant flux throughout its lifetime. As a result, no two ‘time slices’ of it are materially identical. Only in death, when the organism finally succumbs to thermodynamic equilibrium, does its material constitution stop changing.

The challenge that this poses for understanding biological persistence was carefully examined by Jonas (1966), who concluded, very much in line with the biologists who have advocated the SLC, that in an organism form is *emancipated* from matter. Organismic form exhibits a degree of independence that enables it to continue to exist despite incessant material exchange—indeed *because* of it.<sup>22</sup> For Jonas, organisms invert the ontological relation between matter and form found in inanimate objects like a stone or a lump of iron. Whereas in the latter form is subordinated to matter (as form in such instances reflects nothing more than the contingent spatial configuration of a physical body), in the former it is matter that is subordinated to form (as form here specifies a unified, causally efficacious whole).

Machines, however, are considerably different from stones and lumps of iron in that their form is not merely accidental. As with organisms, their matter is arranged into a specific organization that allows them to perform their function. The relevant difference with regard to organisms, as we noted earlier in the chapter, is that their form is manifested as a fixed structure rather than as a persisting flow. But suppose that a machine kept its form intact despite changes to all of its material parts. What then? The famous ‘ship of Theseus’ of antiquity serves as a convenient example to explore this scenario. According to Greek legend, for centuries this ship performed an annual voyage from Athens to the island of Delos. Over time, the ship underwent numerous repairs and replacements of worn-out parts, until eventually it contained none of its original planks, ropes, or sails. In spite of this, Athenians continued to regard it as the same venerable ship. One could imagine the same situation applying to a number of machines today, such as a medieval cathedral clock still in operation, or a painstakingly restored steam locomotive. The question is: do such machines—let us call them ‘Thesian machines’—exhibit the sort of diachronic identity that characterizes organisms?<sup>23</sup>

<sup>22</sup> Note, however, that the independence of form from matter is not absolute. Form never totally transcends the domain of matter altogether, as it can only emancipate itself from a specific material constitution by adopting *another* material constitution. One should therefore be sceptical of claims by proponents of so-called ‘artificial life’ research that the living form can be logically decoupled from any concrete material instantiation and re-created in a computer medium (for an in-depth examination of this issue, see the essays in Boden 1996).

<sup>23</sup> John Locke, in the second edition of his *Essay Concerning Human Understanding* (published in 1694), already considered a version of this question, noting, in relation to the identity of animals compared to that of machines, that, ‘[i]f we would suppose [a] Machine one continued Body, all whose organized Parts were repair’d, increas’d or diminish’d, by a constant Addition or Separation of insensible Parts, with one Common Life, we should have something very much like the Body of an Animal’ (Locke, quoted in McLaughlin 2001: 177).

On the face of it, organisms and Thesian machines display the same dynamic stability of form. Nevertheless, upon closer examination, we are able to see that they differ in three key respects (cf. Jonas 1968). First, the replacements of the material parts of a Thesian machine are caused from the outside, that is, by an agent other than the machine itself. This is by virtue of the fact that machines are extrinsically purposive. In an organism, on the other hand, the material exchange is caused from within, which means that the organism, being intrinsically purposive, is its own agent of change. Organisms thus persist actively, by maintaining themselves, whereas Thesian machines persist passively, by means of external interventions. Second, the replacement of parts in a Thesian machine does not take place continuously, as a matter of course, but is rather a consequence of contingent events. For example, the ship of Theseus would have required repairs after incurring damage during a thunderstorm or after an accidental collision with rocks near the shore, but it could well have *not* required such repairs, if those particular circumstances had been different. In contrast, the material exchange in an organism is—as we have already discussed—a constant, inviolable feature of its persistence through time; it is neither contingent nor accidental. And, third, the form of an organism does not stay fixed during its lifetime. Organisms grow and develop. Some undergo major morphological changes, such as metamorphosis. Nothing comparable happens to a machine (Thesian or otherwise), given that the fixity of its internal structure is precisely what allows it to perform the function it was designed for.

