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The Return of the Organism as a Fundamental Explanatory Concept in Biology

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Abstract

Although it may seem like a truism to assert that biology is the science that studies organisms, during the second half of the twentieth century the organism category disappeared from biological theory. Over the past decade, however, biology has begun to witness the return of the organism as a fundamental explanatory concept. There are three major causes: (a) the realization that the Modern Synthesis does not provide a fully satisfactory understanding of evolution; (b) the growing awareness of the limits of reductionism in molecular biology; and (c) the renewed interest in the nature of life as a genuine scientific problem. This essay examines these recent developments and considers the new epistemological roles being played by the organism in each of them. It also reflects on what the present resurgence of the organism means for the philosophy of biology.

1. *Introduction: The Disappearance of the Organism*

Biology is the science of organisms. Or at least it used to be. The second half of the twentieth century witnessed the disappearance of the organism as a fundamental explanatory concept. The epistemological focus shifted to *sub*-organismic entities (like genes) on the one hand, and to *supra*-organismic entities (like populations) on the other. The category connecting them, the organism as a whole, fell between the cracks of biological enquiry. The organism became 'an undernourished orphan in biology, unwanted because it is not understood by biologists interested in levels above and below [it]' (Russert-Kraemer and Bock 1989: 1055). This is reflected in the philosophy of biology of the period, which was dominated by debates arising at the supra-organismic level, such as the metaphysics of species (e.g. Hull 1978), and debates arising at the sub-organismic level, such as the putative reduction of Mendelian genetics to molecular genetics (e.g. Kitcher 1984). Questions concerning the nature of organisms (for instance, how they maintain their organization, how they coordinate their functions, and more generally how they differ from inanimate systems like machines), which had practically defined the philosophy of biology in the first half of the twentieth century (e.g. Johnstone 1914; Needham 1928; Woodger 1929; Haldane 1931; Bertalanffy 1952), were dismissed as too metaphysical. Organisms no longer seemed relevant to the biological agenda, and few biologists and philosophers felt the need to even mention them. Some even questioned their very existence (Ruse 1989).

Webster and Goodwin (1982) were among the first to denounce the disappearance of the organism from biological theory. They traced this elision to Weismann's separation of the germ line from the soma (i.e. the body) at the turn of the twentieth century. As a result, modern biological thought had come to view the body as a physical manifestation of the action of a central directing agency, instantiated by the notion of the 'genetic program', which directly determines biological structure and function. Although there is a great degree of truth to this diagnosis, the demise of the organism can be more straightforwardly regarded as a major theoretical consequence of the two defining events of twentieth-century biology: the Modern Synthesis of evolution and the molecular biology revolution. The Modern Synthesis combined Darwinian natural selection with Mendelian genetics in the form of population genetics, which was used to bring together many aspects of comparative anatomy, systematics, ecology, and palaeontology under a common set of explanatory principles. Molecular biology adopted the new analytical techniques of biophysics and biochemistry in an attempt to explain—making use of ideas arising in cybernetics, information theory, and computer science—all major cellular phenomena in terms of the structural properties of macromolecules. Taken together, these two developments resulted in an unapologetically genocentric view of life (e.g. Williams 1966; Monod 1971). Such a view left no room for an independent consideration of the organism, which was seen as nothing more than an epiphenomenon of its genes.

In recent years, the situation has begun to change. While no one doubts that the twentieth century will be remembered as 'The Century of the Gene' (Keller 2000), more and more biologists and philosophers have been calling for 'A New Biology for a New Century' (Woese 2004) that will reinstate the organism back to the centre stage of biological theory (e.g. El-Hani and Emmeche 2000; Bateson 2005; Pepper and Herron 2008). A number of edited volumes have appeared reappraising the concept of the organism in light of contemporary findings and evaluating its potential unifying role in biology (Laubichler 2000; Gutmann et al. 2000; Huneman and Wolfe 2010). We can distinguish three main causes for the current resurgence of the organism. The first has been the realization that the theoretical framework of the Modern Synthesis does not provide a complete or fully satisfactory understanding of the evolutionary process. The second is the growing awareness of the limits of reductionistic approaches in molecular biology and systems biology. And the third has been the renewed interest in the nature of life as a basic problem in theoretical biology. In the next three sections, I will examine each of these in turn. I will conclude by reflecting on what the return of the organism means for the philosophy of biology.

