Chapter 7

What constitutes an explanation in biology?

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1. Introduction

"Explaining" and "explanation" are words that tend to feature prominently in even the most basic descriptions of science. This is a big part of what science is about: generating explanations of our world. It seems to be a big part of what biology is all about as well. Research in biology undoubtedly leads to practical applications in pursuits from medicine to agriculture to conservation, but one of its fundamental aims is to generate *understanding* of the living world around—and within—us.

The centrality of explanation to the scientific enterprise is matched by philosophers' enthusiasm for debating the nature of explanation in science. Philosophers of science have been up to our elbows in debates about the nature of scientific explanations since at least the middle of the twentieth century. Pet theories abound, but some basic insights into the broad contours of scientific explanation have also emerged.

In this chapter, I aim to provide a relatively nonpartisan discussion of the nature of explanation in biology, grounded in widely shared philosophical views about scientific explanation. At the same time, this discussion will reflect what I think is important for philosophers and biologists alike to appreciate about successful scientific explanations. So, some points will be controversial, at least among philosophers. Along the way, I indicate which ideas are controversial and say something about the nature of controversy. I make three main points: (1) causal relationships and broad patterns have often been granted importance to scientific explanations, and they are in fact both important; (2) some explanations in biology cite the components of or processes in systems that account for the systems' features, whereas other explanations feature large-scale or structural causes that influence a system; and (3) there can be multiple different explanations of a given biological phenomenon, explanations that respond to different research aims and can thus be compatible with one another even when they may seem to disagree.

2. Causes, Patterns, and Causal Patterns

It is appropriate that this chapter about explanation follows on the heels of a chapter about causation, as today's philosophers of science by and large see these topics as deeply related. At its most basic, the idea is that to explain something is to show what is responsible for that thing—and whatever is responsible for something is its *cause*. You explain the suddenly dark room by appealing to the fact that a fuse was blown; you account for a polymorphism by noting there was frequency-dependent selection; and you account for a high concentration of female caribou antlers by pointing to the fact that this was a calving site (Miller et al., 2013). Philosophers sometimes disagree about what qualifies as a causal explanation or the features causal explanations must have, and some philosophers question whether *all* scientific explanations cite causes. But, to my knowledge, all contemporary philosophers accept that causation is central to at least most scientific explanations. The central role that philosophers accord causation in scientific explanation is akin to the call in biology for identifying the cause, process, or mechanism responsible for something. (Though, as I make clear in the next section, philosophers of science use the concept of mechanism in a more restricted way than this.)

It wasn't always so: philosophers didn't always take causes to be at the heart of explanation. At the start of contemporary discussions of explanation, Carl Hempel famously posited that explanations were derivations. So-called *deductive-nomological* explanations involved explaining a phenomenon by deriving it logically from a scientific law and the initial conditions that, given the law, brought about the phenomenon in question (Hempel, 1965). Thus, to explain something was taken to consist in showing how it resulted from laws of nature, thereby rendering it unsurprising. Later philosophers argued that Hempel had a variety of related ideas here, and though the official deductive-nomological account of explanation faced a number of significant difficulties, the "unofficial" account fared better. This was supposed to be the idea that explanations *unify* by showing how disparate phenomena turn out to arise for the same reason or to fit the same pattern (Friedman, 1974; Kitcher 1981). Newton famously assimilated the movement of celestial bodies in orbit to the freefall of bodies here on Earth. Cooperative behaviors have emerged in many different species and biological communities because there are a set of circumstances in which cooperation can be advantageous to organisms. Such accounts seem to explain by showing how the phenomena in question fit into a pattern.

This has also been touted as an important philosophical insight about scientific explanation: explanations should unify disparate phenomena, cite general patterns, or something along those lines. Some philosophers have endorsed this instead of the idea that explanations should cite causes. A growing number of philosophers argue that not all scientific explanations are causal, that some phenomena are explained by statistical or mathematical facts or other regularities that do not seem to be causal (see, e.g., Reutlinger and Saatsi, 2018). One interpretation of this is advocacy of the explanatory importance of patterns and regularities, some of which are causal and others of which are not.

In my view, both of these ideas—that causal dependence is explanatory, and that patterns and regularities are explanatory—are important insights into the nature of scientific explanation. Some philosophers have combined both insights into a single account of explanation with the idea that scientific explanations should cite patterns in causal influence. On this kind of an approach, it's not just information about causal relationships that's explanatory but also information about the *scope* of those causal relationships, or the range of circumstances in which a given causal relationship holds. This kind of view has been advocated more or less explicitly by James Woodward (2003), Michael Strevens (2004, 2008), and me (Potochnik, 2015, 2017), among others. Thus, I think scientific explanations—at least by and large—depict *causal patterns*. The causal content of an explanation is a way to show a dependence: that the phenomenon to be explained came about due to the featured causes. That an explanation depicts a *pattern* in causal dependence means that it also shows the extent—or scope—of the causal dependence in question.

