

A Manifesto for a Processual Philosophy of Biology

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Abstract

This chapter argues that scientific and philosophical progress in our understanding of the living world requires that we abandon a metaphysics of things in favour of one centred on processes. We identify three main empirical motivations for adopting a process ontology in biology: metabolic turnover, life cycles, and ecological interdependence. We show how taking a processual stance in the philosophy of biology enables us to ground existing critiques of essentialism, reductionism, and mechanicism, all of which have traditionally been associated with substance ontology. We illustrate the consequences of embracing an ontology of processes in biology by considering some of its implications for physiology, genetics, evolution, and medicine. And we attempt to locate the subsequent chapters of the book in relation to the position we defend.

Keywords: philosophy of biology; process ontology; metaphysics of science; organicism; essentialism; reductionism; mechanism; metabolism; life cycles; symbiosis

1. Introduction

This book is a venture in the metaphysics of science, the exploration of the most basic features of the world implied or presupposed by science. One of its main aims is to demonstrate the fundamental importance of such an investigation. Getting this very general picture right makes a real difference to whether we do the science well and understand properly what it tells us. The particular metaphysical thesis that motivates this book is that the world—at least in so far as it concerns living beings—is not, as philosophers have overwhelmingly assumed, made up of substantial particles or things, but of processes. It is dynamic through and through. This thesis, we believe, has profound consequences.

More specifically, we propose that the living world is a hierarchy of processes, stabilised and actively maintained at different timescales. We can think of this hierarchy in broadly mereological terms: molecules, cells, organs, organisms, populations, etc. Although the members of this hierarchy are usually thought of as things, we contend that they are more appropriately understood as processes. A question that arises for any process, as we shall discuss in more detail below, is what enables it to persist. The processes in this hierarchy not only compose one another but also provide conditions for the persistence of other members, both larger and smaller. So if we take, for example, a liver, we see that it provides enabling conditions for the persistence of the organism of which it is an organ, but also for the hepatocytes that compose it. Outside a very specialised laboratory, a hepatocyte can persist only in a liver. And reciprocally, for a liver to persist it requires both an organism in which it resides, and hepatocytes of which it is composed. A key point is that these reciprocal dependencies are not merely structural, but are also grounded in activity. A hepatocyte sustains a liver, and a liver an organism, by doing things. This ultimately underlies our insistence on seeing such seemingly substantial entities as cells, organs, and organisms as processes.

These processes—which have so often been taken for things, or substances—themselves engage in more familiar-sounding processes such as metabolism, development, and evolution; processes that, again, often provide the explanations of the persistence of more thing-like, or continuant processes. Do we not need things to undergo such non-controversially processual occurrences as metabolism, development, and evolution? Should we not be dualists, endorsing a world of both things and the processes they undergo? There are many responses to this line of thought, but the minimal condition for a position to count as the kind of process ontology we endorse is that processes are, in some sense, more fundamental than things. What this means, in very general terms, is that the existence of things is conditional on the existence of processes. Our own preferred view of this kind, which we shall elaborate later, is that things should be seen as abstractions from more or less stable processes. Peter Simons, in his essay in this volume, suggests that things are ‘precipitates’ of processes.

How might one argue for or against a thesis of this kind? One traditional philosophical answer appeals to pure argument or reason. Perhaps, as Kant thought, there are deep truths about the world that must be assumed if it is to be possible for us to gain empirical knowledge of it, presuppositions, therefore, of the possibility of science. Or perhaps the way our language works points to facts that are deeper and more universal than the local discoveries of science, facts therefore foundational to any specific empirical claims.

Without wanting to deny the value of such philosophical strategies, our conception of the metaphysics of science includes a conviction that such a project must proceed in dialogue with what science actually tells us about the world. In common with most of the contributors to this volume, we advocate a naturalistic metaphysics. That is to say, we think that the examination of scientific findings points us towards pictures of the world at a more abstract level than is the immediate target of scientific research. We believe that as such pictures become established they can, in turn, throw new light even on quite specific issues within the science on which they are grounded. To use a term that has become unfashionable in some philosophical quarters, the relation between science and metaphysics is dialectical.

We are commonly asked whether a processual philosophy of biology should really be an ontological project rather than, perhaps more modestly, an epistemological one. Is it not enough to claim that the idea of process provides a more effective conceptual instrument for approaching nature? Several authors in this collection advocate something like this position. But in light of our naturalistic approach to metaphysics, we do not see a great difference between this position and the more metaphysical formulation that we prefer. Given this naturalism, metaphysics is generally to be established through empirical means, and is ultimately therefore answerable to epistemology. Scientific and metaphysical conclusions do not differ in kind, or in the sorts of arguments that can be given for them, but rather in generality and abstraction. If it turns out that process is indeed the right concept to make sense of nature, then this is as good reason as we can expect for taking nature to be ontologically composed of process.

Although metaphysical conclusions are more abstract and general than what are normally taken to be scientific findings, they are not indefinitely so. The essays in this volume offer many reasons for thinking that the living world is a world of processes rather than a world of things, although we do not take this to demonstrate conclusively that the world is universally a process world. We do, as a matter of fact, believe that there are compelling reasons to interpret the physical world more generally in terms of process as well, and if that is right, it is hard to see where we should expect to find exceptions to a universal processualism. But the argument must be made piecemeal.

We proceed as follows. We begin by reviewing what we take to be the major milestones in the history of process philosophy, and we then consider some early twentieth-century attempts to develop a processual view of the living world, which turn out to have considerable relevance for our project. Following this, we outline our particular conception of process ontology, as well as our understanding of what processes are and of how they relate to things, or substances. We then examine some of the key empirical findings of biology that have prompted us to adopt the processualism we defend, and we illustrate the value of taking a processual stance in a number of prominent philosophical debates. Finally, we discuss several important consequences of embracing an ontology of processes in various areas of biology. We conclude by providing a brief overview of the rest of the essays in this volume.

2. Historical Background

The opposition between things and processes as the ultimate constituents of reality is of course an ancient one, commonly traced all the way back to the Presocratics. Heraclitus is the patron saint of process philosophy, at least in the Western tradition.¹ The Greek motto *panta rhei* (i.e. ‘everything flows’) encapsulates the Heraclitean doctrine of universal flux. Heraclitus not only emphasised the pervasiveness of change, but also signalled the importance of change in explaining stability over time (Graham 2015). The antithesis of this view is the atomism of Leucippus and Democritus. The indivisible and unchanging material atoms of this tradition provided paradigms for traditional substances.

Parmenides was another early advocate of substantialism. Although his static view of the world proved too extreme for most subsequent philosophers to accept, his conviction that permanence is more fundamental, and more real, than change became one of the core principles of Western metaphysics. It was enthusiastically adopted by Plato in his changeless realm of eternal Forms or Ideas, and also by Aristotle who, whilst locating these essential Forms in worldly entities, nonetheless remained committed to their unchanging character. Aristotelian substances, which are the basic entities of his metaphysics, are distinguished as substances of particular kinds by their essence, and this essence sets unbreachable limits on the kinds of changes that an individual substance can undergo. It is difficult to overstate how influential this essentialist view has been. Many substantialists to this day follow Aristotle in asserting that to be a thing one must be a thing of a certain kind, and that the kind to which a thing belongs determines what changes it can undergo and still be what it is.

It is interesting to observe that Aristotle’s own thought is in many respects more congenial to a process perspective than that of his followers, and this surely has to do with his lifelong fascination with biology. Aristotle took organisms as exemplars of his conception of substances, and consequently conceived them teleologically so as to recognise and unite the different stages of the developmental cycle organisms go through. But despite his awareness of the distinctive dynamicity of living beings, Aristotle is still best described as a substance ontologist.² Historically speaking, Aristotelian metaphysics provided the foundation for the substantialist philosophy that was developed by scholastic thinkers during the medieval period.

¹ For reasons of space as well as of expertise, we restrict ourselves here to the debate within Western philosophy. It is worth noting, however, that process-centred views of reality are quite prominent in non-Western philosophical traditions, for example in Buddhist thought (see, e.g., Carpenter 2014).

² Accordingly, the deployment of his ideas in modern biological theory raises a number of problems. For example, it seems difficult to see how the essences Aristotle postulated could encompass either the indefinite developmental plasticity now acknowledged to be a characteristic of organisms (West-Eberhard 2003), or the changes that kinds of organisms undergo over the course of evolution.

Although the Scientific Revolution is often thought of as a revolt from Aristotelianism, it was certainly not a rejection of substantialism. A central reason for this was the revival of atomism by Boyle, Newton, and others. An atom is a thing, or substance, if anything is. The atoms of early modern science were eternal and permanent in their intrinsic properties. Changes experienced in our macroscopic world were attributed to the motions of, and rearrangements of the relations between, underlying atoms, which remained unchanged throughout such interactions. It is true that for Locke, perhaps the leading exponent of this philosophy, our lack of access to the microscopic world of atoms led him to a notorious scepticism about the kinds of entities that we encounter at the macroscopic level. As a result, he did not assume that biological kinds, such as cats or dogs, partook of a common underlying essence. However, this did not contradict his substantialist philosophy; it only restricted our ability to know what kind of substance, if any, they exemplified.

Various philosophers in subsequent centuries can be associated to some degree with process thinking. Leibniz criticised Descartes' conception of material substance for its lack of activity, and is often considered a process metaphysician, though we are inclined to think that his system of inherently active 'monads' is too idiosyncratic to lend much support to the process cause, at least as we understand it. Hegel's metaphysics of becoming, wherein nature progressively self-differentiates through the operation of a dialectic that continually integrates conflicting opposites into ever new unities, provides something more unequivocally processual. In fact, attempts to apply dialectical materialism to biology—from Engels' *Dialectics of Nature* to Richard Levins' and Richard Lewontin's *The Dialectical Biologist* (1985)—have many commonalities with the present project. The American pragmatists, especially James and Dewey, deserve a mention as well, as they formulated a distinctly processual philosophy in order to come to terms with the implications of Darwin's theory of evolution, though, given their pragmatism, more from an epistemological than an ontological perspective. Nevertheless, the figure that has come to be most closely associated with process thinking in recent times is unquestionably Alfred North Whitehead, who articulated a comprehensive metaphysical system that conceived the world as a unified, dynamic, and interconnected whole.

Nowadays process philosophy has become almost synonymous with Whitehead's work.³ Without in any way wishing to detract from Whitehead's importance to the development of process thought, for the purposes of our present project we wish to distance ourselves from the association with Whiteheadian metaphysics. One reason for this is that Whitehead's most systematic metaphysical treatise, *Process and Reality* (1929), is generally agreed to be opaque and at times so obscure as to verge on the unintelligible. His system confers unconventional meanings to familiar concepts (e.g. organism, nexus, satisfaction) and it introduces a number of neologisms (e.g. prehension, concrescence, superject) and idiosyncratic technical terms (e.g. actual occasion, subjective aim, extensive continuum) that we have not found particularly helpful in developing the ideas that interest us concerning living systems. We also disagree with Whitehead regarding his insistence on conceiving reality in atomistic terms—a feature of his process metaphysics that we shall return to later. Finally, and perhaps most importantly, the panpsychist foundations of Whitehead's system, not to mention its theological character, are hard to reconcile with the naturalistic perspective we uphold.

³ To illustrate, the journal *Process Studies* defines its subject "as referring primarily, although not exclusively, to the philosophy of Alfred North Whitehead and his intellectual associates". The Australasian journal for process thought is named after one of Whitehead's neologisms, *Concrescence*. And the European Society for Process Thought declares in its mission statement that "[t]he society focuses on Alfred North Whitehead's thought in all its aspects".

For the above reasons, we have found that Whitehead is sometimes as much a liability to process thought—associating it with undesirable philosophical baggage and off-putting prose—as a valuable exponent. In fact, we suspect that process philosophy has not received the attention it deserves partly because of its close association with Whitehead’s work.⁴ So, while we are happy to acknowledge the significance of Whiteheadian metaphysics, the reader will not find in this essay, or in any of the ensuing chapters, exegetical discussions of the Category of the Ultimate, the eight Categories of Existence, the twenty-seven Categories of Explanation, or the nine Categorical Obligations enshrined in *Process and Reality*. All things considered, we are more inclined to risk reinventing the wheel than to look for the concepts and theses we want in Whitehead’s metaphysical system.

3. The Organicist Precedent

Surprisingly, perhaps, we have found Whitehead to be more useful to us through his influence on an important group of early twentieth-century biologists than through direct engagement with his own work. The members of this collective, known as the *organicists*, produced a large body of literature in the philosophy of biology that predates by several decades the publications generally assumed to have given rise to the modern discipline (Nicholson and Gawne 2015). Interestingly, the book by Whitehead that exerted the greatest influence on the organicists was not *Process and Reality*, but *Science and the Modern World* (1925). This earlier work, written in more accessible prose and without much of the conceptual apparatus that characterises his later metaphysical writings, presented a condensed history of scientific ideas and argued that the mechanistic, reductionist, and determinist view of nature that had reigned supreme since the seventeenth century was no longer defensible in light of the revolutionary developments of modern physics.

In place of this obsolete worldview, Whitehead advocated a philosophy of nature that stressed the development, organization, and interdependence of all things, and he recognised that these concepts were far more congenial to biology than to physics. Biology, Whitehead observed, had historically relied for its development on the solid epistemological bedrock of classical physics, but it could no longer afford to do so; it had to spring forth as a unified, autonomous science by carefully scrutinizing and rebuilding its conceptual foundations in accordance with its own needs. As he put it, “the progress of biology [...] has probably been checked by the uncritical assumption of half-truths. If science is not to degenerate into a medley of *ad hoc* hypotheses, it must become philosophical and must enter upon a thorough criticism of its own foundations” (Whitehead 1925: 25). The organicists adopted this as a rallying cry in their cause to develop a new philosophy of biology that would emancipate their science from both the physicochemical reductionism of mechanism and the obscurantist holism of vitalism in coming to terms with life’s dynamic, systemic, and purposive character.⁵

The noted physiologist John Scott Haldane (father of J. B. S. Haldane) was the first to use the label ‘organicism’ to describe his own views. Looking back at his writings it is easy to discern a processual thread running through them. Haldane regarded the organism as an integrated and coordinated whole exhibiting a “delicate regulation [that] is maintained, day after day, and year

⁴ There are notable exceptions, however. Recent attempts to extricate process philosophy from Whitehead’s particular version of it can be found in Nicholas Rescher’s *Process Metaphysics* (1996) and in Johanna Seibt’s *Process Theories* (2003). The Stanford Encyclopedia of Philosophy entry on ‘process philosophy’ (Seibt 2012) also discusses the topic in general terms rather than in the specific context of Whitehead’s own framework.