These differences prevent us from straightforwardly concluding that the maintenance of form, coupled with the exchange of matter, is a sufficient condition for the persistence of organisms—even if it might be for Thesian machines. The maintenance of form in an organism is actually a type of *self-maintenance*. This self-maintenance, moreover, is a *necessary* rather than a contingent occurrence, and it takes place *continuously*, in an uninterrupted sequence of causal events that collectively lead to the progressive modification of the form that is being maintained, as the organism grows and develops. It is clear, then, that, in order to comprehend the persistence of organisms, we must first let go of the MCO in all of its possible manifestations—including hypothetical Thesian ones—and take fully on board their processual nature.

As processes, organisms are extended and differentiated not only in space but also in time. It is wrong to speak of an organism and its history as if the two were somehow separable. Strictly speaking, an organism does not *have* a temporal trajectory; it *is* itself a temporal trajectory. What we perceive as an organism at any point in time represents only a cross section (or a time slice) in the unfolding of the process it instantiates. And it is this entire four-dimensional process, rather than any of its momentary three-dimensional manifestations, that constitutes the actual living entity (cf. Woodger 1930; Torrey 1939).<sup>24</sup> These perdurantist considerations signal

<sup>24</sup> From this perspective, the process of metabolism could be said to take ontological precedence over the organism that undergoes it, given that what appears as an organism at a given time derives its existence from the metabolic process it embodies. This is, I think, what Jonas had in mind when he cryptically remarked that ‘the organism must appear as a function of metabolism rather than metabolism as a function of the organism’ (Jonas 1966: 78).

the importance of *causal continuity* in biological persistence. This criterion of diachronic identity—which indexes the continuous interlinking of temporal states that an entity undergoes—was termed ‘genidentity’ by Kurt Lewin in the 1920s, and it has recently been defended by several philosophers of biology (see Boniolo and Carrara 2004; Guay and Pradeu 2016; and chapters 2, 4, 5, and 11 here).

Let me now try to come to some sort of conclusion. We have seen that it makes no sense to identify an organism over time with the materials that compose it, given that these are constantly being replenished by the whole. The constituents of an organism at any particular instant are only the temporary realization of the self-producing organizational unity of the whole. Unlike the MCO, the SLC accurately reflects the fact that the matter of an organism is necessarily and continuously exchanged while its form is actively maintained. Bringing together the autonomous maintenance of form with the causal continuity of process that makes up a living entity over time, we can draw our second ontological lesson, which is that, as far as organisms are concerned, *persistence is grounded in the continuous self-maintenance of form*.

Two issues require further clarification in relation to this lesson. The first is that, as we have indicated above, to speak of the maintenance of form is not to say that it remains totally fixed over time; form *does* change gradually as the organism develops. It is rather to emphasize that form is stabilized sufficiently to be reidentifiable as an uninterrupted steady state in spite of the constant turnover of matter that realizes it. The second clarification is that the relentless flux of matter entering and leaving the organism does not prevent us from identifying *parts* within it over time.<sup>25</sup> It is important in this context not to confuse material constituents with architectural components. The former are ephemeral and accidental (as they are constantly being exchanged), whereas the latter are persistent and necessary, inasmuch as they contribute—physiologically and morphologically—to the preservation of the organism as a whole.<sup>26</sup>

Before moving on, I wish to draw attention to one more aspect of the diachronic identity of organisms that the SLC can help elucidate, and that is the issue of what may be called ‘cross-generational identity’. If we take seriously the processual idea that the organism is ontologically subsidiary to the self-maintaining metabolic stream that instantiates it at any given moment, then it follows that the identity of this stream can be maintained *across* generations of organisms. Reproduction, in this view, can be reinterpreted as the means by which a self-maintaining metabolic stream perpetuates itself beyond the lifespan of individual organisms (cf. Hardy 1965; Griesemer 2000; Saborido et al. 2011). A key advantage of conceptualizing reproduction in this way is

<sup>25</sup> Part decompositions do not lose their explanatory power when we adopt a processual conception of the organism. Making the case for this epistemological claim, however, would take me beyond the scope of the present discussion.

