1 Why Should Biologists Care about the Philosophy of Science?

TOBIAS ULLER AND KOSTAS KAMPOURAKIS

1.1 Introduction

To many biologists, science and philosophy may appear an odd couple without much in common. Perhaps the word "philosophy" will even bring to mind endless arguments and speculation about whether the chicken or the egg came first, without ever getting anywhere. After all, are philosophers not still arguing over the same things as Aristotle and his fellow Greeks? Well, yes. But biologists too are concerned with the questions that occupied Aristotle: what living beings are and where they come from; how they develop, function, and interact with one another; and why there are so many forms and how those forms should be classified. There has been tremendous progress in biology, of course. But it does not appear that biologists will ever run out of questions. This is because good science does not only reveal new things about the world; it also reveals that there are things we did not even know we could know. So we want to know more.

Not all research is equally effective in promoting the advancement of science, and it is therefore useful to reflect on what works and what does not. In fact, while biologists may think of themselves as busy enough just doing science, they have been and still are preoccupied with metascientific questions and issues, which is what philosophy of science is about: how to think about genes or ecosystems, the nature of species, the causes of evolution, the value of experimentation versus observation, and if molecular or evolutionary biology is the most fundamental of the biological sciences, to take just some examples. Perhaps even more significantly, twentieth-century genetics and molecular and evolutionary

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biology were all shaped by attempts to ensure that the biological sciences meet the criteria of a "hard science," mapped on ideals in physics.

This ideal no longer seems as appealing as it once did. Over the last decades, studies in philosophy of science have revealed that scientific aims, methods, models, and concepts are much more diverse than previously envisaged by either scientists or philosophers. The biological sciences have been important for reaching this conclusion because biologists turn out to be very flexible in their scientific exemplars. What goes on in ecology and molecular or evolutionary biology can at times bear limited resemblance to each other, let alone to traditional exemplars in physics. Yet, the biological sciences are hugely successful and influential. This success is difficult to account for if the standards of mid-twentieth-century physics were the only way to ensure knowledge.

The present volume was put together because we believe that being aware of the rich conceptual and methodological issues of science can make biologists better at what they are doing – as students, teachers, scientists, and professionals. Philosophy of science is not the preoccupation of armchair philosophers or retired scientists, but it is rather central to any scientific endeavor. The problem is that, more often than not, biologists are not educated and encouraged to pursue this kind of reflection. The present volume is an attempt to support them in doing this.

1.2 Science and the Philosophy of Science

While biologists study life, philosophers of science study science (see Lewens 2015 for an accessible introduction to philosophy of science). Not unlike biologists, some philosophers are motivated by the big picture, whereas others are obsessed with a particular problem (Box 1.1). Many philosophers of science work on particular "study systems," such as molecular biology or evolutionary theory. This requires familiarity with the aims, methods, and knowledge of each particular area, which is one reason why philosophers need to engage with scientists. Another reason is that science is shaped by human abilities, interests, and values. Sometimes it is not possible to understand science without understanding the scientists themselves. This work often draws on the history of science to reveal how events actually played out or how facts and values

BOX 1.1 **What Kinds of Questions Do Philosophers of Science Ask?**

Philosophy of science is concerned with what science is, how it works, and what it can tell us. Some of the most fundamental questions concern very general features of science:

- What makes science different from non-science?
- How are scientific knowledge and understanding generated?
- How is science organized?
- What are the limits of science?

Major topics in philosophy of science are those that analyze and clarify the main components of scientific investigation, including

- What is a scientific explanation?
- How are scientific concepts used and transformed?
- What is the role of idealization in science?
- What is the relationship between theory and data?

Answers to these questions often require careful study of more narrowly defined questions, and most philosophers of science are therefore working on particular problem agendas that can range from quite general to very specific:

- What is the difference between reductionist and holistic approaches to the study of life?
- What is a biological mechanism?
- What do biologists mean when they refer to genes?
- What is the utility of Hamilton's rule in evolutionary theory?