⁵ Many of the British organicists came together in what came to be known as the Theoretical Biology Club, a group of biological thinkers interested in interdisciplinary approaches to the problem of organization which held regular meetings during the 1930s (see Abir-Am 1987; Peterson 2016).

after year, in spite of all kinds of changes in the external environment, and in spite of the metabolic changes constantly occurring in all living tissues” (Haldane 1917: 17). He observed that organisms remain physiologically constant over time even though, from a purely physical perspective, they are highly dynamic eddies of matter. “They 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” (ibid.: 90). When we study the living world, according to Haldane, we are not really dealing with material things at all, but with stabilised processes. He even went as far as to remark that “[t]he conception of a ‘thing’, or material unit, is [...] useless in the interpretation of distinctively biological facts” (Haldane 1919: 125).

Another prominent organicist was Edward Stuart Russell, who is probably best known today for his historical treatise *Form and Function* (1916). In his later, more philosophical works, Russell repeatedly emphasised the purposive character of organisms, which are always striving “actively towards an end, whether of self-development, self-maintenance or the continuance of the race” (Russell 1924: 56). Underlying this was a deeply processual understanding of the organism, which Russell described as “essentially an activity in course of passage, changing from one form to another, always developing or regressing, but never standing still” (ibid.). Like most other organicists, Russell criticised the machine conception of the organism for neglecting the inherent dynamicity of life, asserting that “[t]he organism is *not*, like a machine, a static construction, but a constantly changing organization of functional activities” (Russell 1930: 169). Russell also drew attention to the temporal character of the organism, which “at any one moment of its history must be regarded as merely a phase of a life-cycle”, insisting that “[i]t is the whole cycle that is the life of the individual” (ibid.: 171). As he put it in a subsequent discussion, “[i]t is as a life-cycle progression and not as a static organisation that the living thing is ultimately to be conceived” (Russell 1945: 186).

Joseph Henry Woodger was a further exponent of organicism. Although today he is mostly remembered—and derided—for his attempts to formalise biological theories, Woodger published a number of non-formal philosophical works in which he articulated a processual view of life (see Nicholson and Gawne 2014). Like Russell, he felt that “[t]here is an urgent necessity for a consideration of *temporal* relations” (Woodger 1929a: 299), and he was perhaps the first philosopher of biology to examine the issue in a systematic way. The following quotation, taken from his *Biological Principles*, offers a flavour of his discussions of the topic:

An organism, whatever else it may be, is an event—something happening. It is temporally as well as spatially extended. It has temporal as well as spatial parts. Your pet dog to-day and your pet dog yesterday are two *different* temporal parts of the same dog, just as his head and his tail are two different *spatial* parts of the same dog. It is in virtue of the particular kind of continuity of the dog yesterday and the dog to-day that we call it the ‘same’, and this seems to be the proper sense of the term. But it can no more be taken for granted that to-day’s temporal part is the same as yesterday’s than it can be taken for granted that one spatial part, e.g. the head is the same as another, e.g. the tail. We know, in fact, that they are not the same. Organisms are temporally as well as spatially differentiated. (Woodger 1929a: 219)

Conrad Hal Waddington is probably the most familiar of the organicists nowadays, as his work has for some time been an inspiration to philosophers of biology sceptical of various aspects of the Modern Synthesis.⁶ Waddington remained a committed processualist throughout his career

⁶ The Modern Synthesis is the term given to the general theoretical framework of evolutionary biology articulated in the mid twentieth-century that combined Darwinian natural selection with Mendelian genetics in the form of population genetics, and which was used to bring together many aspects of comparative anatomy, systematics, ecology, and palaeontology under a common set of explanatory principles.

(see Waddington 1969). “The fundamental characteristics of the organism”, he wrote in *The Strategy of the Genes*, “are time-extended properties” (Waddington 1957: 189). Biology does not study things; it studies processes occurring at various timescales. According to Waddington, to fully understand an organism one has to consider how it is affected by four distinct types of temporal change—studied, in turn, by four different branches of biology—all of which are proceeding simultaneously and continuously at various rates:

An animal functions from minute to minute or from hour to hour, in feeding, digesting, respiring, using its muscles, nerves, glands and so on. These processes of *physiological* functioning may be repeated within periods of time which are short in comparison with the lifetime of an individual animal. But there is an equally important set of processes, of a slower tempo, which require appreciable fractions of the life-history and are repeated only a few times, if at all, during one life-cycle; these constitute *development*. Still longer-term processes are those of heredity, which can only be realised during the passage of at least a few generations and which form the province of *genetics*. And finally, no full picture of an animal can be given without taking account of the still slower processes of *evolution*, which unfold themselves only in the course of many life-times. (Waddington 1956: 3-4)

But it was not just the British organicists who developed a processual understanding of life. The Viennese organicists Ludwig von Bertalanffy and Paul Alfred Weiss, for instance, also defended a processual ontology in their thinking about biology. Bertalanffy (1952: 134) regarded the organism as “the expression of an everlasting, orderly process” consisting of “a continuous stream of component materials” (ibid.: 133) that flow through it and at the same time constitute it. “What is described in morphology as organic form”, Bertalanffy argued, “is in reality a momentary cross-section through a spatio-temporal pattern” (ibid.: 134). Weiss was equally thorough in his processualism, claiming that biological processes can only be understood in terms of more basic processes, and not in terms of more basic things: “[l]ife is a dynamic *process*. Logically, the elements of a process can be only elementary *processes*, and not elementary *particles* or any other static units” (Weiss 1962: 3). One of the key implications that Weiss drew from this is that a cell “can never be defined in terms of a static inventory of compounds, however detailed, but only in terms of their interactions” (ibid.).

Overall, the ontology of organicism was distinctly processual, and this is in no small part a reflection of the influence exerted by Whitehead, both in terms of his timely diagnosis of the collapse of mechanicism in physics and its exciting implications for biology, and in terms of his insightful examination of time, dynamics, and wholeness in the books he wrote prior to *Process and Reality* (i.e. Whitehead 1919, 1920, and especially Whitehead 1925).⁷ We think it is quite significant that the organicists were able to develop a coherent processual perspective in biology without availing themselves of the grand metaphysical system Whitehead presented in that book, widely regarded today as his masterpiece. In this respect, it is perhaps more appropriate to describe organicism as a philosophy of biology that was inspired by Whitehead than as a genuinely Whiteheadian philosophy of biology.⁸ Be that as it may, what is relevant for our

⁷ Russell, for example, described Whitehead’s *Science and the Modern World* (1925) as “the most valuable philosophical contribution of recent years [...] which is of the highest interest and importance to biology” (Russell 1930: 179). Waddington blamed that same book for his decision to abandon geology for biology in the mid-1920s (Peterson 2011: 306). And Woodger described his own *Biological Principles*, which he wrote before the publication of *Process and Reality*, as an “attempt to extend Prof. Whitehead’s views to biology” (Woodger 1929b: 345).

⁸ Indeed, it is important to distinguish the organicists from authors who have sought to develop a processual understanding of biology on the basis of the panpsychist metaphysics laid out in *Process and Reality*. Early attempts to do so include *A Contribution to the Theory of the Living Organism* (Agar 1943) and *General Biology and*

present purposes is that the organicists showed the way in which one might articulate a processual account of the living world that is naturalistically grounded and empirically informed. We regard the organicists as kindred spirits and consider our project to be continuous with the earlier tradition in the philosophy of biology to which they belong. Of course, a great deal of progress has occurred in biology in the decades since the organicist tradition went into decline, so while many of their core ideas have stood the test of time, their re-evaluation in the light of these more recent developments is long overdue. About a third of the chapters in this volume feature discussions of, or references to, organicist authors.

4. Processes and Things

This manifesto, and the book more generally, defends the thesis that the right way to understand living systems at all levels is as a hierarchy of processes rather than of things. Philosophically, this is a radical thesis: as we have already seen, an ontology of things, or Aristotelian substances, has dominated Western philosophy since the Greeks. As a result, it is generally assumed that substance ontology provides the most ‘natural’ articulation of our common-sense intuitions about the world.⁹ Johanna Seibt, in her contribution to this volume and elsewhere (e.g. Seibt 1996), refers to this as the ‘myth of substance’. This pervasive bias towards things is reflected in our everyday language, and it has a direct effect on how scientific research is conducted and how its results are interpreted. The papers in this collection illustrate many of the problems that arise from taking the ontological primacy of things as a given in the particular context of the life sciences. Though not every contributor to this book is a fully signed-up process metaphysician, all are exploring topics that point in various ways to the advantages of this alternative position.

What is the difference between a thing, or a substance, and a process? In large part, of course, this is the question that this book, and to a lesser extent the present essay, is supposed to help answer. A starting point, however, is the following. Processes are extended in time: they have temporal parts. Whether things have temporal parts is a debated issue. Many philosophers hold that this is not the case. As it is sometimes expressed, a thing is wholly present at any moment when it is present at all. Often this position is combined with presentism, the view that only the present exists at all (Bourne 2006). Both of these theses are contested by four-dimensionalists, who think of things as ‘space-time worms’, extending through time for as long as they exist (Sider 2001). On such a view, only a tiny part of a temporally-extended thing is present at any instant. We shall not say any more about this debate here, except to note that four-dimensionalism is already half way towards a full-blown process ontology. Both populate the world with temporally-extended entities with diverse temporal parts. To see where these positions may still differ will require further attention to what it is that makes temporal parts of an entity parts of the same entity, a question that we shall return to later, and that will also be discussed in subsequent chapters, especially those in Part II of the book.

Equally central to the concept of process is the idea of change. A process depends on change for its occurrence. Traditionally, change has been construed as something that happens to things, or substances, typically conceived as durable integrated entities that are not dependent on external relations for their existence. Things, in this view, are the subjects of change, and processes

Philosophy of Organism (Lillie 1945). Two edited volumes have appeared more recently with a similar agenda, namely *Mind in Nature* (Cobb and Griffin 1977) and *Life and Process* (Koutroufinis 2014).

⁹ Of course, we realise that the concept of substance has lent itself to a wide range of interpretations throughout the history of philosophy, not all of which are mutually compatible. Accordingly, we recognise that substance ontology is not so much a single, distinct doctrine as it is an umbrella term for a collection of philosophical positions that share a commitment to ontologically prioritising substances (however these may be construed) over processes.

merely track modifications in the properties of things over time, or describe means by which things interact with one another. This understanding leads to the assumption that processes always involve the doings of things. Processes, therefore, necessarily presuppose the prior existence of things.

One problem with this view is that many processes do not in fact belong to particular subjects. Rain, wind, electricity, and light are all commonplace examples of subjectless, or ‘unowned’, processes that are not the actions of individual things. There are numerous subjectless processes in the living world as well: osmosis, fermentation, adaptive radiation, etc. As Johanna Seibt shows in her chapter, the autonomous existence of subjectless processes is not compromised by the fact that they lack many of the features of concrete particulars, such as determinate boundaries or, for that matter, a unique or specific spatiotemporal location.

A more fundamental problem is that even what appear to be the subjects of activities can themselves be construed as specific temporal stages of stable processes; they do not have to be understood as things. Though many processes are defined in terms of concrete particulars that undergo them, the notion that only things or objects are qualified to count as concrete particulars is nothing more than a prejudice. Many processes are bona fide individuals—they are concrete, countable, and persistent units. Non-biological examples include whirlpools, flames, tornadoes, and laser beams. In biology, processes are, as we have already mentioned, dynamically stabilised at vastly different timescales: a matter of minutes for a messenger RNA molecule, a few months for a red blood cell, many decades for a human being, and up to several millennia for a giant sequoia tree. This stabilisation can make it easy to mistake them for static things. But more importantly, it allows them to play the role traditionally attributed to things undergoing processes in substance ontology; the only condition is that the relevant processes must be sufficiently stable at the timescale of the further processes that they in turn undergo. Enzymes can be treated as things because they are stable on the timescale of catalysis. Similarly, white blood cells are stable on the timescale of phagocytosis, alveoli are stable on the timescale of respiration, animals are stable on the timescale of reproduction, and so on.

We believe, then, that it is a mistake to suppose that processes require underlying things, or substances. This commonly held belief corresponds, unsurprisingly, to the original meaning of the term ‘substance’, which derives from the Latin word *substantia*—literally, that which stands under. In opposition to this view, we take nature to be constituted by processes *all the way down*.¹⁰ This represents the reversal of the substantialist position described above. Instead of thinking of processes as belonging to things, we should think of things as being derived from processes. This does not mean that things do not exist, even less that thing-concepts cannot be extremely useful or illuminating. What it does imply is that things cannot be regarded as the basic building blocks of reality. What we identify as things are no more than transient patterns of stability in the surrounding flux, temporary eddies in the continuous flow of process.

The thoroughgoing processualism we uphold regards change, or better dynamicity,¹¹ as fundamental, or primitive. This dynamicity is extended in time and, like time itself, it is continuous. It is therefore inappropriate to regard it—or any of the myriad processes that constitute it—as a sequence of particular events. To conceive of processes as series of discrete

¹⁰ If we were to use the concept of substance in its original Latin sense, we would say that processes, not things, are the real substances of the world, the ultimate constituents of reality.

¹¹ Dynamicity appears to be a more suitable concept for our purposes, given that change can carry undesirable substantialist connotations. As we indicated above, if change is described as the alteration of the properties of pre-existing substances, then it is not necessary to conceive it as a basic ontological category in its own right.

temporal episodes is to overlook the very dynamicity that process philosophy is intended to emphasise. As we noted earlier, this is one of the key reasons why we do not situate our project in the Whiteheadian tradition. Whitehead construed reality in atomistic terms, as being ultimately made up of indivisible units, which he called ‘actual occasions’, out of which all larger processes are composed. In place of a discontinuous view of the world as a complex aggregation of ultimate elements, we prefer to think of it as a manifold of nested and interrelated processes that collectively constitute a dynamic continuum. This understanding of nature forces us to rethink a number of traditional problems in philosophy, such as the nature of causation, which is what Rani Lill Anjum and Stephen Mumford set out to do in their essay in this volume.

Processes come in many forms, shapes, and sizes. The spatiotemporal organization of a process and its spatiotemporal and causal relations to other processes determine its persistence and stability, and are also what grounds its properties and causal powers. As we have already noted, processes can be ‘pure’ dynamic activities or they can be individuals exhibiting most of the characteristics typically attributed to things. Whereas things can generally be individuated by their spatiotemporal locations—things typically exclude other things from the regions of space-time they occupy—this is not typically the case for processes. Many processes have boundaries that are fuzzy or indeterminate, a feature with implications that we shall explore later. Processes are individuated not so much by where they are as by what they do. A series of activities constitute an individual process when they are causally interconnected or when they come together in a coordinated fashion to bring about a particular end. Many of the processes found in the living world, moreover, exhibit a degree of cohesion that demarcates them from their environment and thereby allows us to identify them as distinct, integrated systems—as entities in their own right. In his chapter, James DiFrisco considers the extent to which the cohesion criterion, first proposed by John Collier (1988, 2004), can provide an effective means of individuating biological processes.