<sup>26</sup> The organicists drew attention to the contrast between the maintenance of form (both of the whole and of the parts) and the fluidity of matter by distinguishing between the ‘biological’ and the ‘physico-chemical’ viewpoints of the organism. Haldane, for instance, wrote that ‘when we have observed the shape of a friend’s nose we can predict from the *biological* standpoint that it will be the same a year hence, though from a *physical* and *chemical* standpoint a very small portion of the same atoms or molecules may be present in the nose after the year’ (Haldane 1931: 140–1, emphasis added; similar claims can be found in Ritter 1909, Russell 1924, Woodger 1929, and Bertalanffy 1933).

that it is better able to account for *epigenetic inheritance*, as it assumes a far greater degree of continuity between parent and offspring. It is worth elaborating on this point a little. If reproduction essentially boils down to the replication of the genetic material of the parent(s), which—in accordance with the MCO—supplies the blueprint for the *de novo* programmatic construction of the offspring, then epigenetically inherited traits can only be treated as oddities or anomalies. But, if the offspring is construed—in accordance with the SLC—as the offshoot of a self-maintaining metabolic stream (or, in the case of sexual reproduction, as the ‘intersection’ of two such streams), then it is evident that the genetic material is only going to constitute a part (albeit a very important part) of what gets transmitted during reproduction. The essential point is that, within the process-ontological framework of the SLC, the detection of epigenetically inherited traits ceases to be a strange and surprising discovery and comes to be something we would actually expect to find.

#### 4.3. *Third ontological lesson: ‘Order does not entail design’*

We turn now to a third area of biological ontology that can be illuminated by rejecting the MCO and adopting the SLC: the nature and origins of biological order. Organisms and machines are both, to be sure, highly ordered systems. In abstraction from time, their hierarchical structure is quite comparable, which is one of the reasons why the MCO is such a useful heuristic tool. However, when they are considered in time, it becomes apparent that their mode of organization is fundamentally different. Machines exhibit a static organization, in the sense that their physical architecture—as well as the degrees of freedom of their parts—is fixed upon manufacture. Organisms, on the other hand, exhibit a *dynamic* organization in the sense that their form, as we have discussed above, reflects a stabilized pattern of continuous material exchange with their environment. Organismic organization, is dynamic in a further respect, namely in its capacity to modify itself so as to compensate against external perturbations—a feature we have also discussed.

The ontological chasm separating organisms from machines widens even more when we consider the origins of the order they each display. The order of a machine invariably reflects a particular *design*—a preexisting plan, usually in the form of a blueprint or a diagram, which has been implemented by an external agent (i.e. the machine’s creator). The striking thing about the order of all dissipative structures, including organisms, is that it arises in the absence of design. As we noted earlier in the chapter, the recognition that natural systems can spontaneously self-organize from non-linear interactions and become stabilized in far-from-equilibrium conditions through a constant flux of energy and matter is probably the most momentous discovery of non-equilibrium thermodynamics. Nevertheless, it has proven remarkably difficult to incorporate this insight into our biological understanding of organismic order. One reason is undoubtedly that biologists today are more accustomed to thinking about organisms mechanically (in accordance with the MCO) than thermodynamically (in accordance with the SLC).

It is rather ironic that Schrödinger’s *What Is Life?*, which helped to shed light on how life conforms to the second law of thermodynamics, was simultaneously responsible for spawning the modern mechanistic conception of organismic order. Schrödinger argued that the source of all biological order is to be found in the

chemical structure of a single molecule, the self-replicating chromosome, which he conceived as an ‘aperiodic crystal’ in order to account for its stability in the face of thermal fluctuations. In this respect, organisms are no different from machines, which also exhibit rigid, solid-state structures capable of withstanding thermal agitation that enable them to operate in a regular, orderly way. In Schrödinger’s own words, ‘the clue to the understanding of life is that it is based on a pure mechanism, a “clock-work” . . . [that] also hinges upon a solid—the aperiodic crystal forming the hereditary substance, largely withdrawn from the disorder of heat motion’ (Schrödinger 1944: 82, 85).

