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Physical Explanation and the Autonomy of Biology

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Abstract

It is often claimed that biology is autonomous from the physical sciences, but this is seldom made precise. This paper makes explicit, for the first time, five distinct ‘autonomy of biology’ theses. Three moderate theses concerning scientific status, methodological distinctness, and non-reducibility of biology to physics, are correct, and are nearly universally accepted. Two stronger theses concerning the exclusivity of biological explanation and irrelevance of physical laws, are shown to be false on the basis of two case studies of physical explanations of biological phenomena. Which scales and laws are explanatorily relevant for a particular phenomenon must be decided empirically.

1. Introduction

The autonomy of biology from the physical sciences has been a major theme in philosophy of biology. It was important in the vitalism vs. mechanism debate and in the organicist movement, and it continues to feature in contemporary debates. Recent works on biological explanation defend the distinctness of biological explanations (Braillard and Malaterre 2015; Bock 2017; Fang 2022), and there is widespread criticism of reductionist approaches in biology, with some authors advocating a return to organicism, according to which biological explanations must appeal to the organism as a whole (Nicholson and Dupré 2018; Dupré 2021; Reiss and Ruse 2023; various authors in Mossio 2024).

This contrasts with the widespread use of reductionist approaches in contemporary biology, especially in cellular and molecular biology, where "the dominant role played by physical and chemical principles" (Weber 2005, 25) is not seen as problematic, and is arguably part of their success. Despite widespread consensus that biological systems are, or are realised by, physical systems, the question of how biology relates to physics is not settled, and continues to motivate discussions about the autonomy of biology, reductionism, and the role of physical explanations in biology.

Vitalism took living systems to be fundamentally different from non-living matter, either because they contain something primitively lifelike, or because they are not governed by physical laws. Following the demise of vitalism, some philosophers viewed biology as a 'temporary science' that would in time be reduced to physics (Nagel 1951: Smart 1963). Notoriously, Oppenheim and Putnam (1958) proposed a hierarchical model of the sciences that was supposed to correspond to reductive relations between them that were ultimately grounded in microphysics. The thesis of the autonomy of biology was developed by Mayr and others in response to this and other strong forms of reductionism. Today, almost everyone agrees that biology is a legitimate science, with its own concepts, methods, problems, and theoretical approaches.

Yet, given that vitalism is wrong, it is also the case that the entities and processes of actual biological systems are just as subject to physical laws as all other systems in the universe. Organisms and other biological entities have physical components organised in certain ways, and biological processes always involve, depend on, supervene on, or are realised by, a physical basis. Biological function is both constrained by the laws of physics, and enabled by physical processes. Hence, this paper argues, contrary to some strong autonomy theses defended in the recent literature, that some biological explanations are physical explanations, and that the scales and laws that are explanatorily relevant for a particular phenomenon must be decided by scientific discovery, not a priori.[1]

There is not, in fact, one thesis of the autonomy of biology, but several. It is important to distinguish the different senses of autonomy but, unfortunately, they are not made explicit, and so are often conflated. This paper precisely formulates five distinct 'autonomy of biology' theses, and evaluates each one individually.

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[1] Here and throughout what follows, 'physical' is taken to denote physical entities and processes including chemical ones, and does not refer only to fundamental physics.

The next section distinguishes three moderate autonomy theses and summarises the arguments for them. Section 3 presents a much stronger autonomy thesis according to which physical laws are mostly irrelevant, and argues against it. Section 4 presents the strong autonomy thesis that biological phenomena must have biological explanations, and argues against it on the basis of two case studies of physical explanations of biological phenomena. Section 5 concludes the paper.

2. The Autonomy of Biology: Moderate Theses

Historically, an important motivation for arguments in favour of the autonomy of biology was to dispel the worry that biology might not be a legitimate science, and to make the case that biology is “as much a science as the physical sciences” (Mayr 1985, 43). This is unlikely to be opposed by anyone in the twenty-first century.

§1. *Scientific status*: Biology is a genuine science, like physics and chemistry.

There were extreme reductionists in the 1950s and 1960s who thought that that biology was not a genuine science. For example, J. J. C. Smart argued that biology was “not a theory of the same logical sort as physics though with a different subject matter”, being mostly descriptive, and equivalent to just “physics and chemistry plus natural history”

(1963, 57). Such views were plausible to others such as Ernst Nagel (1951), but the extensive predictive and explanatory success of biology in the decades since renders them quaint. Biology has also been deemed not a proper science for failing to be sufficiently *universal*, by allegedly dealing with particular, spatio-temporally restricted entities and events taking place on Earth. There is no reason to think this is true. Despite the current lack of examples of extra-terrestrial life, astrobiology is a thriving discipline, and at least some biological theories, notably evolution by natural selection, are thought to be universal (Dawkins 1983; Sterelny and Griffiths 1999).