The transition we are urging from a substance ontology to a process ontology has one very important epistemological implication. In any scientific enquiry it is necessary to distinguish what requires explanation from what is background, taken for granted. The orthodox substantialist position of modern science typically takes this background to involve stability: if nothing changes, then nothing requires explanation. This is because the default mode of existence of a thing is stasis and consequently the need for explanation only arises when changes happen to it. For a process, however, change is the norm, and it is its relative stability that takes priority in the explanatory order. If the living realm is indeed processual then we should consider the central explanandum of biology to be not change but stability, or to be more precise, stability attained through constant change. Take physiology as an illustrative example. Physiology is concerned with understanding the multitude of internal processes that enable an organism to stay alive by maintaining its organization within a relatively narrow range of parameters. It is quite clear that in the context of physiological enquiry (which encompasses many more specialized areas of biology) the persistence of an organism is not a background assumption at all, but the very phenomenon that cries out most loudly for explanation. The same can be said of enquiries in development or immunology, and even (or perhaps especially) in medicine, as illustrated by the discussion of cancer in the chapter co-authored by one of us (Dupré) with Marta Bertolaso.

5. Empirical Motivations

In this section we shall examine some well-established scientific facts about life that reveal the unsuitability of traditional substance metaphysics for representing biological reality, and which have compelled us to adopt a processual stance towards the living world.

Although this book is primarily concerned with biology, we do not think we should proceed without at least mentioning that the physical sciences already provide powerful motivations of their own for endorsing a process ontology. Nicholas Rescher (1996: 97) has quipped that modern physics “puts money in the process philosopher’s bank account”, and it is easy to see why. The advent of quantum mechanics at the turn of the twentieth century led to the dematerialisation of physical matter, as atoms could no longer be construed as Rutherfordian planetary systems of particle-like objects. This resulted in the demise of the classical corpuscular ontology of Newtonian physics, which had been one of the pillars of substance metaphysics since the Scientific Revolution. What had hitherto been conceived as the ultimate bits of matter became reconceptualised as statistical patterns, or stability waves, in a sea of background activity.¹²

The subsequent development of quantum field theory, which was articulated to reconcile quantum mechanics with special relativity, has lent further support to the process cause. Quantum fields, which are dynamic organizations of energy distributed in space-time, appear to have purged classical notions of elementary particles from the ontological picture. Although contemporary physicists still routinely speak of ‘particles’, these no longer refer to solid micro-entities or tiny impenetrable granules, but to quantised excitations of particular fields. Quantum fields, in other words, are primary, and the various kinds of particles that physicists refer to are derivative entities, appearing only after quantisation. Thus, what contemporary physics seems to be telling us—if we understand the equations realistically—is that the basic ontological constituents of the universe are not elementary particles, understood as minuscule ‘things’, but fields extended in space-time. Though we are not entirely sure whether fields are either processes or things, they do appear to be more like the former than the latter.¹³

If physics directs us towards process metaphysics, and there are additional reasons for thinking that chemistry is likewise amenable to a process ontological interpretation (see, e.g., Stein 2004 and Stephan Guttinger’s essay in this volume), it would be surprising to find that biology pushes us in the opposite direction, towards an ontology of substances. As it turns out, there are good independent reasons for embracing process metaphysics in biology as well, as we shall now see.

5.1. Metabolic Turnover

One of the strongest motivations for adopting a process ontology in biology stems from a very familiar fact about life, namely that organisms have to eat to stay alive. We can express this in more technical terms using the parlance of thermodynamics by stating that organisms are open systems that must constantly exchange energy and matter with their surroundings in order to keep themselves far from equilibrium. The persistence of an organism is dependent on its ability to continuously maintain a low-entropic ‘steady state’ in which there is a perfectly balanced import and export of materials. When this exchange ceases, the steady state is irretrievably lost and the organism succumbs to equilibrium, resulting in death.

¹² Interestingly, the organicists were well aware of the shift towards process that was contemporaneously taking place in physics. Bertalanffy, for example, explicitly compared the processual ontologies of physics and biology, declaring that just “[a]s in modern physics there is no matter in the sense of rigid and inert particles, but rather atoms are node-points of a wave dynamics, so in biology there is no rigid organic form as a bearer of the processes of life; rather there is a flow of processes, manifesting itself in apparently persistent forms.” (Bertalanffy 1952: 139).

¹³ The argument we have sketched here to the effect that modern physics motivates process metaphysics draws from a number of sources, including David Bohm’s classic *Wholeness and the Implicate Order* (1980) and Richard Campbell’s more recent *The Metaphysics of Emergence* (2015).

Because of their particular thermodynamic characteristics, organisms find themselves in the existential predicament of needing to act to continue to exist. Although a car cannot function without fuel, its existence (i.e. its structural integrity) is not compromised when it is deprived of fuel. An organism, in contrast, is *always* acting (or working, in the thermodynamic sense), as it must remain permanently displaced from equilibrium if it is to stay alive. You can leave your typewriter in an empty loft and return a decade later and start using it again. But if you accidentally leave your hamster in the loft, you will not have a hamster for very long.

This continuous activity, which is truly indispensable for life, is known in biology as the process of *metabolism*. Metabolism encompasses the means by which organisms break down the materials they take in from their environment in order to acquire the energy they need to rebuild their constituents and maintain themselves in a steady state far from thermodynamic equilibrium. Metabolism also includes the processes by which organisms dissipate energy and excrete material wastes back in to their environment, thereby conforming to the second law of thermodynamics. This constant metabolic turnover takes place at every level of biological organization. As we indicated at the start of this essay, an organism is not organized as a hierarchy of structures (as a machine is), but as a hierarchy of processes. The lower we go down the biological hierarchy, the faster the rate of material exchange. The stability of each process in the hierarchy is secured by virtue of the constant metabolic turnover of components taking place at the lower level. Accordingly, the stability of a multicellular organism as a whole derives from the continuous regeneration of its tissues, which are themselves maintained by the incessant renewal of their cells, which are in turn stabilized by the ongoing replenishment of their molecular constituents.

The appearance of stasis in biology can be deceptive at any level of organization. Subcellular formations such as the mitotic spindle or the Golgi apparatus seem well-defined structures within a short timescale, but when we consider them for longer temporal intervals it becomes evident that they are but fleeting manifestations of ongoing processes of material exchange. These organelles, like many other molecular assemblies in the cell, do not exist as fixed microstructures but as quasi-stationary patterns—part fluid, part consolidated—which persist for a time before undergoing transformations or disappearing altogether (Kirschner et al. 2000; Misteli 2001). Exactly the same is true for the cells that compose a tissue, for the tissues that constitute an organ, and for the organs that make up an organism. Any given cell, and any given tissue, instantiates a dynamic steady state, only the form of which persists, while its material constitution is constantly being turned over by metabolic events.

Ultimately, this also applies to a multicellular organism as a whole. This is harder to appreciate because the material regeneration of the form of most macroscopic organisms is so slow that it is not easily perceived by the human eye. But consider the following thought experiment. Imagine an extra-terrestrial humanoid life form whose mode of visual recognition was based on the enumeration of the material components that make up particular tokens of general types, rather than on the identification of the general types that are instantiated by particular tokens. Imagine further that this alien lands on Earth at a particular location and encounters two dogs: a living dog and a robotic dog. The alien scans the two dogs, catalogues their material constitution for future identification, and returns home. A few years later, the alien returns to Earth to the same location and faces the two dogs it encountered in its first trip. Despite being in the presence of the same two dogs, the alien's cognitive apparatus means that it is only able to identify the robotic dog and not the living one. From the alien's perspective, the living dog of the first trip has faded out of existence, and an entirely different living dog has taken its place. What this admittedly fanciful thought experiment is meant to illustrate is that if one focuses on matter

rather than form and allows for a sufficiently extended period of time, the stream-like nature of macroscopic organisms becomes perfectly evident. The fact that this does not happen to be easily perceptible to us does not make it any less true or important.

From a metabolic perspective, it is simply a matter of fact that in an organism *everything flows*. Of course, this is not to say that everything flows *at the same rate*. In the human body, for instance, each type of tissue has its own turnover time, depending on the workload endured by its cells. To illustrate: the cells lining our stomach only last around five days; cells of our epidermis are renewed every two weeks; our red blood cells are replenished after four months; our liver as a whole is regenerated on a yearly basis; and our entire skeleton is replaced each decade (Wade 2005). When we consider the turnover time of molecules in our body, the rate of replacement is several orders of magnitude faster. For example, the protein turnover rate in an adult is roughly eight per cent *per day*, and virtually all the protein molecules in our body are replaced during the course of a year (Haynie 2008).¹⁴ This should not be surprising. A cell persists for far longer than any of its molecular constituents, and the same can be said of the lifespan of a tissue compared to that of its component cells. In general, none of the parts in an organism is as old as the organism itself. What this implies, as far as you—the reader—is concerned, is that your physical body is several times younger than your actual age.¹⁵ Sadly, however, wrinkles and grey hair renew themselves just as faithfully as smooth skin and more youthfully tinted tresses.

Overall, the reality of metabolism forces us to recognise that organisms, despite their apparent fixity and solidity, are not material things but fluid processes; they are metabolic streams of matter and energy that exhibit dynamic stabilities relative to particular timescales. As processes, and unlike things or substances, organisms have to undergo constant change to continue to be the entities that they are. The chapter by one of the present co-authors (Nicholson) examines the metabolic character of organisms and its grounding in thermodynamics in greater depth, and explores some of the ontological implications of transitioning from a machine-like to a stream-like conception of the organism. The chapter by Denis Walsh also takes the metabolic aspect of life as a point of departure to argue that organisms are agents rather than objects and to explore the consequences of this ontological shift for our understanding of evolution. And the last chapter in the book, by Anne Sophie Meincke, appeals to the processual nature of metabolism to deal with the puzzle of personal identity.

5.2. Life Cycles

Another equally uncontroversial fact about life that similarly compels us to embrace a process perspective is that all organisms undergo a characteristic series of morphological and behavioural changes over the course of their lifetime; they do not stay the same from the moment

¹⁴ One might be tempted to object that the DNA in our cells constitutes an exception, as it remains unchanged. But what remains unchanged is not the DNA molecules themselves, but their nucleic acid sequence. The actual molecules undergo change when they are replicated during cell division, and indeed the extraordinary precision of replication is only achieved by an elaborate set of editing processes that respond to inaccuracies. It is also worth noting that even the nucleic acid sequence does not stay exactly the same, given that replication errors do occasionally occur, resulting in minute variations which may or may not result in phenotypic changes.

¹⁵ Physiologists, and even members of the general public, have long been aware of this bewildering fact. In the 1905 edition of his novel *The Irrational Knot*, George Bernard Shaw wrote: “At present, of course, I am not the author of *The Irrational Knot*. Physiologists inform us that the substance of our bodies (and consequently of our souls) is shed and renewed at such a rate that no part of us lasts longer than eight years: I am therefore not now in any atom of me the person who wrote *The Irrational Knot* in 1880. The last of that author perished in 1888; and two of his successors have since joined the majority. Fourth of his line, I cannot be expected to take any very lively interest in the novels of my literary great-grandfather” (Shaw 1905: xvii).

they come into existence but rather *develop* progressively over time, acquiring certain properties and capacities and losing others along the way. This is commonly referred to as the process of *ontogeny*, and the precise nature, order, and timing of the changes it comprises varies enormously from one species to another.

Let us take a frog as an example. It begins its life as a fertilized egg, which divides and develops into an embryo. When the egg hatches, it leaves its gelatinous enclosure and attaches itself to a floating weed or blade of grass. It then becomes a tadpole with a cartilaginous skeleton, gills for respiration (external gills at first, internal gills later), and a tail for swimming. Its tail keeps on growing and its hind legs gradually appear, followed by its forelegs. The tadpole's lungs also begin to develop at this point to prepare for its life on land. Many other morphological changes take place during this time: its nervous system becomes adapted for its eventual life on land, its head becomes more distinct through the repositioning of its eyes, its ear organs begin to form internally and externally, its lower jaw transforms into a big mandible, and its gills are gradually grown over by skin until they disappear. As its tail progressively shortens the tadpole appears ever more frog-like, until it emerges from the water as a froglet. Eventually, as an adult frog, it finds a mate—if it is lucky—and the entire process starts anew (see Figure 1).

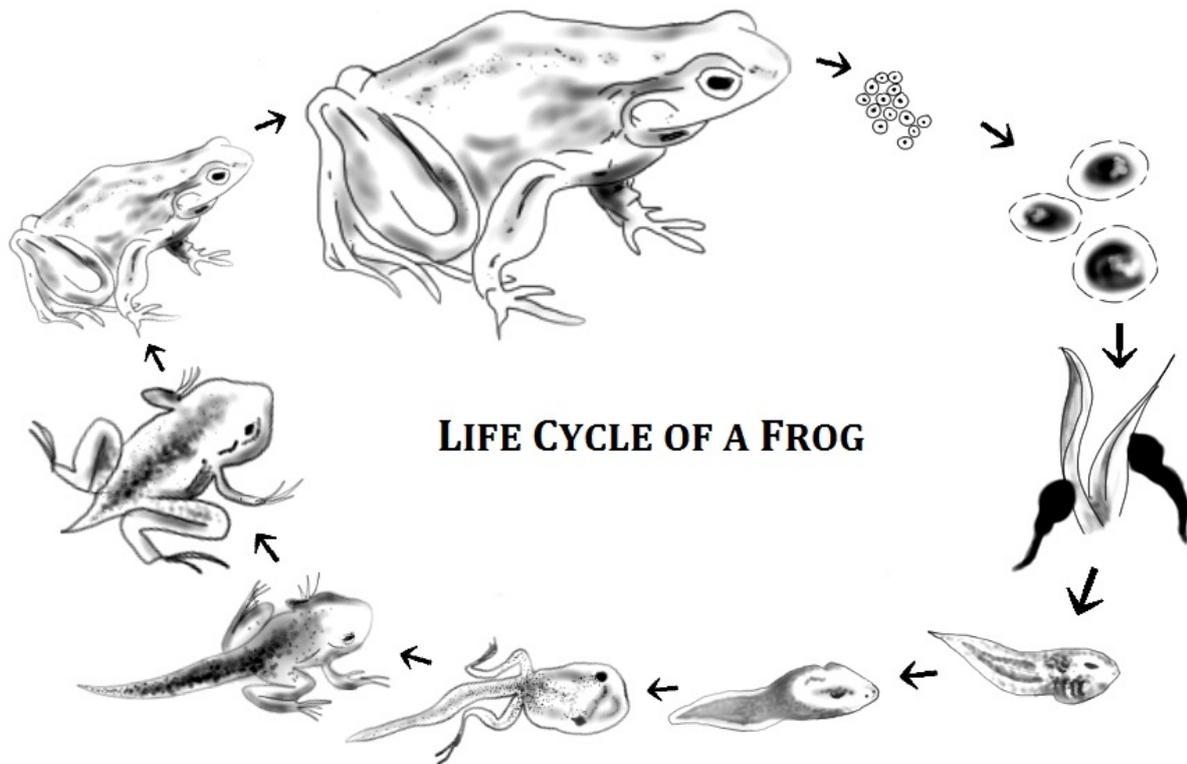


Figure 1. Schematic representation of the various stages in the life cycle of a frog

This familiar example showcases some of the problems with the traditional understanding of organisms as things, or substances. When considering a particular organism, there is a general tendency to privilege or prioritise the adult stage of its life cycle (for instance, in the context of taxonomic discussions), as this is the period during which the organism most closely resembles a thing by virtue of its relative stability. But we should not forget that the organism encompasses the entire life cycle; indeed, it is the life cycle itself that constitutes the organism. Strictly speaking, it is incorrect to speak of an egg developing into a frog, as the egg is really a temporal part of the developmental trajectory that *is* the frog. Organisms cannot be separated from their

history. What we perceive as an organism (e.g. a frog) at any given moment represents only a cross-section, or time slice, in the unfolding of the persistent process it instantiates. It is important to realise that these time slices do not reflect real discontinuities in the process from which they derive. Although an adult frog is undoubtedly very different from a tadpole, the developmental progression from tadpole to frog is smooth and gradual; there is no sharp boundary demarcating them. Knowing what we know about frogs, it simply makes more sense to think of them as processes rather than as things.