According to Schrödinger, organisms and machines are both subject to the same preformationist ‘order-from-order’ principle. Just as the order of a clock derives from the preexisting plan of a clockmaker, so the order of an organism derives from the ‘hereditary code-script’ contained in its genome, which specifies ‘the entire pattern of the individual’s future development and . . . its functioning in the mature state’ (ibid., 21). But genes, for Schrödinger, do not just store the information for development; they are also ‘instrumental in bringing about the development they foreshadow. They are law-code and executive power—or, to use another simile, they are architect’s plan and builder’s craft—in one’ (ibid., 22). These provocative ideas served as the basis for the metaphor of the *genetic program*, which came to dominate late twentieth-century developmental biology (see Keller 2000). This incarnation of the MCO equates the embryo with a computer that executes a predetermined set of operations in accordance with a program encoded in its genes. The genetic program model is fraught with problems but, since I have examined them in detail elsewhere (Nicholson 2014), I will refrain from doing so again here. Suffice it to say that it has taken biology decades to remove the misconceptions that resulted from it; indeed they still linger.

Ultimately, Schrödinger was right to suppose that genes are material carriers of information. There *really is* a code connecting DNA to RNA to the primary structure of proteins—a fact that has become enshrined in every biology textbook as ‘the central dogma of molecular biology’. But he was wrong to localize in the genome all the information required to specify the adult organism, and even more so to invest it with the causal power to initiate, control, and direct the developmental process. Ontogeny, it turns out, is a highly heterogeneous process involving the confluence of numerous intersecting causal factors, only some of which have their physical basis in the DNA. Replacing the MCO with the SLC enables us to make sense of this empirical finding. Once we internalize the notion that the organism is a thermodynamically open dissipative structure, we are able to see that its order cannot possibly derive from any one of its material constituents, and that it must instead be construed as a systemic property emerging from the collective dynamics of the complex web of chemical reactions that underlie it.

Organisms are, of course, rather peculiar dissipative structures in that they do not spontaneously self-organize, like whirlpools or tornadoes. This is precisely where genes come into the picture. Genes can be said to encode a historical record of successful modes of self-organization—a record that liberates organisms from the burden of having to ‘reinvent’ the metabolic pathways of chemical transformation they need to survive every time they undergo a reproductive cycle (cf. Schneider and Kay 1995; Weber and Depew 2001). From the perspective of the SLC, the role of

genes is not to initiate, control, or direct development, but rather to constrain the possible paths of dynamically stable forms of self-organization to those with the highest probability of producing a viable, structurally and functionally differentiated adult. The genome, in this view, constitutes a sort of *catalogue* or *database* of effective self-organization strategies that is transmitted from one generation to the next in a given lineage. What follows from this empirically motivated reconceptualization is the conclusion that biological order does not come preformed in a static ‘order-from-order’ structure (as Schrödinger famously conjectured), but rather emerges progressively, through an epigenetic ‘order-from-disorder’ process.<sup>27</sup> By restating this thesis in simpler, more straightforward terms, we arrive at our third and final ontological lesson, which is that, in biology, *order does not entail design*.

## 5. Conclusions

After the scientific revolution, the notion that nature is a well-oiled machine proved irresistible. The machine metaphor conforms to our naïve, pre-theoretical expectations about the world, which are grounded in good old-fashioned substance metaphysics; and the profitable deployment of this metaphor in different areas of scientific inquiry historically served to reaffirm such preconceptions. This, in turn, helped to legitimize the ontological adequacy of the metaphor, and it vindicated the mechanistic conviction that nature is lawful, deterministic, and totally explainable in reductionistic terms. Over the past century, however, we have slowly been coming to the realization that that this view of nature simply does not work (cf. Whitehead 1925; Prigogine and Stengers 1984; Dupré 1993). Physicists first, and biologists more recently, have begun to challenge the substantialist assumptions that underlie the mechanistic worldview, which emerged with the rise of modern science.