2. *The Organism as* Explanans *and* Explanandum *of Evolution*

The greatest theoretical innovation of the Modern Synthesis in relation to Darwin's own theory was the reconceptualization of evolution as the change in allele frequencies of a population. Evolutionary biologists became concerned not with organisms, but with how populations change over time as a result of the causal powers of genes. In this view, organisms are the liaisons of evolution; a sort of interface between the phenotypic expression of genes and the selecting role of the environment. They have no autonomous agency of their own. Their distinctive features, and indeed their very existence, are to be explained by appealing to the causal capacities of genes. In the words of Dawkins (1976: xxi), organisms are mere 'survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes'. It is the genes that are selected for by the environment (rather than the organisms that contain them), and it is at the level of the genes that evolutionary explanations must be sought. The organism has no explanatory role to play.

The Modern Synthesis view of evolution can be characterized by the theoretical demarcation of three biological processes: (a) inheritance: the inter-organismic process that ensures the resemblance of offspring to parent; (b) development: the intra-organismic process by which the fertilized egg becomes a morphologically and physiologically differentiated adult; and (c) adaptation: the supra-organismic process by which populations come to comprise organisms well suited to their conditions of existence. The three processes are considered relatively autonomous given that the development of an individual does not affect the traits that are inherited by its offspring, and the relative adaptiveness of those traits has no influence on the fidelity of their transmission. Moreover, the process that brings about adaptation does not alter the traits that are inherited and developed; it merely selects between them. In this picture of evolution, the gene plays a central unifying role, as genes are the only entities that are crucial to all three of the aforementioned processes. Genes are the sole units of inheritance. Development is the execution of a program of phenotypic information encoded in the genes. And adaptation results from changes in gene frequencies in a population.

This widely held view of evolution has recently been challenged from various fronts. The different critiques converge in rejecting the premise that genes are the sole, or even the primary, agents responsible for inheritance, development, and adaptation, and also in questioning the assumption that these processes are causally independent from one another. With regard to inheritance, there is growing evidence against the notion that genes are the only transmitters of information from parent to offspring. Jablonka and Lamb (1995, 2005) have drawn attention to a number of 'Neo-Lamarckian' epigenetic inheritance mechanisms (such as chromatin marking processes like DNA methylation, positive feedback loops of gene expression, RNA interference, and the template-based replication of membranes and prions), which enable the acquisition and transmission of phenotypic variation across generations. With regard to development, it is becoming apparent that genes do not constitute a special class of 'master molecules' that direct and control the developmental process. A new theoretical perspective has emerged, called 'Developmental Systems Theory' (see Oyama 2000; Oyama et al. 2001), which conceives organisms as being epigenetically reconstructed in each generation from a wide array of developmental resources (of which genes are only one factor), rather than resulting from the execution of a causally privileged, quasi-preformationist genetic program. Finally, the fact that genes do not determine the phenotype on their own, and that development has an influence on what gets inherited, has important implications for how we think about adaptation. West-Eberhard (2003, 2005) has argued that phenotypic plasticity (i.e. the capacity of a single genotype to generate different phenotypes in response to variable environmental conditions) plays a pivotal role in adaptive evolution because it leads to phenotypic innovations that can later be consolidated by means of genetic accommodation. On her account, novel adaptive phenotypes are not caused by changes in gene frequencies, as the Modern Synthesis view would have it. Instead, it is the adaptive novelties—resulting from the phenotypic plasticity of organisms—that cause changes in gene frequencies.