Now one could attempt to retain the commitment to substance ontology by arguing that, despite the developmental transformations that organisms undergo, they nevertheless remain the same thing, or substance, throughout. The problem with this line of argument is that it is surprisingly difficult to specify what stays the same throughout the life cycle of an organism. To refer back to our example, when we consider a fertilized egg, an embryo, a tadpole, a froglet, and an adult frog, it is not clear what properties they all share beyond being temporal stages of the same individual process. In fact, there may well be no interesting properties shared by all.¹⁶

Before moving on, we wish to emphasise that the idea of a life cycle is broader and more inclusive than the concept of ontogeny. Multicellular organisms undergoing embryological differentiation are not the only biological entities with life cycles. Cells have life cycles as well, typically involving a growth phase that includes DNA replication followed by mitosis and cytokinesis. Accordingly, the same problems we have discussed in the context of multicellular organisms also apply to individual cells. Even viruses have life cycles. In fact, a wide range of conceptual difficulties disappear when we view viruses as processes rather than as things, as one of us has recently argued (Dupré and Guttinger 2016). Viruses pass through an intricate sequence of stages as part of their life cycle. Some of these stages are highly stable (for instance, the virion stage, which is what most people have in mind when they think of viruses). Crucially, however, the very existence of these stable states can only be accounted for by referring to their role in the larger cyclical process that *is* the virus. Finally, we should also mention that just as developmental cycles are not the only kinds of life cycles, life cycles are not the only kinds of cycles that living systems undergo. The field of chronobiology investigates the wide range of cyclic phenomena exhibited by organisms, such as circadian rhythms.

The fact that most biological entities (not just organisms) exist as temporally-extended and temporally-differentiated life cycles provides strong grounds for endorsing a processual view of the living world. The significance of life cycles for biological ontology is examined in the chapters by James DiFrisco, Paul Griffiths and Karola Stotz, and Flavia Fabris.

5.3. Ecological Interdependence

A third motivation for taking a processual stance in biology concerns two features that are often taken as defining characteristics of a thing or substance: the first is that it should have boundaries, even if sometimes vague, more or less determined by its being the kind of thing that it is; and the second is that it should exhibit a certain autonomy or independence, that its dependence on anything external to it should be at most contingent. Neither of these characteristics is easy to reconcile with the well-known fact that organisms do not exist in nature as isolated or even independent entities but rather live in densely interconnected communities that provide many of the conditions of existence that enable the survival of their individual

¹⁶ Again, one may be tempted to nominate the DNA sequence for this role. The problem is that genomes are highly dynamic entities that are subject to many kinds of changes during development (Barnes and Dupré 2008). Moreover, it is not even clear that there is any unique entity that qualifies as the genome of an organism (Dupré 2010a).

members. Indeed, ecology tells us that the environment in which each organism finds itself is partially constituted by the complex network of reciprocal interactions it maintains with other organisms. Some of these interactions are so intimate and so fundamental to the survival of the organism that it has been hotly debated whether the interacting entities are distinct at all, or should rather be understood as constituting a single life.

The nature of these interactions varies widely: they can be specific or generic, permanent or transitory, obligate or facultative. They can occur among individuals belonging to the same species or they can involve organisms of many different species. Traditionally, there has been a tendency to regard conspecific relations as more intimate and significant. Extreme examples are the highly organized collectives formed by eusocial insects such as ants or honeybees, which are so tightly interwoven that they are often described as ‘superorganisms’. However, recent research in various areas of biology has revealed that inter-species associations, generally referred to as *symbiotic* relations, are equally if not more fundamental and are also more pervasive. Indeed, it is becoming increasingly apparent that symbiosis is the rule rather than the exception in the biological realm (Margulis 1998; Gilbert and Eppel 2015).

There are various kinds of symbiotic partnerships. Some are mutualistic (i.e. beneficial to both parties), such as the relationship between sea anemones and clownfish, in which the anemones protect the fish from predators (which cannot tolerate the stings of the anemone) and the fish defend the anemones against butterflyfish (which eat anemones). Others are commensal (i.e. beneficial to one party and neutral to the other), such as epiphytic plants (e.g. mosses, orchids, ferns, etc.), which grow on trees in order to increase their exposure to sunlight. And yet others are parasitic (i.e. beneficial to one party but harmful to the other), such as the ticks, fleas, lice, and leeches that feed on the blood of warm-blooded animals. But the extent of symbiosis goes well beyond associations between multicellular organisms (Dupré and O’Malley 2009). Every multicellular organism is itself engaged in an array of symbiotic relationships of the three aforementioned types with vast numbers of microorganisms. Large organisms (‘macrobes’) are actually multi-species collectives, or *holobionts*, composed of many different kinds of microbial symbionts—bacteria, archaea, viruses, protists, fungi, and microscopic metazoans such as nematodes—which live in symbiotic associations with their macroscopic eukaryotic hosts. Importantly, these microbial symbionts play crucial roles in the survival, reproduction, and evolution of their hosts (Moran 2006; Gilbert et al. 2012). Even the microbes themselves do not live independently, preferring instead to live in complex communal organizations, or *biofilms*, which often consist of multiple species. A familiar example is dental plaque, in which over six hundred distinct microbial taxa have been distinguished (Marsh 2006). Biofilms, just like organisms, have their own distinctive life cycles (Ereshefsky and Pedroso 2013).

Ecological interdependence, then, is one of the characteristic aspects of the living world, and it poses major problems for an ontology of things, or substances. One reason is that this ontology typically regards relations as external to things. A thing is taken to be what it is independently of the relations it enters in. A precondition of this independence is that it has relatively clear boundaries that enable its objective individuation as a discrete entity. Moreover, the properties (often taken to be essential properties) that determine both its boundaries and its continued existence are grounded on features that lie entirely within those boundaries. The interconnectedness of life challenges all of these substantialist assumptions. Organisms persist by virtue of the intricate webs of relations they maintain with one another, which in part endow them with their distinctive properties, capacities, and behaviour. In the light of ecology in general, and of symbiosis in particular, organisms need to be viewed as processes rather than things. As processes, and in contrast to things, organisms are fundamentally relational entities

that affect and are affected by their environment, within which they are firmly embedded, and which is itself constituted by numerous other processes.

Ecological communities or consortia such as biofilms, holobionts, and superorganisms are not collections of relatively autonomous things but deeply entangled meshes of interdependent processes. This entanglement can make it extremely difficult to establish unequivocally the boundaries of a biological individual, or even determine how many individuals we are dealing with in a particular situation. This is why ecological relations are best seen as the intertwining of processes. The biological world presents us with a seamless spectrum of degrees of intertwining. This spectrum ranges from facultative forms of mutualism or commensalism among multicellular organisms to instances of fully obligate endosymbiosis, such as the mitochondria found in virtually all eukaryotic cells. We are generally comfortable with asserting that in the former case we are dealing with two individuals, whereas in the latter case we are dealing with one, as we take the mitochondrion to be fully a part of the cell that contains it. However, for most other forms of ecological association that lie in between these two extremes it is far less clear that we can make such definite estimations.

How intimate must an association become for two individuals to count as one? And where is the dividing line between these two kinds of associations? Think for example of *Buchnera aphidicola*, bacteria that live in specialised cells within aphids and synthesise nutrients that the aphid cannot otherwise produce. These bacteria have greatly reduced genomes that make clear that they could not survive outside the aphid. Does this mean that they cannot be seen as individuals? One of the merits of an ontology of processes—compared to one of substances—is that it makes it possible to embrace the vagueness naturally suggested by such cases. It appears that distinguishing discrete individuals within the deeply entangled flux of interdependent living processes is often a matter of conceptual decision motivated by specific theoretical or practical interests. We shall examine the implications of this in the next section.

Although the early twentieth-century organicists appealed to metabolic turnover and life cycles to motivate their defence of a process philosophy of biology (as can be appreciated from the quotations we offered earlier), they did not really consider ecological interdependence. But it is interesting to note that Whitehead himself recognised its significance.¹⁷ More recently, Charles Birch and John Cobb have used ecological interdependence as the basis of the particular brand of process ontology (which they call ‘event ontology’) defended in their book *The Liberation of Life* (1981). On their view, relations rather than intrinsic properties are the distinguishing features of entities of all kinds. Stephan Guttinger’s chapter in this volume builds on Birch and Cobb’s ecological model to develop a processual account of biological macromolecules. The chapters by Thomas Pradeu and Frédéric Bouchard consider the significance of symbiosis for philosophical discussions of biological identity and biological individuality, respectively. And

¹⁷ In *Science and the Modern World*, Whitehead illustrated the interconnectedness of his worldview with an ecological discussion of the Brazilian rainforest: “The trees in a Brazilian forest depend upon the association of various species of organisms, each of which is mutually dependent on the other species. A single tree by itself is dependent upon all the adverse chances of shifting circumstances. The wind stunts it: the variations in temperature check its foliage: the rains denude its soil: its leaves are blown away and are lost for the purpose of fertilisation. You may obtain individual specimens of fine trees either in exceptional circumstances, or where human cultivation has intervened. But in nature the normal way in which trees flourish is by their association in a forest. Each tree may lose something of its individual perfection of growth, but they mutually assist each other in preserving the conditions for survival. The soil is preserved and shaded; and the microbes necessary for its fertility are neither scorched, nor frozen, nor washed away. A forest is the triumph of the organisation of mutually dependent species” (Whitehead 1925: 206). Whitehead’s remarks seem remarkably prescient, especially in the light of recent discussions regarding the so-called ‘Wood Wide Web’ (Giovannetti et al. 2006).

Argyris Arnellos presents in his chapter a process-based organizational account of life that recognises and attempts to integrate its metabolic and ecological dimensions.

6. Philosophical Payoffs

Process ontology, as we have seen, is far more attuned to and concordant with the understanding of the living world provided by the findings of contemporary biology than its substantialist rival. But apart from the critical question of empirical correspondence, from a pragmatic perspective process ontology also proves to be the more attractive position to adopt in a number of different contexts. One of its great virtues, as we shall see in this section, is that it is able to provide a cogent metaphysical justification for several important critiques that have recently been put forward in the philosophy of biology. Specifically, in what follows we shall discuss how process ontology serves to ground critiques of essentialism, reductionism, and mechanicism.

6.1. Grounding Critiques of Essentialism

In our view, the ability of substance ontology to answer central philosophical questions is deeply connected to its invocation of essentialism. Assuming that there is some essential property of a thing of a certain kind answers two kinds of questions.¹⁸ First, it tells us what kind of thing we are concerned with and so, more generally, it allows us to address questions about the nature of classification. If we ask what kinds of things are there in the world and how are they distinguished from one another, we can answer that things are of different kinds if and only if they have different essential properties. Second, it allows us to answer questions about the persistence of things, such as what it is for the same thing, or substance, to continue to exist through time. These questions will be familiar to those concerned with the puzzle of personal identity, which considers how it is possible for someone to be the same person as they were decades earlier despite undergoing massive change. Essentialism's answer to these questions is that a thing persists for just so long as it possesses the relevant essential property.

As it happens, however, essentialism—at least as far as the living world is concerned—is untenable, or so one of us has argued for many years (Dupré 1993, 2002; see also Hull 1965; Sober 1980). The questions it aims to answer are badly posed. The assumption that there is some unique natural kind to which a given organism belongs is false (Dupré 2002; Ereshefsky 1992). In actual scientific practice, different theoretical interests (e.g. ecological role, phylogenetic history, etc.) dictate different and multiply overlapping ways of dividing biological entities into kinds. A classificatory pluralism that follows from this observation has become quite widely accepted among philosophers of biology.¹⁹ And the failure of essentialism with regards to classification is one of the factors that makes the process perspective so attractive. Indeed, it is possible to see the processual character of biological entities as providing a deep explanation of why a multiplicity of ways of classifying such entities is precisely what we should expect to find. Promiscuous realism, as one of us has denominated this pluralism of classifications (Dupré 1993), thus finds a metaphysical justification in process ontology (Dupré 2017a).

But the pluralist implications of process ontology do not end there. In addition to explaining why we should be pluralists about classification, it also explains why we should be pluralists about

¹⁸ There are philosophical accounts that postulate distinctive individual essences (e.g. Kripke 1980), which could answer the second of the questions we discuss here. We shall ignore these for present purposes.

¹⁹ There are still some defenders of essentialism (e.g. Devitt 2008) as well as philosophers who defend essentialism generally, without much interest in the practical obstacles it faces in the life sciences (e.g. Ellis 2001). At least among philosophers interested in biology (a category that does include Devitt) they are in a distinct minority.

individuation. Biology suggests not only that there is no single way of classifying living entities into kinds, but that even the division of biological reality into distinct individuals may not be a thoroughly determinate and unambiguous matter. As we argued in our discussion of ecological interdependence, the ubiquity of symbiosis can severely complicate the task of defining the boundaries of a biological entity, as well as that of ascertaining whether particular entities are distinct individuals or parts of another entity. Take, for instance, the trillions of microbes that make up the human microbiome, and without which the human host would rapidly become sick and die. Are these parts of the human organism or rather just a large consortium of cooperating others? For some practical purposes, for example when describing the conditions for a healthy human life, it will be natural to treat the whole as one system; for others, for example when tracing the various evolutionary lineages to which the various collaborating cells belong, it may be more natural to treat them as many. Why should we suppose that there is a single unequivocal answer to this question, rather than many different ones depending on the issues we are interested in addressing?