Philosophers of biology are those philosophers of science who are particularly concerned with the biological sciences. Philosophy of biology did not begin in earnest until the 1970s, and earlier philosophy of science was largely concerned with physics or chemistry. However, philosophy of biology is now one of the main areas of inquiry and philosophers of biology have made important contributions to philosophy of science as well as biological theory. For examples, see the Further Reading section at the end of this book.

influence each other over time (see Chapter 13). Being scrutinized can feel uncomfortable for scientists, in particular if they believe that science is – or should be – free of such biases. As illustrated by several of the chapters in this book, this belief is not only mistaken but can actually be detrimental to science itself. The questions, methods, and models that a scientific community considers exemplar are shaped in part by shared attitudes and beliefs. Ignoring these social aspects of science can make biologists less well equipped to identify and solve scientific problems, and it can make them struggle to handle controversies between scientists and between science and other parts of society (see e.g., Chapters 7, 12, and 14)

For philosophy of science to become useful to biologists, scientists and philosophers need to find ways to communicate, share ideas and results, and perhaps occasionally work together. As biologists who have attempted to work with people from other disciplines will testify, collaboration is easier said than done. One main hurdle is simply ignorance about each other's work. Another is to become familiar with terminology and habits of mind that are often specific to particular disciplines. These hurdles can be overcome. Nevertheless, just as it will take time and effort for a cancer researcher to figure out if insights from evolutionary theory will be useful to her, it will take time and effort to figure out if philosophy of science will be useful to you. We hope that this collection of chapters will be helpful for those who are willing to dedicate their time. At the end of the book, we provide suggestions for further reading on both general topics in philosophy of science, as well as topics that are likely to be of particular interest to biologists. In the last chapter we also make concrete suggestions about how topics from philosophy of science could be taught to biology students.

1.3 Kuhn and Popper As Caricatures

Perhaps no philosopher of science is more familiar to scientists than Karl Popper. Popper was concerned with the big questions in philosophy of science, and his work has had a long and lasting intellectual impact, not the least on scientists (Lewens 2015). His idea that scientific hypotheses can never be proven, only falsified, is commonly introduced to beginners in the natural sciences as the fundamental feature of science. Falsification not only separates science from non-science but Popper also meant

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that the repeated failure to falsify hypotheses can account for the growth of scientific knowledge. Another philosopher of science who is likely to be mentioned in introductory science classes is Thomas Kuhn, famous for introducing the idea of a paradigm shift (Kuhn 1996). Scientists tend to be more ambivalent toward Kuhn since he emphasized that science is a collective, social endeavor where scientists sometimes appear irrational. But Kuhn's concept of paradigm shifts can be interpreted as a radical theory change introduced in the face of repeated falsification of established theories. For many biologists, this view of how science works – steadily securing knowledge through hypothesis testing and rarely interrupted by radical theory change when major hypotheses are disproven – may be the entire philosophy of science they are exposed to during their studies, perhaps even for their entire academic career.

No shame on Popper and Kuhn, and scientists are often taught a caricature of their work (like we just did!), but this is not really enough to understand how science works. Believe it or not, philosophy of science has progressed! While falsifiability remains an important litmus test for a scientific hypothesis, it is now widely recognized that the building of knowledge through falsification of *a priori* hypotheses is a poor characterization of many successful sciences, including biology. Scientific knowledge and understanding is generated through much more diverse standards and activities than envisaged by these early philosophers of science. There are good reasons for this diversity. The world is immensely complex, and humans are limited beings. Thus, it is reasonable that different scientific questions demand different approaches or methods. However, a diversity of scientific standards does not imply an absence of standards. It is important to understand what works and why.

In practice, biologists tend to pick up most ideas of what science is and how it works from fellow biologists, typically those who work on similar problems using similar methods. But if there is no universal standard of science, this can make it difficult to recognize or understand the importance of research that uses different standards or, for that matter, the limitations of one's own approach. Such failure can lead to inefficient science, missed opportunities for scientific breakthroughs, or even long and fruitless controversy. In what follows, we reflect on three features of science – its aims, methods, and concepts – to make a case for why biologists can benefit from insights gathered from the philosophy of science.

1.4 Scientific Aims

What are the aims of science? A short list would likely include description, classification, prediction, and explanation. Biologists *describe* and *classify* new species, molecules, and biological processes; they *predict* the effects of human activities on biodiversity or the spread of disease; and they *explain* how cells work and why populations evolve. A main reason for these activities is that many biologists ultimately strive to *understand* living systems, such as cells, organisms, and ecosystems. This understanding has practical consequences for technology, medicine, and many other features that make up societies, and it is therefore important far outside academic circles.