Out of this recent work emerges a view of evolution that is considerably different from the one that dominated late twentieth-century biological thought (cf. Pigliucci and Müller 2010; Gilbert and Epel 2008; Walsh 2006, 2010; Huneman 2010). It is a view in which it is no longer possible to sharply distinguish between the processes responsible for the intergenerational stability of the phenotype (inheritance), those that occur in the growth and differentiation of an organism (development), and those that produce advantageous phenotypic variations (adaptation). Inheritance, development, and adaptation are unified because they are all consequences of the distinctive capacities of organisms, such as their plasticity and robustness (Bateson and Gluckman 2011). Perhaps more importantly, the emerging view of evolution dislodges the gene from its privileged position and restores the organism back to the centre of the evolutionary stage. In this organism-centred view, organisms rather than genes are the primary agents of evolutionary change. Of course, this is not to say that genes are not important. Genes really are among the units of inheritance. Genes really do exert phenotypic control (along with numerous other developmental resources). And adaptation really does consist, among other things, in the change in gene frequencies in a population. But adopting an organism-centred view forces us to rethink some of the central tenets of evolutionary theory.

Take the role of chance in the generation of phenotypic variation, for instance. In the Modern Synthesis view, phenotypic variation is taken to arise by genetic mutation and recombination. These genetic changes are described as 'random' or 'blind' because the incidence of their occurrence is not correlated with the adaptiveness of the traits they code for. Chance thus plays a key role in the introduction of new phenotypic variation upon which selection acts to bring about adaptive change. However, if phenotypic innovation and variation does not arise primarily by mutation and recombination but by means of epigenetic mechanisms, such as developmental rearrangements of core cellular processes (Kirschner and Gerhart 2005) and regulatory interactions between tissues and environmental factors during morphogenesis (Müller and Newman 2003), then adaptive change is not predominantly chancy. Instead, the dynamics of organismic development must be regarded as playing a decisive role in biasing the direction of evolution (Arthur 2004). It would appear that, far from always being random in origin and blind to function, phenotypic variation can be 'targeted' in the sense that it can arise in response to environmental challenges, preferentially affecting the functions and activities of organisms in ways that make them better adapted to survive.

Another aspect of the traditional evolutionary picture that is challenged by the nascent organism-centred view is the conceptualization of the relation between organism and environment. According to the Modern Synthesis view, this is an externalist relation. A causal arrow runs from environment to organism (or rather, its genes), and this arrow explains why organisms are the way they are. Adaptation is conceived as a process by which natural selection effectively moulds organisms to fit pre-established environmental templates. Environments pose 'problems', and the organisms best equipped to deal with them are the ones that survive and reproduce. The problem with this view is that it neglects the active role that organisms play—through their metabolism, their activities, and their choices—in defining and partly creating their own ecological niches. To varying degrees, organisms choose their own habitats, mates and resources, and even construct parts of their local environments by means of nests, dams, holes, paths, webs, chemical gradients, etc. Odling-Smee et al. (2003), building on earlier work by Lewontin (1982, 1983), have dubbed this phenomenon 'niche construction', and refer to it as 'the neglected process in evolution'. The evolutionary significance of niche construction resides in the realization that if organisms do not just adapt to environments, but also help construct them, then the selection pressures that act upon organisms exist partly as a consequence of the niche-constructing activities of past and present generations of organisms. This generates a feedback loop between niche construction and selection that shapes the dynamics of evolutionary change.

Ultimately, the new organism-centred view of evolution has consequences for how we think about the nature of selection itself. In the Modern Synthesis view, selection is interpreted as a force that causes adaptive change by driving populations through changes in gene frequencies (Sober 1984). Selection does not only eliminate detrimental genetic variations but also acts creatively by bringing beneficial genetic variations together. Evolutionary change thus comes about by the capacity of environments to retain and promote genetic variations that favour the survival and reproduction of the organisms that contain them. However, if evolutionary change arises instead from the ways in which organisms deploy their developmental plasticity to respond to environmental challenges that they themselves partially determine, then the traditional view of selection becomes problematic. Rather than conceiving it as a force that causes adaptation, the organism-centred view implies understanding selection as the effect on a population of the sum of the individual activities of organisms as they struggle to survive (Walsh et al. 2002; Matthen and Ariew 2002). According to this interpretation of evolution, natural selection is caused by the differential survival and reproduction of organisms, and not the other way around. It can explain changes in the statistical structure of populations but not the adaptiveness of the individual organisms that comprise them. Some, however, maintain that a causal understanding of selection can still be made compatible with the organism-centred view (Ramsey 2013; Pence and Ramsey 2013).