In analogy to the promiscuous realism one of us has long advocated, the thesis that there are multiple ways of carving biological entities into distinct individuals can be described as ‘promiscuous individualism’ (Dupré 2012). What we wish to emphasise here is that this latter thesis, like the former, can be viewed as a direct implication of an ontology that takes processes as fundamental. To illustrate this, consider the processes made famous by Heraclitus: rivers. A river is a part of a widely distributed process of water flowing to the sea, but the division of this process into discrete parts is a matter of human convenience, not objective fact. The Missouri river is the longest river in North America, and much longer than the Upper Mississippi, but we denominate the former a tributary of the combination of the latter and the (still shorter) Lower Mississippi. Is this a discovery or, on the other hand, a mistake? It is surely obvious that this is a convention resulting from a contingent past decision. Similarly, on the question of classification, distinctions between rivers, streams, brooks, lakes, ponds, and so on are rough and convenient ways of dividing up processes of water flow; they hardly reflect sharp and objective distinctions between natural kinds.

Beyond questions of classification and individuation, substance ontology has traditionally called upon essentialism to answer questions concerning persistence. Things persist, the argument goes, by virtue of their continued possession of certain essential properties that make those things what they are and which remain unchanged over time. The problem for substance ontology has always been that it is extraordinarily difficult to specify any such change-exempt descriptive properties that permanently characterise the essence of things. Indeed, all of the empirical facts that we marshalled in support of the process cause in the previous section cast serious doubts on the existence of essential properties. Firstly, as a consequence of constant metabolic turnover, a biological individual is never materially identical from one moment to the next. Secondly, because of its life cycle, it undergoes massive morphological changes as it progresses through its various ontogenic phases. And thirdly, as a result of its ecological interrelations, the symbiotic associations that compose and maintain it change considerably over its lifetime.²⁰ Overall, substance ontology is not able to deal with the problem of persistence because the constituents of the world—of the living world, at the very least—are not endowed with essential properties. The question is: does process ontology actually fare any better? One of the classic objections to process ontology is that it is incapable of accounting for persistent entities, or continuants, which anchor our representation of the world (cf. Strawson 1953; Wiggins 2016). Is this correct, and if so, where does that leave us?

²⁰ In the human case we mentioned earlier, for instance, the symbionts that make up the microbiome of a neonate are very different from those of an adult.

We offer here some thoughts regarding the persistence of processes, which is a recurring topic throughout the book (see especially the essays by Peter Simons, James DiFrisco, Thomas Pradeu, Daniel Nicholson, and Anne Sophie Meincke). For a start, we do not think that we are dealing with an insoluble philosophical problem, as there is a wide range of uncontroversial physical processes to which we clearly and unproblematically do apply criteria of identity over time. Think of hurricanes, streams, and vortices. A paradigm somewhere between the first and last of these is the Red Spot on Jupiter—a storm that has persisted for at least as long as we have had the instruments to observe it, a period of centuries. The mode of persistence of an organism is in many respects quite similar to that of the Red Spot. Just as the Red Spot persists by drawing in matter and energy from the violent winds that surround and shape it, so an organism persists by securing from its environment the matter and energy it requires to maintain its organization far from thermodynamic equilibrium. The persistence of the Red Spot is not based on the mere persistence of any of its individual properties or constituents; it is rather something the Red Spot *does*—a continuous activity. Even its identity as an individual cannot be taken as a given; it is instead a task that the Red Spot must constantly accomplish. By means of its continuous activity, the Red Spot demarcates itself from the flux of its surroundings. All of these considerations, we believe, are equally applicable to organisms.

So what is it that makes the various temporal stages of the Red Spot temporal stages of the same process? We take it that the answer must be sought in various forms of causal connection and continuity between the relevant stages. The momentum of the material making up the Red Spot at t_1 explains its momentum at t_2 , and the external winds that help maintain the structure of the Red Spot at t_1 continue to do so at t_2 . Indeed, a similar kind of story could be told about those surrounding winds themselves. We suspect that this is the general form of explanation that is needed to account for the persistence of a process. An obvious advantage of this way of explaining persistence is that it poses no restrictions on the amount of change that can take place between the properties of a process at different moments in time.

However, as we illustrated with the example of a river, the ability to track individual processes over time definitively is limited. Rivers split and merge, open up into lakes or deltas, and so on. What counts as the same river is to some degree a matter of convention. Nevertheless, we regard this inherent vagueness as a strength of the process perspective rather than a weakness. We need to come to terms with the fact that many organisms—including all unicellular organisms—are liable to split; those that do not, frequently intertwine and even intermingle as a consequence of their ecological interrelations. The reproduction of a lichen, for instance, requires the independent reproduction of a fungus and a photosynthetic bacterium or alga, and the subsequent merger of the various offspring with suitable new partners (not necessarily of exactly the same kind as their parents) to form new lichens. More generally, as we have already emphasised, the near universality of symbiosis makes the delineation of biological individuals to some degree indeterminate. Given all this, we should certainly not expect the tracking of entities over time to be a fully determinate matter. This may strike us as a problem, but the truth is that it is only a problem if we already assume that it *should* be possible to perfectly track entities through time in the first place, in accordance with the essentialist stance generally associated with substance ontology. An ontology of processes, besides conforming to what biological research actually tells us about the living world, liberates us from the burden of this expectation.²¹

²¹ Strawson (1953) argued convincingly that we could make no sense of a world without persistent individuals that we could reidentify at different times. Note that nothing we have said contradicts this requirement. It is just that the selection of reidentifiable individuals is less objectively determined than Strawson supposed. Or so we claim.

6.2. Grounding Critiques of Reductionism

Process ontology also helps us account for the problems with reductionism in biology. One of us has been arguing for decades against the temptations of reductionism, temptations that have been exacerbated in recent times by the successes of molecular biology (Dupré 1993, 2010b; Powell and Dupré 2009). Despite these successes, it has become increasingly clear to many biologists as well as philosophers that reductionism is at best a severely limited approach to understanding living systems. While much progress has been made in understanding wholes, such as cells, in terms of their organelles, macromolecules, and other subcellular assemblies, a consensus is emerging that understanding these entities cannot be fully accomplished without essential reference to the systems of which they are parts (e.g. Boogerd et al. 2007; Noble 2012).

In the context of substance ontology, however, it is difficult to understand where the failure of reductionism comes from. What could a whole possibly be beyond the set of constituents that compose it and the physical relations among them (i.e. spatial locations and connecting forces)? A classic argument of this kind is due to Kim (2005), who has convinced many that it is incoherent to attribute any behaviours to a physical whole that are not ultimately either deductive consequences of the behaviours of the parts that make them up, or causally impotent epiphenomena. This conclusion is often expressed via the widespread assertion that higher levels must at least supervene on lower levels. If the state of the lower level is fully specified, then everything at the higher level must be fully determined at the same time. Any other possibility is often taken to be logically incoherent.

Such considerations have their basis in the conventional structural hierarchy of substance ontology, which views the world in terms of successive levels of organization: elementary particles, atoms, molecules, cells, organisms, and so on. At each level of this hierarchy, it is in principle possible to determine the intrinsic properties of the relevant things. From the properties of things at one level, and the relations between them, we can infer the properties of the things at the higher level. Thus, the properties of all things are consequences of the properties of their constituents plus the relations between their constituents, down to the most elementary level (assuming there is one). It is difficult to see what else there could be that could contribute to determining a thing's properties.

Matters look quite different when we view the biological world as being organised not as a structural hierarchy of things, but as a dynamic hierarchy of processes, stabilised at different timescales. At no level in the biological hierarchy do we find entities with hard boundaries and a fixed repertoire of properties. Instead, both organisms and their parts are exquisitely regulated conglomerates of nested streams of matter and energy. The processes that make up the biological hierarchy not only compose one another but also provide many of the enabling conditions for the persistence of other processes in the hierarchy at both higher and lower levels. In other words, the visible and tangible entities at each level are not simply given (as they are in a structural hierarchy of things), but are rather dynamically maintained by continuous activity taking place at higher and lower levels in the same hierarchy.

One of the most significant consequences of the processual hierarchy of the living world, then, is that it makes the physicalist dream of absolute reductionism impossible. The complex web of causal dependencies between the various levels means that we cannot fully specify the nature of an entity merely by listing the properties of its constituents and their spatial relations. It also means that we cannot pick out any level in the hierarchy as ontologically or causally primary. Whereas a substance ontology that presupposes a structural hierarchy of things only allows

bottom-up causal influences, a process ontology has no trouble in recognising that causal influences can flow in different directions. Once we transition from an ontology of substances to an ontology of processes it is no longer incoherent or mysterious to assert that the properties of the parts are partially determined by the properties of the whole—a claim, by the way, that biologists (especially physiologists and embryologists) have been making for centuries on the basis of their empirical investigations. This point has important philosophical ramifications. The ‘downward causation’ that naturally results when a process at one level in the hierarchy is stabilised from a level above it has often seemed metaphysically grotesque to philosophers tacitly or explicitly working within a substance ontology. To a process philosopher, on the other hand, such notions present no special problem.

In a world of processes, reductionism makes little sense. We already anticipated this claim in our discussion of ecological interdependence. Processes are inherently relational entities. They influence and are influenced by their surroundings. These surroundings, in turn, are made up of even further processes. In abstraction from their surroundings, processes are nothing at all; they have no independent existence. One needs only to think of waves in an ocean or of gusts of wind in a storm. A process has the properties it does in no small part because of its relations with other processes. Consequently, it cannot be fully explained independently of these relations. A necessary condition for reductionism is that it must be possible to treat entities independently from one another, considering their structure and constitution independently of the context in which they exist. But this is precisely what an ontology of processes denies. When we accept that the living world is a process world, we are able to understand why reductionism in biology, despite its countless if limited successes in local and fixed contexts, can never fully succeed as a global explanatory enterprise, even in principle.

6.3. Grounding Critiques of Mechanicism

Ever since the Scientific Revolution, substance ontology has been associated with mechanicism, the view that nature—and everything in it—is a machine that operates in a regular and predictable manner and which can be fully explained in mechanical terms. Mechanicism is, of course, a natural expression of substance thought, as machines instantiate many of the properties traditionally attributed to substances; they are fixed material entities with clearly defined boundaries, and which exist independently of the activities they engage in and of the relations they maintain with other entities. It is not surprising, then, that mechanicism is perfectly consistent with both essentialism and reductionism; a machine is taken to belong to a particular kind because it exhibits certain unchanging properties, and its organisation and operation can be completely accounted for in terms of its components and their interactions.

Although physics emancipated itself from the mechanistic worldview at the turn of the twentieth century (which is partly what led Whitehead to embrace process metaphysics, as we indicated earlier), mechanicism never really lost its grip on biology; on the contrary, it tightened it following the rise of molecular biology. Nowadays it is not uncommon to regard protein complexes as ingeniously designed molecular machines, cells as intricate sets of circuits that can be partially re-engineered to function in accordance with our needs, development as the computable execution of a deterministic genetic program, or the products of evolutionary change in analogy with optimally-designed artefacts. However, it is becoming ever more apparent that all of these views are deeply problematic, as both of us have argued in earlier work (Dupré 2008; Nicholson 2013, 2014).

One very appealing aspect of the process perspective is that it makes the ontological inadequacy of the machine conception of the organism explicit. If organisms are processes rather than substances, then conceiving them as machines inevitably leads to a distorted understanding of them. Looking back once more at the three empirical motivations we discussed for adopting a process ontology, it is significant that all of them also provide reasons for resisting the ontological assimilation of organisms to machines. Firstly, the reality of metabolic turnover means that the very structure of every organism, unlike that of any machine, is wholly and continuously reconstituted as a result of its operation. Secondly, the life cycle an organism undergoes is unlike anything a machine ever experiences. Machines do not develop, nor do they reproduce; their form and configuration is fixed upon their manufacture, as opposed to that of organisms. And thirdly, as a consequence of ecological interdependence, no organism can function or even persist independently of the entangled web of interrelations it maintains with other organisms. In contrast, the persistence or operation of machines does not depend on their capacity to maintain relations with other machines. Your microwave does not require the presence of other microwaves to heat your food, let alone to persist in your kitchen. By adopting process ontology we are far less likely to be tempted by the machine conception of the organism, which for many biologists (and some philosophers) still constitutes the default, and often tacit, ontological understanding of living systems.

But process thinking allows us to do even more. In addition to legitimating and encouraging the recourse to machine analogies in the living world, mechanicism has permeated modern biology in another, more subtle way, namely by popularising the view that living systems can be explained by describing the causal mechanisms that are said to be operating within them. The word ‘mechanism’ of course derives etymologically from the concept of machine, but today the term refers more loosely to a set of components that causally interact in a regular fashion to produce a phenomenon of interest. The recent realisation that biologists frequently invoke mechanisms in their explanations of phenomena has led to an explosion of interest in the philosophy of science as a growing number of philosophers have tried to come to terms with the nature and scope of so-called mechanistic explanations (e.g. Machamer et al. 2000; Glennan 2002; Bechtel 2006; Craver 2007; Craver and Darden 2013). Although it is undeniable that the elucidation of biological phenomena in terms of mechanisms has proven to be an enormously productive scientific strategy, mechanistic explanations are inherently limited in what they can tell us about living systems, or so we have both claimed in previous publications (Nicholson 2012; Dupré 2013). The value of the process perspective in this context is that it helps us explain these limits.

The view that mechanistic explanations are in principle capable of providing a complete understanding of living systems is problematic because it presupposes an ontology in which substances at least play the central role.²² The ontological picture that typically motivates appeals to mechanisms is that living processes ultimately derive from, and can therefore be explained by, the systematic rearrangement of the pre-existing thing-like entities that compose them. But on the view we have been developing, the components of an organism, be it multicellular or unicellular, are just as much processes as the organism itself. The constituents of a higher-level process do not suffice to explain it because they themselves—or, more specifically, their stability and activity—cannot be fully understood without reference to that same process, as well as those above it. The mereological, bottom-up character of mechanistic explanations means that their

²² We do not say they presuppose a substance ontology *tout court* because, following the canonical statement by Machamer et al. (2000), some philosophical accounts of mechanisms are explicitly dualistic, endorsing both ‘entities’ (i.e. substances) and ‘activities’ (i.e. processes). Nevertheless, processes in mechanistic accounts tend to play a role similar to that of properties in standard substance ontology.

deployment in a world of processes is inevitably subject to the same limits as more traditional forms of reductionism.

Why, then, have mechanistic explanations turned out to be as successful in biology as they undoubtedly have been? A process perspective allows us to answer this question as well. The reason why mechanistic explanations provide insights (to the extent that they do) is that the components of the mechanisms being described are sufficiently stable on the timescale of the phenomena under investigation. For example, it is possible to explain the phenomenon of muscle contraction in mechanistic terms because the entities primarily responsible for it, namely the actin and myosin filaments in the muscle fibre, are sufficiently stable during the temporal interval in which contraction occurs to be treated as thing-like components of a mechanism. However, this does not mean that actin and myosin filaments really are inherently stable constituents of muscles, for if we change our research question and inquire instead about the growth of muscular tissue during development—a phenomenon that takes place over a much longer timescale—it is not possible to discern any specific muscle fibres, let alone any actin and myosin filaments within those fibres, that persist for the entire duration of development. In this epistemic context, we can no longer characterise actin and myosin filaments as thing-like components of a mechanism, as they themselves now appear to be dynamic and transient entities. Mechanism descriptions, therefore, are accurate only on the particular timescales of the phenomena they are called upon to explain.