If biology was a *subfield* of another science such as physics then it could seem to fail to be a proper science in the sense intended above. However, biology is not a subfield of physics in the way that, for example, optics is. Nevertheless, biology does fall within the scope of physics insofar as all systems at all scales obey physical laws, and this is equally true of biological systems as it is of geological ones. Biological systems and processes involve physical systems and processes at many scales to which physical laws apply. This does not make biology a subfield of physics or less than fully scientific.

A second moderate autonomy thesis is methodological.

> §2. *Methodological distinctness*: Biology has its own concepts, methods, problems, and theoretical approaches.

The methodological distinctness of biology is explained by several distinctive features of biological systems: (1) the *uniqueness and variability* of living things; (2) their *high complexity*; and (3) the presence of *historically acquired information* in organisms (Mayr 1985, 1996, 2004).

Biological species are not classes of identical things, but “variable populations consisting of uniquely different individuals” (Mayr 1996, 101). Even genetically identical clones raised in the same environment differ phenotypically in traits ranging from appearance to personality and life span, due to developmental variation, epigenetic differences, and the stochastic nature of cellular processes (Kirkwood et al. 2005; Vogt et al. 2008; Bierbach et al. 2017).

In general, biological systems tend to be much more complex than most non-biological systems. They have a high degree of hierarchical organisation, complex causal and regulatory networks, and high interdependency among their parts. The functioning of organisms involves the coupling of processes at very different scales (Ladyman and Wiesner 2020, 128). Specific methodologies are required to investigate these kinds of complexity.

Biological systems are also unique in the degree to which they store historically acquired information. While many non-biological systems also preserve information, biological systems have *evolved mechanisms* for storing information. As products of evolution, living beings “carry a lot of the history of life with them”, and this history “is encoded in both mechanisms and structure” (Ladyman and Wiesner 2020, 128). The presence of historically acquired information in living systems legitimates ‘why’ questions that are inappropriate in other scientific contexts, and gives an important explanatory role to historical narratives in evolutionary biology.

That differences in the nature of the subject matter should motivate methodological differences is not surprising. But these differences are mainly a matter of degree, resulting in a difference in emphasis and preponderance, rather than a sharp methodological break between biology and the physical sciences (Hull 1974, 133). Neither is biology an entirely historical discipline; nor is historical contingency unique to it – consider the importance of history for geology and cosmology and, more generally, the relevance of initial conditions for the study of any dynamical system.

Another moderate autonomy thesis is formulated in terms of explanatory reduction.[2]

> §3. *Explanatory irreducibility*: Biology cannot be explanatorily reduced to physics.

The idea that biology would one day be explanatorily reduced to physics and chemistry was popular in the 1950s and 1960s. For example, Nagel thought that the autonomy of biology made sense only as a temporary research strategy, allowing the discipline to be “cultivated as an autonomous branch of science, *at least during a certain period of its*

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[2] For reasons of space we do not discuss here ontological reduction.

development" (1951, 38, emphasis added). Francis Crick famously said that the "ultimate aim of the modern movement in biology is to explain all biology in terms of physics and chemistry" (1966, 10). Today, in contrast, explanatory reductionism is almost universally opposed (Pradeu 2018, 451).

There are three main arguments against explanatory reductionism. Firstly, the *argument from functional and teleonomic explanation* states that biology is explanatorily autonomous from physical science due to the prevalence of functional and/or teleonomic explanations, which find no counterpart in physics. For example, it is hard to explain the mechanical properties of wings without reference to their *function* of providing lift and thrust in self-powered flight. If functional explanations are ineliminable and unique to biology, then biology cannot be explanatorily reduced to physics. Secondly, the *argument from multiple realisability* states that biological kinds are multiply realisable, meaning that many different arrangements of physical components can realise the same biological kind; thus, they cannot be reduced to physical kinds. Thirdly, according to the *argument from dual causality*, biological phenomena uniquely require both proximate and evolutionary/historical/ultimate causation. The first can be equated to nomological-deductive explanations (Bock 2017), whereas the latter reflect an organism's evolutionary history. Since evolutionary causation is unique to biology, biology is not reducible to the physical sciences.

The next two sections examine stronger, and more problematic, autonomy theses.

3. Strong Autonomy I: The Irrelevance of Physical Laws for Biological Explanations

A stronger autonomy thesis is the thesis that physical laws are mostly irrelevant for biological explanations.