Overall, evolutionary biology is currently experiencing a shift from a gene-centred to an organism-centred perspective. Having been the traditional *explanandum* of evolution, it is now clear that organisms must also be part of the *explanans*. It remains to be seen how the emerging organism-centred view will coexist with the old Modern Synthesis view—whether it will come to displace it, or if some sort of compromise will be reached between the two theoretical perspectives. What can no longer be denied, in any case, is that the concept of the organism has a fundamental explanatory role to play in evolutionary theory.

3. The Organism as an Antidote to Explanatory Reductionism

The present resurgence of the organism is also the consequence of the unbridled reductionism that characterized molecular biology in the second half of the twentieth century. Watson and Crick's discovery of the structure of DNA in 1953 triggered a vigorous experimental research programme that was extremely successful in identifying and characterizing the basic macromolecular constituents of living systems. In turn, this led to extraordinary advances in the understanding of cellular structure and function. The reductionistic strategy of breaking up the organism (in this case, the cell) into its component parts proved to be such an effective methodology that there was little reason to doubt that studying all of the parts individually would ultimately result in a complete explanation of the organism as a whole, if only because the parts collectively constitute the whole. The general belief in the explanatory power of reductionism was coupled with the more specific conviction that biological information flows unidirectionally from DNA to proteins (the so-called 'central dogma' of molecular biology) and that consequently genes are the primary determinants of an organism's form, function, and behaviour (e.g. Crick 1966). The invention of genome sequencing techniques eventually led to the inception of the Human Genome Project (HGP), which was conceived in order to acquire the complete 'catalogue' of all the genes in a human being. The HGP developed under the explicit assumption that this collection of data

> constitutes the complete set of instructions for development, determining the timing and details of the formation of the heart, the central nervous system, the immune system, and every other organ and tissue required for life (DeLisi 1988: 489).

However, as the twentieth century drew to a close, widespread support for genetic determinism—so enthusiastically advocated by the early champions of molecular biology—was rapidly fading (see Lewontin 1993; Rose 1997; Strohman 1997). It had become clear that DNA sequences in and of themselves do not contain the information required to specify how gene products (i.e. proteins) interact to produce organismic function. There is, in fact, no simple, one-to-one correspondence between genes and phenotypes (Morange 2001; Moss 2003). As a result, the publication of the sequence of the human genome in 2001 failed to deliver in its promise to revolutionize biomedical research by enabling the prediction and treatment of human disease (Bains 2001). Even the architects of the HGP have been forced to acknowledge the impossibility of predicting the lives of organisms from their genomes: 'one of the most profound discoveries that I have made in all my research is that you cannot define a human life or any life based on DNA alone' (Venter 2007: 3). Perhaps the most significant finding of the HGP was that humans have far less genes than expected. Initial estimations circled around the 100,000 mark (Kevles and Hood 1992), but the actual number is closer to 20,000. The realization that organismic complexity is not correlated with gene number has been branded the 'N value paradox' (Claverie 2001), but the truth is that this is only a paradox if one already assumes that there *should* be such a correlation in the first place.