A key implication that we take to follow from this is that the mechanisms described in mechanistic explanations should not be treated, in accordance with the assumptions of the older mechanistic tradition, as real things that ontologically make up organisms (in the way they might be supposed to make up machines). Rather, mechanisms in biology are more appropriately understood as heuristic explanatory devices—as idealised spatiotemporal cross-sections of living systems that conveniently abstract away the complexity and dynamicity of their biotic and abiotic surroundings, and pick out only the causal relations that are taken to be most relevant for controlling and manipulating the phenomena being investigated (Nicholson 2012; Dupré 2013). To suppose that mechanisms are the ontological building blocks of living systems is to commit what Whitehead famously called “The Fallacy of Misplaced Concreteness” (Whitehead 1925: 52), which occurs every time we confuse our conceptual schemas, models, and analogies with the way things really are. What biologists describe as mechanisms (and their components) are actually manifestations of specific patterns of stability of different processes concurrently unfolding in living systems. Process ontology enables us to understand the limits of mechanistic explanations in biology whilst simultaneously recognising and accounting for the scope of their effectiveness.

7. Biological Consequences

The move from substance ontology to process ontology has many interesting biological consequences. We have examined some of them over the course of this essay, and many more are explored by other authors in the remainder of this book. Some of these consequences are far from obvious. Ann-Sophie Barwich, for instance, shows in her chapter how a process perspective on perception results in a far more contextual understanding of olfaction than has been traditionally supposed. Moreover, not all of the consequences discussed in the chapters of this book are purely theoretical in character; quite a few of them are closely tied to practical issues. For example, Eric Baptiste and Gemma Anderson argue in their chapter that an increasing appreciation of the evolutionary role of biological processes requires new ways of representing them for analytical purposes.

Before we conclude, we wish to discuss a few rather significant consequences of embracing an ontology of processes in biology that are not directly covered in subsequent chapters. We present these reflections in order to give the reader a fuller sense of the wide-ranging implications of our project, as well as to offer a glimpse of the work that still remains to be done. Below we consider some specific consequences for physiology, genetics, evolution, and medicine.

7.1. Physiology

Physiology has traditionally been concerned with the study of function. This emphasis on function in turn has tended to direct physiological research towards the analysis of structure. The reason for this is that it has generally been assumed, in accordance with substance ontology, that structures somehow ground the capacities that constitute functions. Structures are taken to be more or less fixed, and ontologically prior to the functions that are associated with them. This substantialist understanding pervades the longstanding philosophical debate on function, where, despite major disagreements, the function of an entity—whether or not it is tied to the explanation of its selective advantage—is seen as a contribution of that entity to a larger system, and this contribution is made possible by its structural properties. One consequence of the process perspective in biology is that it calls into question this familiar and widespread view.

The various structures that an organism exhibits are not really fixed, but are instead continuously maintained by a large number of carefully regulated processes that endow them with their relative stability. These structures cannot be taken for granted in our physiological explanations, as they must themselves be accounted for by the various functional activities that enable them to persist through time. It is therefore incorrect to assume that structures are prior to functions, or that functions are determined by structures. The processual nature of organisms means that changes in their functional demands will tend to result in changes in how they maintain and regenerate their respective structures. In biology the relation between structure and function is not linear and unidirectional, as is often supposed, but circular and symmetrical. Neither of the two can be privileged over the other nor even be understood without appealing to the other.

This key insight was already recognised by the organicists working to develop a processual biology in the early decades of the twentieth century. Most of them explicitly argued that structure and function are mutually interdependent features of organisms. As Haldane elegantly expressed it, “[s]tructure and functional relation to environment cannot be separated in the serious scientific study of life, since structure expresses the maintenance of function, and function expresses the maintenance of structure” (Haldane 1931: 22). Structures are not simply given, but instead reflect the stability of functional activities, which are themselves maintained by stable structures. In the last analysis, it makes no sense to separate structure and function, as the two represent different yet complementary ‘ways of seeing’ the processual reality of living systems: one emphasizing stability and the other emphasizing dynamicity. According to Bertalanffy, “[t]he old contrast between ‘structure’ and ‘function’ is to be reduced to the relative speed of processes within the organism. Structures are extended, slow processes; functions are transitory, rapid processes” (Bertalanffy 1941: 251).

We are inclined to think of structure and function in biology as alternative forms of abstraction from the continuous flow of underlying processes. Structural descriptions abstract away the temporal dimension, as well as selecting non-arbitrary but underdetermined spatial limits for the entities of interest. Functional descriptions bring back the temporal dimension, but they do so at the cost of focusing on a highly specific set of properties of the entities under consideration.

More probably needs to be said about how structural and functional characterisations abstract.²³ The relevant point for now is that even though linear explanations of function in terms of structure serve valuable purposes in biological research, we need to keep in mind that they provide limited perspectives on biological phenomena. It is always possible, it seems to us, and ultimately even necessary, to treat biological structures as explananda as well as explanantia.

7.2. Genetics

Adopting a process ontology in biology also has an impact on how we think about inheritance. Genetics is generally thought to have originated with Mendel's famous experiments on peas, which concerned dichotomous characteristics that eventually came to be explained in terms of underlying invisible factors called genes. The consequent view that all the heritable information transmitted from parent to offspring resides in material particles, or genes, which replicate during reproduction and trigger the developmental construction of the new individual, has proved remarkably resilient even as its empirical basis has been increasingly eroded. This understanding fits naturally with a substance ontology, as it regards what is inherited as a collection of things (i.e. genes), together with their defining properties, namely the dispositions to cause phenotypic effects. A process perspective brings to the foreground two major problems with this substantialist picture. The first has to do with the supposed atomistic nature of genes, and the second concerns the view of reproduction as the transmission of a set of things, construed as a sort of passing of genetic batons.

When genes were first imagined as discrete entities carrying phenotypic information, their ontological status was entirely hypothetical. Although the reality of these entities progressively became accepted, no consensus was reached on their nature until the famous elucidation of the structure of DNA in 1953. As the implications of that discovery became apparent, the view emerged that genes are stretches of DNA defined by a specific sequence of nucleotides, the four chemical structures that alternate in the DNA molecule and which, in turn, provide the information necessary to generate a protein, conceived as the paradigmatic functional molecule. Genes for all kinds of phenotypic traits—from fur colour to sexual preference—were conceived as sequences of nucleotides that have the power to cause or alter these developmental outcomes.

This traditional picture has, however, been very widely rejected (see, e.g., Keller 2000). The development of most traits is now understood to involve features widely distributed across the genome as well as influences from many aspects of the external environment. This has led to growing doubts about the ontological significance of genes as discrete components of genomes, which in turn has prompted a more direct focus on the genome itself (Barnes and Dupré 2008). The genome, far from being the fixed source of developmental information, is now increasingly seen as a thoroughly processual entity. The stability of the nucleotide sequence, which is so crucial to its functioning, is dependent on multiple processes of correction and editing that drastically reduce the error rate of its replication. Moreover, the functioning of the genome involves constant changes in its physical conformation that allow appropriate parts to be more or less accessible for transcription. These changes are in turn partly controlled by the attachment and detachment of a variety of molecules to particular points on the genome, a process referred to as the *epigenetic* modification of the genome. Epigenetic effects are at the end of a causal chain that can begin far away, for example with maternal interaction with an infant organism (Champagne et al. 2006). Importantly, such causal processes allow environmental factors to affect the functioning of the genome.

²³ It would appear—we note in passing—that distinguishing biological mechanisms involves abstractions of both kinds.

Taking a broader view, what these genomic activities indicate is that, far from the one-way control of the cell by the genome that is still sometimes imagined, the genome is in constant two-way interaction with its cellular context and beyond. The persistence of both, in fact, depends on their interrelations. In short, where once we saw a genome as a set of discrete units or things mechanically controlling their wider environment, now we see dynamic interactions of a complex dynamic entity with its even more complex surroundings.

Genetic replication is another vital process ripe for reconsideration from a process perspective. Whereas in the context of substance ontology it may seem natural to conceive of replication as simply the copying and production of one thing on the basis of another—something akin to making a photocopy (cf. Dawkins 1982)—the generation of one process by another is a rather different matter. As James Griesemer (2000, 2005a, 2005b) has emphasised in a series of papers, biological reproduction, unlike photocopying in which only a re-production of information is required, involves a degree of material continuity between the original and the descendent. Indeed, in the replication of DNA new double helices are partially constituted from the material of the old double helices. Treating replication as copying has the inadvertent consequence of diverting attention from the causal process that generates it. DNA does not ‘self-replicate’, as it is sometimes claimed, but is instead completely dependent for its replication on the participation of an intricate molecular ‘machinery’. To think of replication, and by implication of reproduction, in analogy with copying is to abstract away the causality and materiality of the connection between parent and offspring, reducing it to an essentially informational relation.

While mechanistic biologists convinced of the machine-like nature of living systems will be comfortable comparing the role of replication in reproduction with the digital duplication of software systems, a biologist committed to a processual understanding of the living world is far less likely to be seduced by such analogies. When parents are recognised as self-maintaining metabolic processes from which offspring somehow branch off, it becomes clear that reproduction must involve material overlap between the two. Accounts of reproduction that fail to include this aspect neglect one of its essential features. Classical models of transmission genetics, Weismann’s famous separation of germ and soma, and the more contemporary notion of the genetic program have enabled geneticists to study inheritance as mere relations between things, but at the cost of abstracting from the actual processes of reproduction and development that generate these relations. Although such models have proven to be useful heuristics for scientific research, an adequate theory of inheritance must ultimately include these fundamental processes.

In the end, a process ontology forces us to expand our understanding of inheritance itself. Recognising the material overlap between parent and offspring in reproduction makes it obvious that what gets transmitted is much more than just the DNA. The material (i.e. cytoplasmic) continuum that exists between parent and offspring includes many molecular systems that can be inherited apart from the genome, such as macromolecular steady states and self-sustaining metabolic loops (see Jablonka and Lamb 2005). Because these epigenetic inheritance systems typically depend on chemical diffusion and molecular transport processes, they exhibit far lower degrees of fidelity than the nucleic acid coding mechanism characteristic of genetic replication. But this does not mean that they are not capable of affecting developmental outcomes; they are, and they do. Once we adopt a processual point of view, the detection of epigenetically inherited traits ceases to be an odd discovery and becomes something we would actually expect to find.

7.3. Evolution

While it is self-evident that evolution is a process, it is less clear how we should think about the nature of the entities that participate in this process. The traditional substantialist stance has been to regard them as things. Process ontology, of course, leads us to understand them as processes. If organisms are developmental cycles, then we should regard these developmental cycles, rather than the thing-like time slices that we abstract from them, as the actual entities that compose the evolutionary process. In fact, this is the view of evolution that developmental systems theorists have been advocating for many years, with the vital corollary that evolution can be driven by changes to any of the factors that contribute to reproducing the developmental cycle (see Griffiths and Gray 1994 and the essay in this volume by Griffiths and Stotz).

We have to be careful here, however, with the unusual grammar of the word ‘evolve’. Although humans evolve, no particular human ever evolves. What evolve are populations. Even the concept of population is not quite appropriate, as it lacks temporal extension. Populations are temporal cross-sections of lineages, so it really is the lineages that undergo evolutionary change. To say that humans evolve is to say that humans existing at one stage of the human lineage differ in some systematic way from those existing at an earlier stage. The evolving lineages generally considered to be the central subjects of evolutionary change are the entities we usually refer to as species.²⁴

One of the earliest debates in modern philosophy of biology concerned the metaphysical status of species. Because species have historically been treated as paradigmatic classificatory concepts, they were long supposed to designate kinds. But then Michael Ghiselin (1974) and David Hull (1976, 1978) advanced the thesis that species are not kinds but individuals. Although the species-as-individuals view has since become widely accepted, it continues to encounter some resistance on the grounds that it is puzzling and counterintuitive. It is objected, for example, that as the members of a species are discrete and relatively independent, it is not clear how they can be identified as parts of an individual. Another common complaint is that species have very fuzzy boundaries, whereas individuals typically do not. Interestingly, once we see species not just as individuals, but as individual *processes*, we are able to address both of these concerns. Causal relations between the temporal stages of a lineage, and between the spatial parts of these temporal stages, are responsible for providing it with whatever integrity it has as an individual process. And the problem of vague boundaries turns out not to be a problem at all, as processes tend to lack clearly defined boundaries to begin with (think of the boundaries of a thunderstorm, for instance). The expectation that individuals should have clear boundaries is merely a prejudice of substance thought that we simply bypass when we assume a process ontology.

If species or lineages are individual processes, how do they manage to maintain their coherence and stability over time? It would seem that just as organisms persist by renewing the cells that compose them through constant metabolic turnover, so lineages persist by replacing the organisms that make them up through continuous cycles of reproduction. Now recall that reproduction, properly understood, comprises not only inheritance processes (such as genetic replication) but also developmental ones, and these in turn draw on a highly heterogeneous range

²⁴ This is again not quite right, as species typically consist of a number of populations—they are often described as ‘metapopulations’—that may not be connected to one another reproductively or otherwise. Consequently, the unit we really want as the locus of evolutionary change is that of which the metapopulation is a cross-section, something for which, as far as we know, there is no standard term (unless, of course, we count ‘species’!). For present purposes, we can overlook this complication.

of causal factors (Oyama et al. 2001), which means that all of these contribute as well to the stabilisation of a lineage. In addition, a lineage persists by virtue of the reciprocal interactions its members maintain with their environment. Members of a lineage not only adapt to their environment but also modify it as a consequence of their activities and in accordance to their needs. This process is known as niche construction (Odling-Smee et al. 2003).²⁵ Last but by no means least, the persistence of a lineage is dependent on natural selection, understood here not as a cause of change but as a stabilising force. Stabilising selection leads to the continued production of very similar phenotypes in a lineage (namely the most adaptive ones), and this helps maintain its stability over long periods of time.