As far as the living world is concerned, non-equilibrium thermodynamics demonstrates with piercing clarity that organisms are not fixed things with predefined sets of unchanging properties, but resilient *processes* exhibiting dynamic stabilities relative to particular timescales. What I have sought to convey in this chapter is that the findings of thermodynamics render elaborate philosophical arguments in support of a processual view of life almost unnecessary. The idea that an organism is an open system which must constantly exchange energy and matter with its environment in order to keep itself far from equilibrium is not a metaphysical claim but a scientific fact. Of course, a great deal needs to be said philosophically about what kind of processes organisms are and what exactly follows from their processual nature. But the crucial point is that, if we want an ontology of life that is grounded and informed by natural science, then a processual account is unavoidable. Whatever else

<sup>27</sup> Interestingly, Schrödinger actually discussed an ‘order from disorder’ principle in *What Is Life?*, but he took it to apply exclusively to the sort of order described by statistical mechanics, which arises from the statistical averaging of vast numbers of molecules that, taken together, display regular, law-like patterns of behaviour (e.g. diffusion). The very possibility of order spontaneously emerging in far-from-equilibrium conditions did not even occur to him.

organisms may be, what cannot be denied is that they are stable metabolic flows of energy and matter.

As the MCO is the perfect biological embodiment of the commitments of substance metaphysics, in order to come to terms with the processual nature of life we require a different theoretical conception of the organism. We have seen that the history of biological thought already furnishes us with one such alternative, the SLC, which, although harking back to Heraclitus, only became fully articulated in the nineteenth and twentieth centuries—often in explicit opposition to the MCO. By metaphorically appealing to familiar non-living dissipative structures, the SLC enables us to grasp, in simple and evocative terms, the dynamic, far-from-equilibrium features of organisms that a thermodynamic perspective compels us to consider. And, just as the MCO has an impressive range of incarnations (the organism has been variously construed as a clock, a steam engine, a chemical factory, or a computer, depending on context and historical period), so does the SLC prove to be remarkably versatile in its manifestations, invoking as it does streams, vortices, whirlpools, or flames, depending on the aspects of the organism being highlighted. Of course, organisms are quite different from all of these entities, and consequently their correspondence with them is necessarily incomplete. But the SLC is still a considerable improvement on the MCO, as it accurately portrays the physical conditions of life and provides the foundation for a scientifically grounded understanding of the organism capable of making sense of its processual nature.

Taking the SLC as the cornerstone of our biological ontology has a number of interesting philosophical consequences. We have had the opportunity to explore in some depth three such consequences, which we have formulated as ‘lessons’ in order to underscore the pedagogical payoff of reconceptualizing the organism from complex machine to flowing stream. Importantly, this process of reconceptualization does not render the MCO useless or irrelevant; on the contrary, it highlights its enormous heuristic value. We should not underestimate the fact that it is only by uncovering how the MCO *fails* to truthfully capture the organism that we have managed to elucidate its processual nature and derive our three ontological lessons. Bertalanffy was quite right to remark that ‘we cannot speak of a machine “theory” of the organism, but at most of a machine fiction’ (Bertalanffy 1933: 38). It remains, nevertheless, an *extremely useful* fiction.

With regard to the SLC itself, our discussion has shown that it displays a number of features that we tend to look for in a scientific theory: it is able to organize a large body of facts, establish connections between seemingly disparate concepts, and make sense of unexpected empirical findings. By adopting the SLC we have found a way to think naturalistically about normativity and agency, we have grasped the ineliminable role that history plays in shaping biological behaviour, and we have accounted for the inextricable link between organism and environment. The SLC has also given us a new handle on the problem of persistence, and it has allowed us to understand why organismic order needs to be construed as a systemic property. In addition, it has helped us come to terms with certain phenomena, such as niche construction and epigenetic inheritance, which seem perplexing and intractable when viewed from the perspective of the MCO. Finally, at a most general level, we have seen how the SLC brings biological principles into closer contact with physical ones by means of



non-equilibrium thermodynamics, thereby paving the way for a non-reductionist, non-mechanicist reconciliation of biology with physics.