> §4. *Irrelevance of physical laws*: Physical laws (and perhaps laws in general) are irrelevant for biological explanations.

One reason that physical laws are thought to have little relevance for biological explanations is because physical goings-on are assumed to take place at different levels or scales from biological entities and phenomena. This might be the result of equating physics with microphysics. For instance, Mayr claimed that “disturbances at the level of elementary particles are ordinarily of no effect whatsoever at the higher levels of biological integration” (1985, 45), and Gilbert and Sarkar argue that “[w]hen you have an entity as complex as the cell, the fact that quarks have certain spins is irrelevant” (2000, 3). Physical explanation is often accepted “at the cellular-molecular level” (Mayr 2004, 36) but is claimed to have no relevance for higher levels of integration, such as multicellular organisms, and particularly for their evolution.

However, physical laws pervade biology at all scales, as Green and Batterman (2017) acknowledge. Physics is not confined to molecules; macroscopic organisms and their parts are also physical entities and their physical properties afford them their functionality. Even evolutionary explanations of highly contingent events rely on physical laws. Ghiselin (1989) gives the example of a palaeontologist trying to reconstruct the feeding habits of fossil cephalopods. It is no use relying on taxonomic generalisations – though all extant cephalopods are carnivorous, early cephalopods might not have been. Therefore, the palaeontologist must rely on physical laws (Ghiselin 1989, 63), focusing on the mechanical properties of skeletons, teeth, shells, etc, which condition their possible functionality.

Another argument for the irrelevance of physical laws for biological explanations is based on the alleged irrelevance of laws in general for biology. Dupré (2021, 7) claims that in philosophy of biology "the concept of law has largely been abandoned, and replaced by an analysis of scientific understanding through models", and Fang argues that the biological sciences do not rely on either biological or physical laws, but instead "typically use models to explain biological phenomena" (2022, 153).

However, such models themselves rely on physical laws. For instance, Fang (2022, 136-142) discusses a model of intraspecific competition in access to food (Senior et al. 2015). The modelling of "nutrient excesses and deficits when eating nutritionally imbalanced foods" (Senior et al. 2015) relies on the chemistry that underlies metabolic processes. More broadly, the model addresses how organisms deal with trade-offs involving energy acquisition and expenditure. These trade-offs are largely determined by biophysical constraints on "the uptake, transformation, and expenditure of energy and materials from the environment" (Carazo 2022), which are governed by physical laws. Hence, it is not the case that all models in biology dispense with laws; physical laws are essential background assumptions in many such models.[3]

Evolutionary explanations in biology also rely on physical laws and principles. Since the functionality of biological systems is determined by the physical properties of the system and its environment, functional explanation always presupposes physical principles. For example, the evolutionary history of bird flight relies on physical principles of aerodynamics that govern the functionality of wings and other traits.

4. Strong Autonomy II: The Primacy of Biological Explanation

Another strong autonomy thesis is the claim that biological phenomena must have biological explanations.

> §5. *Primacy of biological explanation*: Biological phenomena must have biological explanations.

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[3] Some of the philosophical literature on mechanisms also downplays the importance of laws of nature in biology (e.g. Machamer et al. 2000), but similar arguments apply to this case; namely, that the activities of the entities that compose the mechanism themselves require of presuppose certain physical laws (Weber 2005, 31-32).

Although this view is seldom explicitly defended, it is often implied in discussions of the 'failure' of reductionism in biology (e.g. Kaiser 2011; Nicholson 2014; Dupré 2021). For example, Dupré (1993, 93) claims that "biological phenomena must be explained in terms of biological laws and principles". Similarly, Pradeu (2018, 451) says that "we cannot adequately explain biological processes by means of physicochemical theories and terms". While it's unclear whether these claims should be taken to mean that biological phenomena must be explained *only* in terms of biological terms and principles, both authors certainly suggest that physical explanations are not typically adequate, and are, at best, complementary to biological explanations.

Dupré says that reductive explanation may play a role in accounting for "*how* things of a certain kind do what they do; but they typically do not help us to understand or to predict *what*, among the behaviours of which it is capable, a complex thing will do" (Dupré 1993, 106). He is right that the explanation and prediction of a predator's behaviour requires an understanding of biological and ecological principles, but facts about its heterotrophic metabolism and ATP production mechanism in cells are relevant for the explanation of why it needs to eat, why it has certain evolved traits that allow it to feed on other organisms from which it obtains organic compounds for oxidation, and so on. Physical and reductive explanations are not limited to explaining the *how*, i.e., the functioning of biological mechanisms.