The collapse of genetic determinism—encapsulated in the anti-climax that followed the sequencing of the human genome—was widely regarded as an indication that if one is to succeed in grasping the complexity of an organism, one must not only catalogue and characterize the complete set of genes, but also the complete set of RNA transcripts (i.e. the 'transcriptome'), the complete set of proteins (i.e. the 'proteome'), and the complete set of molecules involved in metabolism (i.e. the 'metabolome'). To this end, high throughput technologies have begun to be used on a massive scale, resulting in the large-scale production of vast pools of data which biologists are now trying to decipher using mathematical models and computer simulations. This new research programme has been called 'systems biology' (Kitano 2001; Alon 2007), and it is generally perceived to offer a way of overcoming the limits of the reductionism of molecular biology by shifting the focus from molecules to systems (see Boogerd et al. 2007).

Despite its aspirations, a number of authors have recently made the acute observation that systems biology as it is currently practised, far from transcending reductionism, is only serving to perpetuate it (Cornish-Bowden 2006; Saetzler et al. 2011). This is because most systems biologists examine intracellular networks (such as those involved in metabolism, signalling or transcription) by characterizing each of the components in the networks individually and then modelling the interactions between them using computational tools. The expectation is that by means of these bottom-up models, systems biology will arrive at a full understanding of the cell as a whole. Such an approach is thoroughly reductionistic given that, like molecular biology, it privileges the molecular level in biological explanation. This is reflected in the way many systems biologists think of their own discipline when they define it as 'the study of the behavior of complex biological organization and processes *in terms of the molecular constituents*' (Kirschner 2005: 504, my emphasis). If this is all that it amounts to, then systems biology does not constitute a significant departure from molecular biology. The former is merely a continuation of the latter (de Backer et al. 2010). In turn, this means that systems biology is subject to the same explanatory limitations as molecular biology. If molecular biology could not grasp biological complexity, then neither can systems biology.

As a result of these concerns, an increasing awareness is emerging that an *ad hoc* approach to systems is not enough. In order for systems biology to succeed where molecular biology failed, it needs to embrace a truly systemic perspective. It must move beyond the study of individual molecules, and even of the interactions between them, and examine systems *as* systems rather than as collections of parts. Understanding the whole requires studying the whole. It means recognizing that by virtue of the organization of the whole, the parts interact nonlinearly causing qualitatively new properties to emerge that are not possessed by the parts, neither when considered individually nor when assembled in other combinations. It also means appreciating that although one can analyse the various activities of a biological system in isolation, the system actually carries them out simultaneously by harmoniously coordinated interactions that cannot always be predicted computationally or replicated experimentally. It has been suggested that systems biology should reorient at least part of its research efforts towards the identification and characterization of the organizing principles that underlie these and other distinctive features of living systems (Mesarovic et al. 2004; Rosslenbroich 2011).

Although this approach is still in its infancy, it is already possible to glean the first theoretical insights it has generated (Bard et al. 2013; Bizzarri et al. 2013). One of the most intriguing is what Noble (2012) has termed the 'theory of biological relativity', which postulates that there is no privileged level at which biological functions are determined. In most cases, the whole and the parts reciprocally determine each other's function. Noble's favourite example is the pacemaker rhythm of the heart, which is not only caused by the activity of the ion channels at the molecular level, but is also dependent on the functioning of the organ, and even the body as a whole. Other instances of the apparent circular causality underpinning complex biological phenomena have been examined by Soto and Sonnenschein (2006).

It is in the context of these current efforts to put the 'systems' back into 'systems biology' that the organism is making a return as a fundamental explanatory concept. The recognition that an understanding of the whole in terms of the parts needs to be complemented with an understanding of the parts in terms of the whole (Cornish-Bowden et al. 2004) reflects the renewed priority afforded to the organism in the explanation of biological complexity. The fact that the properties and behaviour of the parts are partially determined by the organization and activity of the organism as a whole implies that these cannot be fully accounted for without considering the influence exerted upon them by the whole. There is a complementarity and interdependence between molecular-level and system-level explanations (Powell and Dupré 2009). To understand any cellular or organismic phenomenon, it is necessary to situate the 'local' molecular process causally responsible for it within the 'global' context of the organized system that makes it possible in the first place. This realization has prompted Hofmeyr (2007) to suggest that Dobzhansky's adage for the Modern Synthesis that 'Nothing in Biology Makes Sense Except in the Light of Evolution' (1973) should be reformulated for systems biology as 'Nothing in an organism makes sense except in the light of context'.