A phenomenon can be said to be understood when one can give it a satisfactory explanation (see Chapter 2).[1] Given that we explain phenomena all the time, it will perhaps come as a surprise to learn that it is neither obvious what it means to explain something, nor what, if anything, that makes scientific explanations different from everyday explanations. The traditional point of view on behalf of philosophers of science is that scientific explanations consist of statements that demonstrate that the phenomenon to be explained follows from natural law (Woodward 2017). This account of explanation is heavily influenced by physics, and biologists hardly find it very appealing since there is a widespread skepticism toward the existence of biological laws.

A more promising idea is that explanation is linked to causality, manipulability, and control (e.g., Woodward 2003).[2] It will feel natural to biologists to think of causes as difference-makers (Illari & Russo 2014). Rain causes seeds to germinate because if it had not rained the seeds would remain dormant. Loss of genetic variation causes population extinction because if it were not for the loss of genetic variation the population might have adapted to the environment. One view of scientific explanation is that it is achieved when the information provided by the explanation allows one to answer a range of such what-if-things-had-been-different questions (e.g., Woodward et al. 2003; Strevens 2008; Potochnik 2017). For example, an explanation for how ATP is generated

[1] Philosophers speak of the phenomenon to be explained as the *explanandum* and the sentences that do the explaining as the *explanans*.

[2] There are various versions of this theory of causal explanation, Woodward 2003 and Strevens 2008 are useful starting points.

may refer to biochemical features of glycolysis. This explanation reveals something about the causal tapestry of the world; the molecular detail makes it possible to grasp the consequences of a change in the concentration of pyruvate or the chemical structure of the reacting molecules. According to some philosophers, this is what it means to understand how ATP is generated, and the more what-if-things-had-been-different questions about ATP production we can answer the better we understand it.

Not all explanations in biology are mechanistic like this, however, and many explanations in biology look more like historical explanations (see Chapter 10). An explanation for the extinction of dinosaurs may refer to a meteorite that struck the earth and caused long-term changes in the earth's climate. Nevertheless, the reason why this explanation generates understanding is similar to the case of ATP; reference to the meteorite and its effect on climate makes it possible to grasp what would have happened to the dinosaurs if the meteor had not have struck the earth, or if it had been smaller, or if there had been no competing mammals around. There may be other kinds of scientific explanations, but being able to give answers to what-if-things-had-been-different questions appears to at least be one important feature of many scientific explanations.

A good thing about this notion of explanation is that one need not take truth too seriously. What really is "out there" may forever be out of reach, but representations of the world can be sufficiently good approximations that enable one to foresee what would have happened if things had been different. It is not always possible to support the explanation through active intervention, of course (this is difficult for the dinosaur extinction, for example). But scientists can nevertheless ensure that their theories are empirically justified – or true enough – by imagining and studying a range of different situations. This is why it is important that scientific theories are falsifiable; if a theory makes no falsifiable claims, it also appears impossible to predict the consequences of an intervention.

Another helpful feature of the causal theory of explanation is that it brings attention to the fact that scientists need to manage causal complexity (Potochnik 2017). Biological systems are enormously complex, and any representation of a living system will only capture some of its actual causes. This is in itself not a problem. In fact, too much detail makes it harder to grasp what would have happened if things had been different. A diagram of all causal interactions in a cell would describe the cell but not explain how it works. To explain phenomena, scientists leave things out (abstraction) and make assumptions that are false (idealization). Abstraction and idealization play positive roles in explanation because they foreground the causal relations that are of interest – idealization makes the phenomenon appear as if it were produced by the focal causes alone (Potochnik 2017). As a result, how one thinks about biological processes influences which of the myriad of actual causes of a particular phenomenon that are picked out as being explanatory causes.

It may be helpful to illustrate this feature of idealization using a nonbiological example. Consider the frequent delays of trains arriving into Stockholm Central. One possible cause of these delays is that late departures of trains that are not headed toward Stockholm can propagate through a jammed train system – a kind of cascading effect. To see if this can explain the arrival delays into Stockholm C, transport planners may benefit from assuming that trains run at a constant speed unless they have to stop to let other trains pass. Plugging in real data on train speeds and how they vary seems unnecessarily complicated. Doing so might even make it harder to grasp how improving departure punctuality of trains throughout Sweden will affect arrival times of trains bound for Stockholm C.