Indeed, reductive explanations are typical in biology and often they are the only kind of explanation that is available; for example, there is no correct explanation of how plants make sugars other than the mechanism of photosynthesis understood as a redox reaction. In the next two subsections we consider two case studies that show that some biological explanations are physical explanations, in the sense that they explain certain biological phenomena in terms of physical laws. Weber (2005, 29) argues that this kind of explanation is in fact the *goal* of much of contemporary biology. Before moving on to the case studies, there are three important points to be noted.

Firstly, the notion of explanatory reduction has two senses that need not always coincide. One is that of the reduction of an explanation in one theoretical framework, to an explanation in another, for example, from thermodynamics to statistical mechanics. This is the kind of reduction of biology to physical science that is at issue in the arguments about *Explanatory irreducibility*. The second sense of explanatory reduction is when the behaviour of a whole is reduced to behaviour of its parts. This sense applies to the reduction of thermodynamics too, but also to many other reductive explanations in science to which the first sense does not. Such explanations are found in biology; for example, the collective behaviour and coordination of social insects is explained in terms of their individual traits and interactions.

Secondly, reductive explanation essentially involves interactions among the parts. Some critics of reductive explanation mistakenly take it to require considering only the parts in isolation and ignoring their interactions. For example, Mayr claims that, “by failing to consider the interaction of the components, [reduction] fails to fulfil what it promises”

(2004, 80). Powell and Dupré argue against a systematic adoption of reductionism on the grounds that “[r]arely can explanations be given *solely* in terms of the properties of isolated components” (2009, 62), and point out that biologically interesting causal powers are often “grounded not in the internal structures of the entities we analytically distinguish, but in the relations between them” (63). Meincke (2019) characterises the non-reductionist approaches of systems biology as arguing that organisms “cannot be understood by looking at their parts only; it is the specific interplay of the parts” that needs to be studied.

In contrast, Dupré’s (2010, 34) characterisation of reductionism in the following terms is much fairer: “the reductionist claim should be that the lynx is nothing but a collection of physical parts *assembled in a certain way*”. Similarly, Weber characterises reductionism as the belief that “once the parts of a system *and their interactions* are understood, there is nothing left for science to explain” (2005, 18, emphasis added). It is the aggregative result of the iteration of many interactions that features in many reductive explanations. This is no less true for reductive explanation of this second kind in physics. Anderson’s famous slogan ‘More is Different’ about condensed matter physics is only true because the numerosity in question includes interactions as well as individuals (Ladyman and Wiesner 2020, 66-68). Complexity science is founded on the recognition of how generally this applies and how it illuminates emergence.

The third point to note is that it is often assumed that reductive explanations of the second kind in biology ‘bottom out’ at the molecular level (Machamer et al. 2000), and that reductive explanation in biology must be sought in “the interaction of macromolecules” (Rosenberg 2006, 54). However, there is no good reason why biological phenomena cannot have explanations at scales both above and below the molecular. Green and Batterman (2017, 31) point out that many explanations in biophysics and mechanobiology appeal to explanatory properties above the molecular scale, such as tissue stiffness. But scales lower than the molecular can be important too – for example, quantum tunnelling is important for respiration (Lane 2011); and particle spin may be crucial for explaining navigation in bird migration (Arndt et al. 2009).

4.1 Case Study: Eye Lens Protein

Certain mutations in the human γ-D crystallin protein cause early-onset cataracts that manifest in childhood. The explanation of why these mutations cause cataracts in children is a physical explanation, as detailed below – the explanandum is biological, and the explanans involves only *physical* concepts (in addition to the biological concepts in the explanandum).

A biophysical study of the human γ-D crystallin protein shows that although single point mutations at site 23 do not produce any significant structural change in the protein, they dramatically alter its solubility profile. Specifically, the removal of proline from this region of the protein causes changes in the binding energy that are strongly temperature-dependent. While the solubility of the native protein increases with temperature, the opposite happens with the mutant protein: it crystalises when the temperature is raised (McManus et al. 2007). The mutation has a negligible effect on the properties of the protein in the solution phase, whereas the properties of the solid phase are very different. This discrepancy is explained in terms of highly anisotropic interprotein interactions (McManus et al. 2007).

This study is a good example of a biological phenomenon (how a particular mutation causes cataracts in children) that has a physical explanation: the binding energy of mutant γ-D crystallin protein strongly increases with temperature, resulting in a phase transition at physiological temperatures that causes lens opacity. The study also demonstrates that protein function is not entirely determined by its structure, but also depends on interprotein interactions. The fact that the interactions between protein molecules are an important part of the explanation illustrates the point that reductive explanations rely on the interactions between parts.