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## References

- Alberts, B. (1998). The Cell as a Collection of Protein Machines: Preparing the Next Generation of Molecular Biologists. *Cell* 92: 291–4.
- Barandiaran, X., Di Paolo, E., and Rohde, M. (2009). Defining Agency: Individuality, Normativity, Asymmetry and Spatio-Temporality in Action. *Journal of Adaptive Behavior* 17: 367–86.
- Barham, J. (2012). Normativity, Agency, and Life. *Studies in History and Philosophy of Biological and Biomedical Sciences* 43: 92–103.
- Bertalanffy, L. von. (1932). *Theoretische Biologie*, vol. 1: *Allgemeine Theorie, Physikochemie, Aufbau und Entwicklung des Organismus*. Berlin: Gebrüder Borntraeger.
- Bertalanffy, L. von. (1933). *Modern Theories of Development: An Introduction to Theoretical Biology*. Oxford: Oxford University Press.
- Bertalanffy, L. von. (1942). *Theoretische Biologie*, vol. 2: *Stoffwechsel, Wachstum*. Berlin: Gebrüder Borntraeger.
- Bertalanffy, L. von. (1950). The Theory of Open Systems in Physics and Biology. *Science* 111: 23–9.
- Bertalanffy, L. von. (1952). *Problems of Life: An Evaluation of Modern Biological and Scientific Thought*. New York: Harper & Brothers.
- Bertalanffy, L. von. (1967). *Robots, Men, and Minds: Psychology in the Modern World*. New York: George Braziller.
- Bickhard, M. H. (2000). Autonomy, Function and Representation. *Communication and Cognition* (Special issue) 17: 111–31.
- Black, M. (1962). *Models and Metaphors: Studies in Language and Philosophy*. Ithaca, NY: Cornell University Press.
- Boden, M. A. (ed.). (1996). *The Philosophy of Artificial Life*. Oxford: Oxford University Press.
- Boniolo, G. and Carrara, M. (2004). On Biological Identity. *Biology & Philosophy* 19: 443–57.
- Brillouin, L. (1949). Life, Thermodynamics, and Cybernetics. *American Scientist* 37: 554–68.
- Brooks, D. R. and Wiley, E. O. (1986). *Evolution as Entropy: Toward a Unified Theory of Biology*. Chicago: University of Chicago Press.
- Brown, T. L. (2003). *Making Truth: Metaphor in Science*. Urbana: University of Illinois Press.
- Campbell, R. J. (2009). A Process-Based Model for an Interactive Ontology. *Synthese* 166: 453–77.
- Cannon, W. B. (1929). Organization for Physiological Homeostasis. *Physiological Reviews* 9: 399–431.

- Christensen, W. (2012). Natural Sources of Normativity. *Studies in History and Philosophy of Biological and Biomedical Sciences* 43: 104–12.
- Coleman, W. (1977). *Biology in the Nineteenth Century: Problems of Form, Function, and Transformation*. Cambridge: Cambridge University Press.
- Collingwood, R. G. (1945). *The Idea of Nature*. Oxford: Oxford University Press.
- Cuvier, G. (1833). *The Animal Kingdom, Arranged in Conformity with Its Organization*. New York: G. & C. & H. Carvill.
- Dawkins, R. (1986). *The Blind Watchmaker*. New York: Norton.
- Dawkins, R. (1998). Universal Darwinism. In D. L. Hull and M. Ruse (eds), *The Philosophy of Biology* (pp. 15–37). Oxford: Oxford University Press.
- Dear, P. (2006). *The Intelligibility of Nature: How Science Makes Sense of the World*. Chicago: Chicago University Press.
- Dijksterhuis, E. J. (1961). *The Mechanization of the World Picture*. New York: Oxford University Press.
- Dupré, J. (1993). *The Disorder of Things: Metaphysical Foundations of the Disunity of Science*. Cambridge, MA: Harvard University Press.
- Gilbert, S. F. (1982). Intellectual Traditions in the Life Sciences: Molecular Biology and Biochemistry. *Perspectives in Biology and Medicine* 26: 151–62.
- Griesemer, J. (2000). Reproduction and the Reduction of Genetics. In P. Beurton, R. Falk, and H.-J. Rheinberger (eds), *The Concept of the Gene in Development and Evolution: Historical and Epistemological Perspectives* (pp. 240–85). Cambridge: Cambridge University Press.
- Guay, A. and Pradeu, T. (2016). To Be Continued: The Genidentity of Physical and Biological Processes. In A. Guay and T. Pradeu (eds), *Individuals Across the Sciences* (pp. 317–47). New York: Oxford University Press.
- Haag, J. W., Deacon, T. W., and Ogilvy, J. (2011). The Emergence of Self. In J. W. van Huyssteen and E. P. Wiebe (eds), *In Search of Self* (pp. 319–37). Grand Rapids: William B. Eerdmans.
- Haldane, J. B. S. (1940). *Keeping Cool and Other Essays*. London: Chatto & Windus.
- Haldane, J. S. (1917). *Organism and Environment, as Illustrated by the Physiology of Breathing*. New Haven: Yale University Press.
- Haldane, J. S. (1919). *The New Physiology and Other Addresses*. London: Charles Griffin.
- Haldane, J. S. (1931). *The Philosophical Basis of Biology*. London: Hodder & Stoughton.
- Hardy, A. C. (1965). *The Living Stream: A Restatement of Evolution Theory and Its Relation to the Spirit of Man*. London: Collins.
- Henderson, L. J. (1913). *The Fitness of the Environment*. New York: Macmillan.
- Henning, B. G. and Scarfe, A. C. (eds). (2013). *Beyond Mechanism: Putting Life Back into Biology*. Lanham: Lexington Books.
- Hobbes, T. (1996). *Leviathan*, ed. by R. Tuck. Cambridge: Cambridge University Press.
- Huxley, T. H. (1870). Address to the British Association: Liverpool Meeting, 1870. *Nature* 2: 400–6.
- Jacob, F. (1973). *The Logic of Life: A History of Heredity*. New York: Pantheon.
- Johnstone, J. (1921). *The Mechanism of Life in Relation to Modern Physical Theory*. London: Edward Arnold.
- Jonas, H. (1953). A Critique of Cybernetics. *Social Research* 20: 172–92.
- Jonas, H. (1966). *The Phenomenon of Life: Toward a Philosophical Biology*. Evanston: Northwestern University Press.
- Jonas, H. (1968). Biological Foundations of Individuality. *International Philosophical Quarterly* 8: 231–51.
- Kapp, R. O. (1954). Living and Lifeless Machines. *British Journal for the Philosophy of Science* 5: 91–103.