The transport planners will feel satisfied if there is a good fit between their model and actual arrival times into Stockholm C. They could claim that they now understand why trains are delayed, because they can explain it in terms of cascading effects of delayed departures of trains bounded for other destinations. However, imagine that it turns out that, contrary to what the model predicts, the actual arrival times are unaffected by such departure delays. One possible explanation for this mismatch between model and reality is that train drivers adjust the speed to compensate and ensure that trains headed for Stockholm have a free pass. This may appear to imply that train speed is a cause of punctuality but not of delays. But this cannot be the case because slow-downed trains can also jam tracks and propagate delays.

What is happening here? Firstly, note that train speed initially appeared unable to account for the arrival delays because it was idealized away from the model. Secondly, it is only when the proposed model was unable to account for the phenomenon that we looked for another cause. This is why train speed appeared as a possible explanation for why trains were not delayed, but not an explanation for why they were delayed. But there is no fundamental causal asymmetry here. Interventions on either departure times or train speeds can cause arrival delays of trains bound for Stockholm C because both can result in interference between trains. As a result, a satisfactory explanation for the late arrivals may require the use of multiple different idealizations, each one suitable for picking out the contribution of a particular cause or set of causes. Trying things out and keeping what appears important may eventually allow more complex representations that have greater explanatory power.

The challenges that transport planners face are also faced by biologists. Biological phenomena are produced and sustained by many factors, and these are often causally intertwined. As a result, there can be several legitimate explanations of the same phenomenon, each drawing on only some of its causes. These explanations are often sufficiently different to happily coexist. One example is the distinction between what biologists commonly refer to as ultimate and proximate explanation. Roughly speaking, ultimate explanations are considered historical explanations that trace events that occur within a population or a lineage, whereas proximate explanations are considered mechanistic explanations at the level of the individual. An ultimate explanation for why mammals maintain a high body temperature may, for example, refer to its fitness benefits in cold climate, which implies that this trait became increasingly common and sophisticated as a result of natural selection. A proximate explanation for the same phenomenon may refer to the autonomic, neuronal, and molecular mechanisms that underlie the ontogenetic development of endothermy.

Following the highly influential work of Ernst Mayr (1961), it is customary in evolutionary biology to consider that causes that feature in proximate explanations should not be invoked to explain evolutionary adaptation (e.g., Dickins & Rahman 2012). However, a closer look at the rationale for this distinction reveals that it relies on an idealization of the evolutionary process that foregrounds fitness differences and screens off other putative causes of adaptive change (see Walsh 2015; Pocheville 2019; Uller & Helanterä 2019). This reflects that the main agenda for evolutionary biology has been to understand the role of natural selection in adaptive evolution, not the role of development, physiology, or behavior. The assumptions made in evolutionary theory tend to turn the latter into constraints; they can account for the absence of adaptive fit but not its presence.

This line of thought is so common to biologists that many take it for granted. However, a comparison to the explanations for the delayed train arrivals is a reason to treat this conclusion with caution. That is, that one particular idealization of evolution by natural selection privileges genes and natural selection does not imply that there is an inherent causal asymmetry in evolutionary processes (Laland et al. 2011). The role of proximate causes in adaptive evolution is in fact one of the most persistent controversies in biology (Amundsen 2005). Contemporary examples include the disagreement over the explanatory role of development, plasticity, extra-genetic inheritance, and niche construction in evolution (see Laland et al. 2014, 2015). One possible reason that these issues are difficult to resolve is that the genetic representation of evolution is commonly taken at face value, rather than being understood as an idealization designed to explain evolutionary phenomena in terms of natural selection. An increased awareness of the relationship between idealization and explanation may reduce the risk that causes that are idealized away become permanently neglected, facilitate capitalization of insights from other disciplines, and put a restraint on unproductive scientific controversy.

While there are good reasons why a biological phenomenon like adaptation can have several explanations, biologists may sometimes wish to determine which of a number of different explanations is the most satisfactory (see Chapter 3). Consider cichlid fish, famous for the ability to evolve very similar morphologies in different lakes (Seehausen 2006). Evolutionary biologists have demonstrated that this convergence happened because the local habitat and foods are often similar in different lakes, which favors a limited set of life styles such as bottom-dwelling grazers and open water predators (e.g., Muschick et al. 2012). Thus, natural selection explains the convergent evolution of cichlid fish. But biologists have also pointed out that some of the recurring features of these fish, such as the shapes of bodies and jaws, tend to be plastic (Schneider & Meyer 2017). That is, those characters respond to the habitat or diet that individual fish encounter during their lifetime. Some biologists believe that plasticity has contributed to the striking