The neglect of the organismic context, and the consequent disregard of Hofmeyr's dictum, causes various problems. In explanations of developmental differentiation, it leads to genetic determinism. In explanations of cellular activity, it results in what may be described as 'molecular animism'. This is the tendency to anthropomorphize molecules by calling them 'regulators', 'integrators', 'organizers', etc., and crediting them with the regulatory, integrative, and organizing effects that actually arise from the coordinated activity of the whole system. The proclivity towards molecular animism is particularly pronounced in research involving gene knockout experiments, which although by themselves can only demonstrate that the expression of a gene is necessary for a specific process, all too frequently are used as evidence to conclude that the gene product in question is the 'regulator' of the process (Davies 2009). The mistaken habit of bestowing privileged causal roles to molecules in explanations of cellular phenomena stems from the failure to understand that everything that happens inside a cell (e.g. DNA replication, protein synthesis, membrane trafficking, etc.) happens by virtue of the enabling conditions afforded by the pre-existing functional organization of the cell as a whole.

On the whole, as Woese (2004) has observed, the molecular biology revolution of the latter half of the past century proved to be a mixed blessing. Those problems (or portions thereof) that were amenable to a reductionistic approach were elucidated and explained in molecular terms. Those not commensurate with the molecular perspective were either ignored or dismissed as irrelevant, and hence have remained largely underdeveloped. Systems biology's ongoing efforts to put the organism back into the picture by emphasizing the importance of organization, integration, and regulation serve to enrich the explanatory toolkit of biology and provide a much needed antidote to the excessive reliance on molecular-level explanations.

4. The Organism as a Means of Grasping the Nature of Life

Life comes in the form of organisms. The fact that late twentieth-century biology managed to go so far focusing exclusively on sub-organismic and supra-organismic entities is indicative of the extent to which biology during this period lost sight of the problem of life itself. What makes something living? How are living systems distinct from inanimate systems? These questions were once at the forefront of theoretical biology. But after the publication of Schrödinger's *What is Life?* (1944) and the subsequent rise of molecular biology, the question of life vanished from the biological discourse (Shostak 1998). In recent years, as dissatisfaction with reductionism in biology has steadily grown, the nature of life has again begun to attract the attention of biologists and philosophers (e.g. Morange 2008; Bedau and Cleland 2010; Letelier et al. 2011). One of the basic shortcomings of reductionistic approaches is that they tend to focus on the material constitution of living systems whilst neglecting the fact that life itself is not a property of the matter of a system, but of its organization. To grasp the crucial difference between a living entity and a non-living one, one must focus on organization. It is here that the concept of *organism* plays a pivotal explanatory role.

The concept of organism is not simply a synonym for 'living being' or 'biological individual', but it also tacitly conveys a specific theoretical understanding of a living being as a self-organized integrated system (Wolfe 2010). Interestingly, an enquiry into the etymology of the word 'organism' reveals that it was coined at the turn of the eighteenth century to designate the kind of organization displayed by living beings in contradistinction to the kind of organization exhibited by machines. Only in the second third of the nineteenth century did 'organism' come to be used generically to refer to individual living beings (Cheung 2006). In a sense, to invoke the concept of organism is already to refer, if only implicitly, to the particular organization of living beings. From a philosophical perspective, it no longer suffices to declare that 'Organisms are "nothing but" atoms, and that is that' (Hull 1981: 282). As an interest in the nature of life as a genuine scientific problem is being rekindled, it is becoming necessary to unpack the theoretical commitments that follow from the technical usage of this concept. In other words, what precisely does the notion of organism capture when it is employed to describe the organization that makes living systems alive?