- Kauffman, S. (1995). *At Home in the Universe: The Search for Laws of Self-Organization and Complexity*. Oxford: Oxford University Press.
- Keller, E. F. (1995). *Refiguring Life: Metaphors of Twentieth-Century Biology*. New York: Columbia University Press.
- Keller, E. F. (2000). *The Century of the Gene*. Cambridge, MA: Harvard University Press.
- Keller, E. F. (2008). Organisms, Machines, and Thunderstorms: A History of Self-Organization, Part One. *Historical Studies in the Natural Sciences* 38: 45–75.
- Kirschner, M., Gerhart, M., and Mitchison, T. (2000). Molecular ‘Vitalism’. *Cell* 100: 79–88.
- Lewontin, R. C. (2000). *The Triple Helix: Gene, Organism, and Environment*. Cambridge, MA: Harvard University Press.
- Lillie, R. S. (1945). *General Biology and Philosophy of Organism*. Chicago: University of Chicago Press.
- Maasen, S., Mendelsohn, E., and Weingart, P. (eds). (1995). *Biology as Society, Society as Biology: Metaphors*. Dordrecht: Kluwer.
- Maturana, H. R. and Varela, F. J. (1980). *Autopoiesis and Cognition: The Realization of the Living*. Dordrecht: Reidel.
- McLaughlin, P. (2001). *What Functions Explain: Functional Explanation and Self-Reproducing Systems*. Cambridge: Cambridge University Press.
- Monod, J. (1971). *Chance and Necessity: An Essay on the Natural Philosophy of Modern Biology*. Glasgow: Williams Collins Sons.
- Moreno, A. and Mossio, M. (2015). *Biological Autonomy: A Philosophical and Theoretical Enquiry*. Dordrecht: Springer.
- Mossio, M., Saborido, C., and Moreno, A. (2009). An Organizational Account of Biological Functions. *British Journal for the Philosophy of Science* 60: 813–41.
- Needham, J. (1928). Recent Developments in the Philosophy of Biology. *Quarterly Review of Biology* 3: 77–91.
- Nicholson, D. J. (2013). Organisms  $\neq$  Machines. *Studies in History and Philosophy of Biological and Biomedical Sciences* 44: 669–78.
- Nicholson, D. J. (2014). The Machine Conception of the Organism in Development and Evolution: A Critical Analysis. *Studies in History and Philosophy of Biological and Biomedical Sciences* 48: 162–74.
- Nicholson, D. J. and Gawne, R. (2015). Neither Logical Empiricism nor Vitalism, but Organicism: What the Philosophy of Biology Was. *History and Philosophy of the Life Sciences* 37: 345–81.
- Nicolis, G. and Prigogine, I. (1977). *Self-Organization in Non-Equilibrium Systems: From Dissipative Structures to Order through Fluctuations*. New York: J. Wiley & Sons.
- Odling-Smee, J., Laland, L., and Feldman, M. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton: Princeton University Press.
- Oparin, A. I. (1961). *Life: Its Nature, Origin and Development*. Edinburgh: Oliver & Boyd.
- Prigogine, I. and Stengers, I. (1984). *Order Out of Chaos: Man’s New Dialogue with Nature*. Toronto: Bantam Books.
- Rescher, N. (1996). *Process Metaphysics: An Introduction to Process Philosophy*. Albany: SUNY Press.
- Ritter, W. E. (1909). Life from the Biologist’s Standpoint. *Popular Science Monthly* 75: 174–90.
- Rosen, R. (1991). *Life Itself: A Comprehensive Inquiry into the Nature, Origin, and Fabrication of Life*. New York: Columbia University Press.
- Russell, E. S. (1924). *The Study of Living Things: Prolegomena to a Functional Biology*. London: Methuen.
- Saborido, C., Mossio, M., and Moreno, A. (2011). Biological Organization and Cross-Generation Functions. *British Journal for the Philosophy of Science* 62: 583–606.