Of course, despite these numerous forms of stabilisation, lineages do gradually change, and this results in their evolution. A key implication of the process perspective is that it encourages us to embrace a much more pluralistic understanding of evolutionary change than the one assumed by orthodox Neo-Darwinism, which regards it almost exclusively in terms of natural selection acting on different alleles in a population. Selection cannot take place unless some other process has already provided the pertinent variants, and the Modern-Synthesis assumption that random genetic mutations alone can fulfil this role is increasingly coming under attack (Pigliucci and Muller 2010). Lineages are sustained by a wide range of processes, including reproduction, niche construction, and stabilising selection, as we have already noted, but also by parental effects, conspecific interactions, and symbiotic associations. It is conceivable that changes in, or disruptions of, any of these stabilising activities might affect the temporal trajectory of a lineage, and we should therefore consider including them in our explanations of evolutionary change.²⁶

We offer one last, more speculative suggestion. Processual systems such as organisms and cells respond to their environment in ways that are conducive to their persistence. A growing number of theorists maintain that such responses are not merely automatic reactions elicited by environmental stimuli, but rather reflect purposive actions on behalf of those systems prompted by emerging challenges and opportunities in the environment. It seems uncontroversial to suggest that natural selection should favour organisms that do what is most conducive to their survival over those that produce fixed responses to a determinate range of environmental stimuli, though traditionally it was supposed that the former was something achievable only through high degrees of intelligence. In her chapter, Flavia Fabris shows that Waddington thought that such adaptive strategies can be found much more widely (a view that Waddington shared with many of his organicist contemporaries), and that such systemic responses could be explained in terms of the adaptive deployment of hidden genetic variation. Perhaps, as Denis Walsh suggests in his provocative chapter, we should see evolutionary change as resulting primarily from such agent-like capacities of organisms and other processual systems.

7.4. Medicine

The process perspective also has interesting consequences for medicine, specifically for how we think about the concept of disease, as has been recently argued by Pierre-Olivier Méthot and

²⁵ It is important not to confuse niche construction with the extended phenotype (Dawkins 1982), as they imply opposite ontologies. The former can be seen as an implication of process ontology, whereas the latter is indicative of substance ontology. The extended phenotype extends the boundaries of things (i.e. organisms) beyond their material bodies and onto their environments, but these boundaries remain fully determined by the intrinsic properties of the things themselves. Niche construction, in contrast, suggests that organisms and their environments are causally intertwined and mutually constitute one another.

²⁶ One of us has recently elaborated these claims in more detail elsewhere (Dupré 2017b).

Samuel Alizon (2015).²⁷ The history of medical thought reveals that the understanding of disease has oscillated back and forth between two opposing conceptions. According to the so-called ‘physiological’ conception, diseases result from disturbances in the functional equilibrium of the body, and their cure reflects the harmonious restoration of this equilibrium. In contrast, the so-called ‘ontological’ conception views diseases as foreign entities that enter the body, and their cure implies the expulsion of the intruders. The ontological conception is aligned with substance ontology, as it regards diseases as particular things (or properties of things) which are discrete and exist independently of the body they infect, whereas the physiological conception is more congenial to process ontology, as it views diseases as temporally-extended disruptions in the carefully regulated meshwork of interconnected processes that constitutes the body.

With the rise of medical microbiology in the late nineteenth century the ontological conception became the dominant theory of disease, and so it has remained, more or less, to the present day. The modern notion of ‘pathogen’ is clearly derived from it, which accounts for why pathogens have long been considered a discrete category, distinguished from other microbes by their inherent capacity to cause disease in appropriate hosts. Conceiving the biological realm in processual terms leads us to question the adequacy of such a strongly substantialist understanding of the aetiology of disease. Taking a processual stance today does not mean returning to the old physiological conception of disease. But it does suggest that pathogenicity may not be an intrinsic property of a microbe at all, but rather, as Méthot and Alizon (2015) argue, a contingent property afforded by the particular ecological context in which the microbe finds itself, and by the complex and ever changing symbiotic relation it maintains with its host.

Remarkably, this is precisely the view that appears to be emerging from recent microbiological research. The traditional question ‘Is this microbe a pathogen?’ is gradually giving way to the question ‘Under what ecological conditions is this microbe likely to become a pathogen?’. This shift is partially being prompted by the discovery that microbes thought to be engaged in commensal or mutualistic relations with their host can become pathogenic (i.e. parasitic) as a result of changes in the host environment (this is the case for the microbes that make up the normal microbiota of the human gut, for instance). Conversely, microbes that are usually pathogenic can end up protecting their host against more virulent parasites. Virulence itself, which refers to the degree of damage capable of being inflicted by a pathogen on its host, is not a constant property of the pathogen; it is arguably not even a property *of* the pathogen, but rather the outcome of a specific kind of interaction of the pathogen with its host.

It is becoming increasingly clear that there is nothing about pathogens, as far as their structure is concerned, that fundamentally sets them apart from non-pathogens. There is also growing evidence that infections are frequently caused by more than one type of microbe. Viewing pathogenicity as a property of an individual microbe can therefore be misleading, as it is often a collective property that emerges from the interactions of various kinds of microbes with a host. In addition, it needs to be kept in mind that the microbes themselves are not unchanging things, but are constantly evolving—and microbes can evolve very rapidly! Sometimes they evolve the capacity to be pathogens. Indeed, an infection that is initially harmless to one host can become pathogenic in subsequent infections.²⁸

²⁷ Pierre-Olivier Méthot participated in the workshop at the University of Exeter where many of the papers collected in this volume were first presented but unfortunately was not able to contribute a chapter. The ensuing discussion considers some of the ideas he presented, many of which are featured in the aforementioned paper.

²⁸ The potentially great rapidity of this process can be attributed to the lateral transfer of so-called virulence factors, which are often packaged as mobile genetic units, such as plasmids, that are transferrable to other cells within the microbiome.

The above considerations strongly suggest that there are no definite criteria by which we can unequivocally classify a particular microbe as a pathogen. The more empirical research is conducted, the further away we seem to be from being able to make such classifications, and for good reason. Attempts to classify microbes in this way are misguided because they seek to attribute a property to the microbe that is in reality a function of the host, the microbe, and their interactions. To attribute pathogenicity to an individual microbe is to commit an indefensible act of abstraction, as it implies ignoring the complex processual context that makes it possible. A microbe is not a thing or a substance, and pathogenicity is not an unchanging characteristic that it carries with it like an essence; it is rather a process, and as such it is to be expected that its characteristics will be found to be transient, context-dependent, historically contingent, and ever subject to ecological and evolutionary changes.²⁹

8. Conclusions

This essay has concerned itself with a number of issues pertaining to the metaphysics of science. It has shown, we hope, that these issues are of such fundamental importance that they cannot be avoided by anyone seriously concerned with science, be it through philosophical reflection or empirical investigation. Scientists as well as philosophers are inevitably committed to certain metaphysical views, regardless of whether they are aware of them or not. These views, as Waddington recognised, “are not mere epiphenomena, but have a definite and ascertainable influence on the work [a scientist] produces” (Waddington 1969: 72). We believe that being explicit about the metaphysical stance one takes to be right for biology is crucial if we are to prevent what Whitehead described as the “canaliz[ation of] thought and observation within predetermined limits, based upon inadequate metaphysical assumptions dogmatically assumed” (Whitehead 1933: 151). Our aim in this manifesto has been to defend the metaphysical thesis that a process ontology is the right ontology for the living world.

We are well aware that previous attempts to defend process ontology have often been met with considerable scepticism, if not downright hostility. One reason for this, in our view, is that process philosophers have frequently felt the need to introduce a new lexicon in order to come to terms with the processual nature of existence. Whitehead, of course, is the most notorious example, and his influence on modern process philosophy, including on how it is perceived by those who oppose it, has been enormous. However, as we hope this essay has demonstrated, it is not necessary to appeal to neologisms or resort to opaque prose to make the case for process. Thing-locutions, despite their pervasiveness, do not have to be taken at face value. After all, our linguistic conventions do not always match with our ontological convictions; which is why, for instance, we continue to speak of ‘sunsets’ and ‘sunrises’ even centuries after the Copernican Revolution. It suffices that we realise that English grammar, like that of other Indo-European languages, exhibits a clear bias towards substances, which may well be rooted, at least in part, in our cognitive dispositions.

Beyond any such inherent bias, we surmise that the widespread prevalence of substance ontology also reflects the fact that in many circumstances it does the job sufficiently well. The relation between substance and process ontology is not completely unlike the relation between classical and modern physics. Just as classical physics provides a convenient approximation of middle-sized physical entities moving at relatively slow speeds but does not constitute an accurate description of physical reality, so substance ontology provides a serviceable characterisation of

²⁹ Further implications of process ontology for evolutionary microbiology are explored in Baptiste and Dupré 2013.

biological entities, especially as considered over short temporal intervals, despite being a fundamentally inappropriate description of the living world. But although it might seem more intuitive to regard organisms as things than as processes, the situation quickly begins to reverse when we start giving due consideration to time. Many of the methods used to study living entities abstract away from the temporal dimension to facilitate their investigation—one only needs to think of conventional anatomical techniques such as desiccating, pickling, staining, fixing, and freezing. It may be that these methods have led biologists to think in substance terms, or perhaps these methods rather reflect their awareness of the difficulty of dealing adequately with dynamic material and therefore highlights their appreciation of the processual nature of life. Yet even if the latter is the correct diagnosis, it seems to us that the use of such techniques has concealed the deficiencies of theorising grounded in substance-based ontology (this claim is further developed by Laura Nuño de la Rosa in her chapter).

Our argument in this essay has been that process ontology is far more concordant with the understanding of the living world provided by contemporary biology than its substantialist rival. The more we learn about life, the more necessary a process perspective becomes. This is particularly the case with regards to the increasing realisation of the omnipresence of symbiosis, which directly challenges deeply entrenched substantialist assumptions about the living world. Thus, even if it is less intuitive than substantialism, the empirical findings of biology are inexorably driving us towards processualism. It is interesting to observe that physics, which has traditionally been regarded as the more advanced science, was pushed towards process ontology about a century ago (as was argued by Whitehead and others), and now biology—if we and the other contributors to this volume are correct—is following suit. Might this perhaps be an indication that the shift from substantialism to processualism is just something that all sciences go through as they develop? This intriguing possibility was recently suggested by Mark Bickhard:

Every science has progressed beyond an initial conception of its phenomena in substance terms to understanding that they are in fact process phenomena. Fire is no longer modeled in terms of the substance phlogiston, but instead in terms of the process of combustion; heat no longer in terms of caloric, but in terms of random kinetic processes; life no longer in terms of vital fluids, but in terms of special kinds of far from thermodynamic equilibrium processes. And so on. (Bickhard 2009: 553)

Be that as it may, what is evident is that an ontology of processes is more consistent with the facts of biology than an ontology of substances. Metabolic turnover, life cycles, and ecological interdependence—to mention the three phenomena we have discussed in most detail—all provide compelling empirical motivations for adopting a process ontology in biology. Philosophers sceptical of our naturalistic approach to metaphysics will doubt whether any amount of empirical evidence could settle, or even be relevant to, the debate between substantialism and processualism. To them we can at least offer our arguments that processualism can deal more effectively than substantialism with a wide range of philosophical issues, including classification, individuation, persistence, explanation, and abstraction. And for those who share our discomfort with the interconnected doctrines of essentialism, reductionism, and mechanicism, processualism, as we have seen, provides resources for grounding this discomfort not available to the substantialist. If the value of an ontological position is to be measured, at least in part, by its ability to solve problems, then processualism can draw support from its application both to biology and to philosophy.

Finally, this essay has illustrated how a processual stance serves as an invaluable heuristic guide in biology. It has a number of interesting and sometimes unexpected consequences for fields as diverse as physiology, genetics, evolution, and medicine, where it forces us to question deeply engrained assumptions and revise basic theoretical tenets. Processualism sheds new light on old problems and even encourages us to change our research questions, and it therefore has the potential to open up novel avenues of empirical investigation. After reading the rest of the essays collected in this volume, we hope that the reader will be convinced at least of the usefulness, and we hope even of the truthfulness, of a processual philosophy of biology.

9. Overview of Contributions

Although we have already alluded to the seventeen other contributions to the volume over the course of this essay, it might be useful to end by saying something about how the book as a whole is organised. Following this extended introduction, the chapters in this volume are classified into four thematic clusters: ‘Metaphysics’, ‘Organisms’, ‘Development and Evolution’, and ‘Implications and Applications’.

The five chapters in Part II of the book deal with general metaphysical issues relating to the goal of developing a process ontology for biology. Peter Simons argues that a fundamentally processual understanding of the living world requires that we reconceptualise the continuant things that biologists study as secondary ‘precipitates’ of primary processes. Rani Lill Anjum and Stephen Mumford suggest that biology is better served by a dispositionalist theory of causation than by more traditional Humean accounts, given that only the former can do justice to the dynamicity, continuity, and context-sensitivity of biological phenomena. James DiFrisco attempts to strengthen the case for a process ontology in biology by providing causal—and suitably processual—accounts of individuation and persistence in terms of cohesion and genidentity, respectively. Thomas Pradeu explores in more detail the fertility of the concept of genidentity in biology, showing how it leads us to prioritise processes over things. Finally, Johanna Seibt considers how a systematic ontological framework of subjectless processes she has developed over many years, called General Process Theory, can be used to address questions of individuality, composition, and emergence in the philosophy of biology.

The four chapters in Part III of the book concern themselves with the concept of the organism—that most central of biological categories—from a processual perspective. Daniel Nicholson calls for a shift in how we think about what organisms are, replacing the conventional machine-like conception with a stream-like one that better captures their processual nature. Denis Walsh claims that recognising the unique character of organisms as processual agents requires an agential theory to make sense of how they evolve. Frédéric Bouchard maintains that evolutionary individuality comes in degrees, as it reflects various levels of functional integration between intersecting processes. Finally, Argyris Arnellos proposes a process-based organizational ontology for biology in order to account for the integrity of individual organisms while simultaneously explaining their collaborative dimension.

The four chapters in Part IV of the book adopt a process ontology in the specific contexts of development and evolution. Paul Griffiths and Karola Stotz show that developmental systems theory is deeply committed to a processual view of life, and they offer a number of reasons why processes need to be taken as fundamental in both development and evolution. Flavia Fabris reappraises the core concepts of Waddington’s theory of epigenetics, and she suggests that the genetic assimilation of acquired characters is best explained in processual terms. Laura Nuño de la Rosa looks at how new microscopy, molecular, and computer technologies for modelling

biological processes are themselves contributing to a processual understanding of development. Finally, Eric Bapteste and Gemma Anderson discuss how an increasing appreciation of the evolutionary role of intersecting biological processes requires new ways of representing these processes for analytical purposes.

Lastly, the four chapters in Part V of the book explore broader implications and applications of a processual philosophy of biology. Stephan Guttinger makes the case for a processual understanding of macromolecules, drawing on ecological ideas to argue that only a process view can elucidate their fundamentally relational character. Marta Bertolaso and John Dupré articulate a processual perspective on cancer, and express their surprise that it does not occur more often in light of the fact that cancer reflects a failure in the highly complex regulatory system that maintains a multicellular organism over time. Ann-Sophie Barwich submits that a process perspective on perception—motivated by recent findings in cognitive neuroscience—results in a far more flexible and contextual understanding of olfaction than has been traditionally supposed. Finally, Anne Sophie Meincke defends the claim that the dilemma of personal identity can be overcome by conceiving persons as biological higher-order processes.