It has recently been suggested that the concept of organism is grounded in two key organizational relations: (a) the *parts–whole* relation, according to which an organism is construed as a structurally and functionally differentiated whole, and (b) the *inside–outside* relation, according to which an organism is construed as an autonomous system capable of maintaining itself in the face of changes to its environment (Ruiz-Mirazo et al. 2000; Nuño de la Rosa 2010). The intricate relation between parts and whole was first recognized by Kant in his *Critique of the Power of Judgment* (2000/1790), in which he observed that living beings are self-organizing systems in the sense that their parts reciprocally produce one another in accordance to the organization of the whole. The whole can be said to be ontogenically prior to the parts because an organism, unlike a machine, is not assembled from well-defined, pre-existing components. Instead, the parts of an organism only acquire their identities *qua* parts as the whole progressively develops from an originally undifferentiated yet already integrated system. Moreover, the whole exhibits a greater degree of invariance than its parts because it maintains its organization by continuously breaking down and replacing the constituents that make it up. Consequently, it makes no sense to identify an organism with the sum of its parts, as these are constantly being replenished by the whole. The parts of an organism at any given moment are only the temporary manifestation of the self-producing organizational unity of the whole (Nicholson 2013). Although organisms are not the only kind of thermodynamically open systems that maintain themselves in far from equilibrium conditions by exchanging energy and matter (flames, tornadoes, and convection cells are other familiar examples), they are distinctive in that they regulate their interaction with the outside environment by means of physical boundaries (like membranes or skin) that they themselves generate. This endows organisms with an internally defined identity—what Bernard (1957/1865) called the *milieu intérieur*—that enables them to act on their own behalf by compensating against external perturbations in order to ensure their continued existence. It is in this sense that organisms are autonomous systems (Mossio and Moreno 2010; Ruiz-Mirazo and Moreno 2012).

This more nuanced characterization of the organism as a self-organizing and self-maintaining autonomous system far from thermodynamic equilibrium can be used to elucidate a number of features associated with life. Specifically, it may hold the key to naturalizing rather elusive notions like function, normativity, and agency. Let us begin with function. Several authors have recently articulated an *organizational* account of biological function according to which the attribution of functions to the parts of an organism is deemed to be determined by the means in which each of the parts individually contribute to the realization of the systemic organization that generates and maintains them. In a way, it is the organism itself that adjudicates the ascription of functions to its parts according to how they help it meet its physiological needs and cope with its environmental surroundings (see Schlosser 1998; Collier 2000; McLaughlin 2001; Christensen and Bickhard 2002; Edin 2008; Mossio et al. 2009; Saborido et al. 2011). What is interesting is that this view avoids the familiar problems with the two classical philosophical accounts of function: the etiological and the dispositional. The etiological account, grounding function in selected effects, is too narrow to accommodate function talk in areas of biology not directly concerned with historical explanations (such as physiology, development, and molecular biology), whereas the dispositional account, by interpreting any means–ends relation as functional, is too broad to discriminate genuine functions from other kinds of causal relations. The merit of the organizational account is that it explains why some traits are functional while others are not (like the etiological account), whilst focusing on current contributions of function bearers rather than on their histories (like the dispositional account). For this reason, it appears to provide a rather promising means of coming to terms with the functional aspect of life.

Moving now to the notions of normativity and agency, although these are frequently considered to belong exclusively to the human domain, there is an important sense in which they can be said to apply to all organisms that becomes apparent when their distinctive organizational dynamics is considered. Because they subsist in far from equilibrium conditions, what organisms are (i.e. their structure) and what organisms do (i.e. their activity) are deeply intertwined. The very existence of an organism depends on the effects of its own activity. This means that an organism's activity is intrinsically relevant to itself. Such intrinsic relevance generates a naturalized criterion for determining what norms the organism *should* follow. An organism (as well as its parts) *must* act in accordance to the particular operational norms that enable it to maintain its organization through time. If it stops following these norms, it ceases to exist. It is therefore possible to speak of what is intrinsically 'good' or 'bad' for an organism by evaluating its activities and actions according to the contribution they make towards the maintenance of its organization. Similarly, it becomes perfectly reasonable to regard an organism as an agent once it is construed as a self-producing organization that engages the world by actively regulating its exchanges with it in order to ensure its continued viability (Barandiaran and Moreno 2008; Barham 2012).