- Schneider, E. D. and Kay, J. J. (1995). Order from Disorder: The Thermodynamics of Complexity in Biology. In M. P. Murphy and L. A. J. O'Neill (eds), *What Is Life? The Next Fifty Years* (pp. 161–73). Cambridge: Cambridge University Press.
- Schrödinger, E. (1944). *What Is Life? The Physical Aspect of the Living Cell*. New York: Macmillan.
- Sherrington, C. S. (1940). *Man on His Nature*. Cambridge: Cambridge University Press.
- Sinnott, E. W. (1955). *The Biology of the Spirit*. New York: Viking Press.
- Taylor, R. (1950). Comments on a Mechanistic Conception of Purposefulness. *Philosophy of Science* 17: 310–17.
- Torrey, T. W. (1939). Organisms in Time. *Quarterly Review of Biology* 14: 275–88.
- Waddington, C. H. (1957). *The Strategy of the Genes*. London: George Allen & Unwin.
- Weber, B. H. and Depew, D. J. (2001). Developmental Systems, Darwinian Evolution, and the Unity of Science. In S. Oyama, P. E. Griffiths, and R. D. Gray (eds), *Cycles of Contingency: Developmental Systems and Evolution* (pp. 239–53). Cambridge, MA: MIT Press.
- Weber, B. H., Depew, D. J., Dyke, C., Salthe, S. N., Schneider, E. D., Ulanowicz, R. E., and Wicken, J. S. (1989). Evolution in Thermodynamic Perspective: An Ecological Approach. *Biology & Philosophy* 4: 373–405.
- Whewell, W. (1840). *The Philosophy of the Inductive Sciences*, vol. 2. London: John W. Parker.
- Whitehead, A. N. (1925). *Science and the Modern World*. Cambridge: Cambridge University Press.
- Wicken, J. S. (1987). *Evolution, Thermodynamics, and Information: Extending the Darwinian Program*. Oxford: Oxford University Press.
- Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton: Princeton University Press.
- Woese, C. R. (2004). A New Biology for a New Century. *Microbiology and Molecular Biology Reviews* 68: 173–86.
- Woodger, J. H. (1929). *Biological Principles: A Critical Study*. London: Routledge & Kegan Paul.
- Woodger, J. H. (1930). The 'Concept of Organism' and the Relation between Embryology and Genetics, Part I. *The Quarterly Review of Biology* 5: 1–22.