References

- Abir-Am, P. G. (1987). The Biotheoretical Gathering, Transdisciplinary Authority and the Incipient Legitimation of Molecular Biology in the 1930s: New Perspective on the Historical Sociology of Science. *History of Science* 25: 1–70.
- Agar, W. E. (1943). *A Contribution to the Theory of the Living Organism*. Carlton: Melbourne University Press.
- Baptiste, E., & Dupré, J. (2013). Towards a Processual Microbial Ontology. *Biology and Philosophy* 28: 379–404.
- Barnes, J. & Dupré, J. (2008). *Genomes and What to Make of Them*. Chicago: Chicago University Press.
- Bechtel, W. (2006). *Discovering Cell Mechanisms: The Creation of Modern Cell Biology*. Cambridge: Cambridge University Press.
- Bertalanffy L. v. (1941). Die organismische Auffassung und ihre Auswirkungen. *Biologie* 10: 247–258 & 337–345.
- Bertalanffy, L. v. (1952). *Problems of Life: An Evaluation of Modern Biological and Scientific Thought*. New York: Harper & Brothers.
- Bickhard, M. (2009). The Interactivist Model. *Synthese* 166: 547–591.
- Birch, C. & Cobb, J. B. (1981). *The Liberation of Life. From the Cell to the Community*. Cambridge University Press: Cambridge.
- Bohm, D. (1980). *Wholeness and the Implicate Order*. London: Routledge.
- Boogerd, F. C., Bruggeman, F. J., Hofmeyr, J.-H. S., & Westerhoff, H. V. (2007). *Systems Biology: Philosophical Foundations*. Amsterdam: Elsevier.
- Bourne, C. (2006). *A Future for Presentism*. Oxford: Oxford University Press.
- Campbell, R. (2015). *The Metaphysics of Emergence*. New York: Palgrave Macmillan.
- Carpenter, A. D. (2014). *Indian Buddhist Philosophy*. Durham: Acumen.
- Champagne, F. A., Weaver, I. C., Diorio, J., Dymov, S., Szyf, M., and Meaney, M. J. (2006). Maternal Care Associated with Methylation of the Estrogen Receptor-Alpha1b Promoter and Estrogen Receptor-Alpha Expression in the Medial Preoptic Area of Female Offspring. *Endocrinology* 147: 2909–2915.
- Cobb, J. B., & Griffin, D. R. (1977). *Mind in Nature: Essays on the Interface of Science and Philosophy*. University Press of America.
- Collier, J. (1988). Supervenience and Reduction in Biological Hierarchies. *Canadian Journal of Philosophy* 14: 209–234.
- Collier, J. (2004). Self-Organization, Individuation and Identity. *Revue Internationale de Philosophie* 58: 151–172.
- Craver, C. F. (2007). *Explaining the Brain: Mechanisms and the Mosaic Unity of Neuroscience*. Oxford: Oxford University Press.
- Craver, C. F., & Darden, L. (2013). *In Search of Mechanisms: Discoveries across the Life Sciences*. Chicago: Chicago University Press.
- Dawkins, R. (1982). *The Extended Phenotype: The Long Reach of the Gene*. Oxford: Oxford University Press.
- Devitt, M. (2008). Resurrecting Biological Essentialism. *Philosophy of Science* 75: 344–382.
- Dupré, J., (1993). *The Disorder of Things: Metaphysical Foundations of the Disunity of Science*. Cambridge, MA: Harvard University Press.
- Dupré, J., (2002). *Humans and Other Animals*. Oxford: Oxford University Press.
- Dupré, J. (2008). *The Constituents of Life*. Amsterdam: Van Gorcum.
- Dupré, J. (2010a). The Polygenomic Organism, In. S. Parry & J. Dupré (eds.), *Nature After the Genome* (pp. 19–31), Oxford: Blackwell.

- Dupré, J. (2010b). It is Not Possible to Reduce Biological Explanations to Explanations in Chemistry and/or Physics. In J. Ayala & R. Arp (eds.) *Contemporary Debates in Philosophy of Biology* (pp. 32–47). Oxford: Wiley-Blackwell.
- Dupré, J. (2012). *Processes of Life: Essays in the Philosophy of Biology*. Oxford: Oxford University Press.
- Dupré, J. (2013). Living Causes. *Proceedings of the Aristotelian Society Sup. Vol. 87*: 19–38.
- Dupré, J., (2017a). Processes, Organisms, Kinds and the Inevitability of Pluralism. In O. Bueno, R.-L. Chen, & M. B. Fagan (eds.), *Individuation across Experimental and Theoretical Sciences* (pp. XX-XX). Oxford: Oxford University Press.
- Dupré, J., (2017b). The Ontology of Evolution. *Interface Focus*.
- Dupré, J. & Guttinger, S. (2016). Viruses as Living Processes. *Studies in History and Philosophy of Biological and Biomedical Sciences* 59: 109–116.
- Dupré, J., & O'Malley, M. (2009). Varieties of Living Things: Life at the Intersection of Lineage and Metabolism. *Philosophy and Theory in Biology* 1.
- Ellis, B., (2001). *Scientific Essentialism*. Cambridge: Cambridge University Press.
- Ereshefsky, M. (1992). Eliminative Pluralism. *Philosophy of Science* 59: 671–690.
- Ereshefsky, M. & Pedroso, M. (2013). Biological Individuality: The Case of Biofilms. *Biology and Philosophy* 28: 331–349.
- Ghiselin, M. (1974). A Radical Solution to the Species Problem. *Systematic Zoology* 23: 536–544.
- Gilbert, S. F. & Epel, D. (2015). *Ecological Developmental Biology: The Environmental Regulation of Development, Health, and Evolution*. Sunderland: Sinauer Associates.
- Gilbert, S. F., Sapp, J., & Tauber, A. I. (2012). A Symbiotic View of Life: We Have Never Been Individuals. *Quarterly Review of Biology* 87: 325–341.
- Giovannetti, M., Avio, L., Fortuna, P., Pellegrino, E., Sbrana, C., & Strani, P. (2006). At the Root of the Wood Wide Web: Self Recognition and Non-Self Incompatibility in Mycorrhizal Networks. *Plant Signaling & Behavior* 1: 1–5.
- Glennan, S. (2002). Rethinking Mechanistic Explanation. *Philosophy of Science* 69: S342–S353.
- Griesemer, J. (2000). Reproduction and the Reduction of Genetics. In P. Beurton, R. Falk, & H.-J. Rheinberger (eds.), *The Concept of the Gene in Development and Evolution. Historical and Epistemological Perspectives* (pp. 240–285). Cambridge: Cambridge University Press.
- Griesemer, J. (2005a). Genetics from an Evolutionary Process Perspective. In E. M. Neumann-Held, C. & Rehmann-Sutter (eds.), *Genes in Development: Re-Reading the Molecular Paradigm* (pp. 343–375). Chapel Hill: Duke University Press.
- Griesemer, J. (2005b). The Informational Gene and the Substantial Body: On the Generalization of Evolutionary Theory by Abstraction. In M. R. Jones, & N. Cartwright (eds.), *Idealization XII: Correcting the Model, Idealization and Abstraction in the Sciences* (pp. 59–115). Amsterdam: Rodopi.
- Griffiths, P. E., & Gray, R. D. (1994). Developmental Systems and Evolutionary Explanation. *Journal of Philosophy* 91: 277–304.
- Graham, D. W. (2015). Heraclitus. *The Stanford Encyclopedia of Philosophy*, E. N. Zalta (ed.): <<http://plato.stanford.edu/entries/heraclitus/>>.
- 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.
- Haynie, D. T. (2008). *Biological Thermodynamics*. Cambridge: Cambridge University Press.
- Hull D. L. (1965). The Effects of Essentialism on Taxonomy: Two Thousand Years of Stasis. *British Journal of Philosophy of Science* 15: 314–326 & 16: 1–18.

- Hull, D. L. (1976). Are Species Really Individuals? *Systematic Zoology* 25: 174–191.
- Hull, D. L. (1978). A Matter of Individuality. *Philosophy of Science* 45: 335–360.
- Jablonka, E. and Lamb, M. J. (2005). *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*. Cambridge: MIT Press.
- Keller, E. F. (2000). *The Century of the Gene*. Cambridge: Harvard University Press.
- Kim, J. (2005). *Physicalism, or Something Near Enough*. Princeton: Princeton University Press.
- Kirschner, M., Gerhart, M., & Mitchison, T. (2000). Molecular “Vitalism”. *Cell* 100: 79–88.
- Koutroufinis, S. A. (2014). *Life and Process: Towards a New Biophilosophy*. Berlin: De Gruyter.
- Kripke, S. (1980). *Naming and Necessity*. Cambridge: Harvard University Press.
- Levins, R. & Lewontin, R. (1985). *The Dialectical Biologist*. Cambridge: Harvard University Press.
- Lillie, R. S. (1945). *General Biology and Philosophy of Organism*. Chicago: Chicago University Press.
- Machamer, P., Darden, L., & Craver, C. F. (2000). Thinking about Mechanisms. *Philosophy of Science* 67: 1–25.
- Margulis, L. (1998). *The Symbiotic Planet*. London: Weidenfeld & Nicolson.
- Marsh, P. D. (2006). Dental Plaque as a Biofilm and a Microbial Community—Implications for Health and Disease. *BMC Oral Health* 6: S14.
- Methot P.-O., & Alizon, S. (2015). What is a Pathogen? Toward a Process View of Host-Pathogen Interactions. *Virulence* 5: 775–785.
- Misteli, T. (2001). The Concept of Self-Organization in Cellular Architecture. *Journal of Cellular Biology* 155: 181–185.
- Moran N. A. (2006). Symbiosis. *Current Biology* 16: R866–R871.
- Nicholson, D. J. (2012). The Concept of Mechanism in Biology. *Studies in History and Philosophy of Biological and Biomedical Sciences* 43: 152–63.
- Nicholson, D. J. (2013). Organisms ≠ 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: 162–174.
- Nicholson, D. J., & Gawne, R. (2014). Rethinking Woodger’s Legacy in the Philosophy of Biology. *Journal of the History of Biology* 47, 243–292.
- Nicholson, D. J. & Gawne, R. (2015). Neither Logical Empiricism nor Vitalism, but Organicism: What the Philosophy of Biology Was. *History and Philosophy of the Life Sciences* 37: 345–381.
- Noble, D. (2012). A Theory of Biological Relativity: No Privileged Level of Causation. *Interface Focus* 2: 55–64.
- Odling-Smee, J., Laland, L., & Feldman, M. (2003). *Niche Construction: The Neglected Process in Evolution*. Princeton: Princeton University Press.
- Oyama, S., Griffiths, P. E., & Gray, R. D. (2001). *Cycles of Contingency: Developmental Systems and Evolution*. Cambridge: MIT Press.
- Peterson, E. L. (2011). The Excluded Philosophy of Evo-Devo? Revisiting Waddington’s Failed Attempt to Embed Alfred North Whitehead’s ‘Organicism’ in Evolutionary Biology. *History and Philosophy of the Life Sciences* 33: 301–332.
- Peterson, E. L. (2016). *The Life Organic: The Theoretical Biology Club and the Roots of Epigenetics*. Pittsburgh: Pittsburgh University Press.
- Pigliucci, M., & Muller, G. (2010). *Evolution: The Extended Synthesis*. Cambridge: MIT Press.
- Powell, A., & Dupré, J. (2009). From Molecules to Systems: The Importance of Looking Both Ways. *Studies in History and Philosophy of Biological and Biomedical Sciences* 40: 54–64.

- Rescher, N. (1996). *Process Metaphysics: An Introduction to Process Philosophy*. Albany: SUNY Press.
- Russell, E. S. (1916). *Form and Function: A Contribution to the History of Animal Morphology*. London: John Murray
- Russell, E. S. (1924). *The Study of Living Things: Prolegomena to a Functional Biology*. London: Methuen.
- Russell, E. S. (1930). *The Interpretation of Development and Heredity: A Study in Biological Method*. Oxford: Clarendon Press.
- Russell, E. S. (1945). *The Directiveness of Organic Activities*. Cambridge: Cambridge University Press.
- Seibt, J. (1996). The Myth of Substance and the Fallacy of Misplaced Concreteness. *Acta Analytica* 15: 119–139.
- Seibt, J. (2003). *Process Theories: Crossdisciplinary Studies in Dynamic Categories*. Dordrecht: Springer.
- Seibt, J. (2012). Process Philosophy. *The Stanford Encyclopedia of Philosophy*, E. N. Zalta (ed.): <<https://plato.stanford.edu/entries/process-philosophy/>>.
- Shaw, G. B. (1905). *The Irrational Knot*. London: Constable.
- Sider, T. (2001). *Four-Dimensionalism: An Ontology of Persistence and Time*. Oxford: Oxford University Press.
- Sober, E. (1980). Evolution, Population Thinking, and Essentialism *Philosophy of Science* 47: 350–383.
- Stein, R. L. (2004). Towards a Process Philosophy of Chemistry. *HYLE-International Journal for Philosophy of Chemistry* 10: 5–22.
- Strawson, P. F. (1953). *Individuals: An Essay in Descriptive Metaphysics*. London: Methuen.
- Waddington, C. H. (1956). *Principles of Embryology*. London: George Allen and Unwind.
- Waddington, C. H. (1957). *The Strategy of the Genes: A Discussion of Some Aspects of Theoretical Biology*. London: George Allen and Unwind.
- Waddington, C. H. (1969). The Practical Consequences of Metaphysical Beliefs on a Biologist's Work: An Autobiographical Note. In C. H. Waddington (ed.), *Towards a Theoretical Biology. Vol. 2: Sketches* (pp. 72–81). Edinburgh: Edinburgh University Press
- Wade, N. (2005). Your Body Is Younger than You Think. *The New York Times* (2nd August 2005).
- Weiss, P. A. (1962). From Cell to Molecule. In J. M. Allen (Ed.), *The Molecular Control of Cellular Activity* (pp. 1–72). Toronto: McGraw Hill.
- West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution*. New York: Oxford University Press.
- Whitehead, A. N. (1919). *An Enquiry Concerning the Principles of Natural Knowledge*. Cambridge: Cambridge University Press.
- Whitehead, A. N. (1920). *The Concept of Nature*. Cambridge: Cambridge University Press.
- Whitehead, A. N. (1925). *Science and the Modern World*. Cambridge: Cambridge University Press.
- Whitehead, A. N. (1929). *Process and Reality: An Essay in Cosmology*. New York: MacMillan.
- Whitehead, A. N. (1933). *Adventures of Ideas*. Cambridge: Cambridge University Press.
- Wiggins, D. (2016). Activity, Process, Continuant, Substance, Organism. *Philosophy* 91: 269–280.
- Woodger, J. H. (1929a). *Biological Principles: A Critical Study*. London: Routledge & Kegan Paul.
- Woodger, J. H. (1929b). Some Aspects of Biological Methodology. *Proceedings of the Aristotelian Society (New Series)* 29: 351–358.