Finally, attending to the characteristic organization of organisms has broader implications for biological ontology. By virtue of their thermodynamic openness, organisms are more accurately conceived as dynamic processes than as stable things. The identity of organisms hinges on the fact that they are continuously undergoing change. Although it is often useful to abstract away the temporal dimension of organisms so that they can be studied as static things, such abstractions do not come without costs. Ultimately, the processual nature of life has important implications for how we think about causation and explanation in biology that are only beginning to be explored (Dupré 2012, 2013; Nicholson 2012, 2013).

Overall, the concept of the organism is becoming a useful means of narrowing down the focus of discussions concerning the nature of life by placing the epistemological spotlight on the distinctive organizational dynamics of living systems.

5. Conclusions: Organicism Redux?

Just as early twentieth-century biology experienced 'The Eclipse of Darwinism' (Bowler 1983), late twentieth-century biology witnessed the eclipse of the organism. The organism was dislodged from its central place as the basic phenomenon of life, as a major explanatory resource, and as a theoretical problem in its own right. Although organisms were deemed to have been explained away, in retrospect a more accurate assessment is that they were merely abstracted away. In molecular biology, the complexity of the organism's organization was taken for granted as the experimental focus shifted towards the detailed mapping and analysis of metabolic pathways, signalling cascades, and the regulation of gene expression. Likewise, in the Modern Synthesis view of evolution, the agency and autonomy of organisms were not even recognized as theoretical problems but were simply presupposed in the models of population genetics and behavioural ecology.

In the first decade of the twenty-first century the situation has started to change, which is why the timing is now right to reassess the place of the organism in the light of current knowledge. Having been conspicuously absent from the philosophical literature for decades, the organism is again reclaiming the attention of philosophers of biology. Indeed, our examination of recent work at the forefront of evolutionary developmental biology, systems biology, and theoretical biology raises serious doubts over whether there can really be a 'philosophy of biology' worthy of its name without an adequate understanding of the concept of the organism.

In a sense, the return of the organism means that philosophy of biology has come full circle. The philosophy of biology in the early twentieth century—especially in the interwar period—was very much influenced by *organicism*, which was a school of thought that rose out of the long-standing dispute between mechanicism and vitalism as a naturalistic, scientifically grounded critique of the reductionistic excesses of mechanicism (Hein 1972). Early twentieth-century organicists considered the organism the fundamental category of biology upon which all theorizing about life should be ultimately based. Judging by the growing calls for the vindication of the centrality of the organism arising concurrently in different biological fields, it is not inappropriate to propose that organicism itself may be re-emerging in the philosophy of biology, as several authors have already suggested (Gilbert and Sarkar 2000; Etxeberria and Umerez 2006; Denton et al. 2013). Perhaps the major item in the revived organicist agenda is to reunite the sub-organismic and supra-organismic perspectives in order to facilitate the eventual formulation of a general theoretical framework for biology that does full justice to all the characteristics proper to life.

Short Biography

Daniel J. Nicholson's research is located at the intersection of theoretical biology and the history and philosophy of science. He holds a PhD in Philosophy (University of Exeter) as well as master's degrees in Molecular and Cellular Biology (University of Bath) and History and Philosophy of Science (University of Leeds). Prior to his present appointment at the Exeter Centre for the Study of Life Sciences, he was a postdoctoral research fellow at the Cohn Institute for the History and Philosophy of Science and Ideas at Tel Aviv University, and at the Konrad Lorenz Institute for Evolution and Cognition Research near Vienna. His doctoral thesis presented a critical examination of mechanistic thinking in biology. Since then, he has become particularly interested in the role of machine models in biological explanation, in the task of providing a naturalistic account of organismic purposiveness, and in philosophical arguments for the autonomy of biology. He also has a long-standing interest in the history of the philosophy of biology, as well as in general topics in the philosophy of science.

Note

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