Kaiser (2011, 469) suggests an alternative reading of what studying a system's "parts in isolation" means in the context of reduction: it means "investigating them not *in situ*, that is, in the context of the system they are a part of, but detached from the system (e.g., *in vitro*)". She argues that, in systems involving complex integration and interdependence of parts, the insights that can be obtained from studying parts in isolation (in this sense) is limited (2011, 471). However, used in this sense, the study of parts in isolation is an essential feature of methodological reduction. In the study above, it would not have been possible to analyse the chemical potentials involved "without using temperatures that ranged well away from physiological" (Thurston 2007, 18878).

As for the claim that reductive explanations are less adequate the more complex and highly integrated a system is (Kaiser 2011, 471), this is not always the case. Which level of explanation is the most adequate should be determined by empirical investigation, and depends on the specific features of the phenomenon under study. As the human γ-D crystallin protein explanation of childhood cataracts demonstrates, for some biological phenomena, a physical explanation is not only possible but correct.[4]

4.2 Case Study: Water Transport in Trees

Another interesting case of a physical explanation of a biological phenomenon is the cohesion-tension theory of water transport in trees (Dixon and Joly 1895; Tyree and Ewers, 1991; Niklas and Spatz 2012).

Trees require a specialised water transport system that is able to carry large amounts of water against gravity, from the roots up to the leaves. Water is transported from the roots up to the leaves through the xylem, which consists of long thin capillary vessels composed of dead cells (tracheids and vessel elements). Xylem vessels are filled with a continuous water column, and the pull from above is provided by transpiration in leaves, which occurs through specialised structures, the stomata. This produces a negative pressure gradient that

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[4] Of course, there can be more than one correct explanation of a phenomenon, for example, both genotypic and physical, as discussed in Love et al. (2017).

pulls the water upwards against gravity. The continuous water column maintains its stability due to water cohesion and adhesion to the inner surfaces of the tracheids, and its tensile strength is remarkably high (Niklas and Spatz 2012, 95-96).

The main principles involved in the physical explanation of water transport in trees are the following: the high cohesive force of water molecules, surface tension, evaporation, and hydraulic principles that govern the flow of liquids through pipes.

The high cohesive force between water molecules and surface tension result from physical properties of the water molecule, namely its polarity (Bagcchi 2013). The asymmetric distribution of electrons across the oxygen and 2 hydrogen nuclei means that the oxygen end of the molecule is partially negatively charged, whereas the hydrogen end is partially positively charged. This causes water molecules to electromagnetically attract each other, forming hydrogen bonds between then, which results in a high cohesion among water molecules that generates a strong surface tension when in contact with a non-polar surface such as air (Bagcchi 2013, 9).

Water evaporation takes place in specialised structures in the leaves, the stomata, and depends on the water potential at the interface between the liquid and gaseous phases, which in turn is related to water vapour pressure (Niklas and Spatz 2012, 95). Usually, the water vapour pressure is higher within the stoma than in the atmosphere, driving evaporation.

The physical explanation of water transport in trees is particularly interesting for two reasons: firstly, it is unexpected that the mechanism responsible for the transport of water many meters upward against gravity turns out to depend on the physical properties of water molecules, and on purely physical hydrodynamical principles. Secondly, it is an example of a problem faced by certain plant lineages under evolutionary pressure to grow taller which was solved by evolution by countering one physical force (gravity) with another (electromagnetic forces between water molecules). This solution neatly illustrates the fact that physical laws both constrain and enable the functioning of biological systems. One reason why physical explanations play important roles in biology is because physical laws are often at the heart of both the problems encountered by evolving biological systems and the solutions they find for them.

5. Conclusion

There are various ways in which biology is autonomous from physical science. Biology is a genuine science (*Scientific status*) that has its own concepts, methods, problems, and theoretical approaches (*Methodological distinctness*). Biological explanations are not reducible to physics (*Explanatory irreducibility*). However, the case studies show that there are physical explanations of biological phenomena, and physical laws are relevant to biological explanations in general (the associated autonomy claims *Irrelevance of physical laws* and *Primacy of biological explanation* are false). The case studies also illustrate that explaining things in terms of their components and their interactions is not the same as explaining things in terms of components behaving as they do in isolation (though studying components in isolation may be scientifically fruitful to some extent). However, whether there are reductive explanations is nothing to do with whether everything can be reduced to fundamental physics, because there are reductive explanations of biological phenomena to other biological phenomena, and reductive explanations within physics itself, that do not involve the entities and processes of fundamental physics. Furthermore, biological systems are made of physical components at many scales, and obey physical laws at those scales, not just microphysical ones. Which scales and laws are explanatory in a given case is discovered empirically and cannot be known a priori. Biology and physics are much more integrated than is sometimes claimed.

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