Consider, for example, explaining the bright coloration of the scarlet ibis (*Eudocimus ruber*). Pointing out the bird's ability to metabolize carotenoids in its diet to influence its pigmentation is explanatory causal information. Likening this to the source of the flamingo's pink, the cardinal's red, and the goldfinch's yellow indicates something about the scope of this causal pattern. The scarlet ibis's coloration is due to one main form of avian pigmentation, a process that can create red, pink, orange and yellow coloration. It can also be enlightening to point out a difference between the scarlet ibis and white ibis: the former but not the latter has a substantial volume of a carotenoid carrier protein in its blood. This indicates why the scarlet ibis is able to metabolize carotenoids in this way while the related white ibis is not—also indicating something about the scope of the explanatory causal pattern.

The idea that causal patterns explain is a causal approach to explanation, but it is not merely a causal approach. On this view, simply providing some causal information is not sufficient for explanation. An explanation also needs to indicate the scope of the explanatory causal dependence, the range of circumstances in which similar causal dependence obtains. The explanatory value of this relates to the insight that explanations should unify by showing how disparate phenomena arise for the same reason or fit the same pattern. With the explanation of scarlet ibis coloration mentioned just above, insight is provided into conditions in which similar coloration occurs. Such explanations show how (potentially disparate) phenomena fit the same pattern. One might even say that causal pattern explanations are akin to the original deductive-nomological view of explanation, for they show how phenomena result from regularities in our world, though the regularities are not universal laws but limited in scope and may have exceptions.

I have suggested that the idea that causal patterns explain relates comfortably to a range of other ideas philosophers have had about explanation. But why think it is true? That is, why think that causal patterns are the sort of things that help us explain our world? Grasping the nature of a causal dependence and the scope in which that dependence holds is key to determining the causal structure of the world, which Gopnik (1998) has influentially argued is the endpoint of explanation. Grasping what I call causal patterns is also, as Woodward (2003) and others have argued, key to effective action. This indicates how and in what conditions we can act to bring about or prevent the focal phenomenon. Additionally, research in cognitive science suggests that causal information and broad generalizations are both the kinds of information that strike our intellects as explanatory (Lombrozo and Carey, 2006) and that we learn more through the act of explaining (Lombrozo, 2011). Uncovering causal patterns thus seems to do exactly the tasks we expect from our scientific explanations, and grasping causal patterns seems to look a lot like explaining.

Perhaps in some explanations, the causal dependence does more of the explanatory lifting than information about the scope of dependence, and vice versa in some other explanations. Explaining the production of ATP in anaerobic respiration by detailing the steps of glycolysis seems to get more explanatory "oomph" from the detailed causal information about the chemical reactions involved than from indications of the scope of this pattern, that is, the conditions in which anaerobic respiration occurs. In contrast, explaining a trait as a product of natural selection assimilates it to a broad range of phenomena—all physical and behavioral traits that have been positively selected—while giving relatively little causal detail. Natural selection, after all, has myriad ecological sources and leads to an astonishing variety of outcomes. It may be that some explanatory dependence patterns aren't even causal in nature. The statistical pattern of regression to the mean has a broad scope of applicability; this pattern can explain a number of phenomena, such as why the outliers in some quantitative trait tend to have offspring with less extreme values for that trait. But this pattern does not seem to be causal. The insight that causal patterns are explanatory can accommodate this variety. I will say more below about which causal patterns are explanatory in which circumstances, but I suspect most scientific explanations occur between these extremes. Science generates understanding by depicting causal dependence and the patterns of when that dependence holds. That is, scientists by and large explain phenomena by depicting causal patterns.

3. From Mechanisms to Large-Scale Causes

My first point about explanation was the idea that information about causal dependence and information about the scope of that dependence are both important to scientific explanations. Scientific explanations feature causal patterns. The second point is that not all explanations cite components and processes. There is sometimes a tendency among philosophers and biologists alike to expect that information about causal dependence boils down to information about the parts of an entity or system and the processes they collectively carry out. Attending to the role of not just causes but also patterns in causal action makes clear this is not so. Biological explanations vary from component- and process-based to those that feature large-scale or structural causes. By ‘large-scale causes,’ I mean influence from some spatial or temporal distance, and by ‘structural causes,’ I mean contextual influences that shape a phenomenon but that do not change to precipitate the phenomenon. These varieties of causal influence are just as important, just as causal, and just as explanatory as components of a system and the processes they carry out.

Let us begin this discussion by returning to the idea, mentioned at the beginning of the previous section, that there is regularly a call in biology to identify the cause or mechanism responsible for something. Some philosophers of science take very seriously such appeals to mechanisms. The so-called “new mechanists” have put a lot of work into defining exactly what a mechanism is, and they think explanation in biology and related disciplines consists in describing mechanisms. These philosophers disagree about some details regarding the nature of mechanisms and their role in explanation, but the general picture is that mechanisms are integrated networks of components that carry out certain activities, thereby bringing about predictable outcomes. Paradigmatic examples of mechanisms are the ATP cycle (Bechtel and Richardson, 1993), protein synthesis (Darden, 2006), and the action potential (Craver, 2006).

This view of mechanisms emphasizes the explanatory value of identifying processes carried out by the components of an entity. This approach fits very well with some areas of research in biology, but advocates of mechanisms tend to go further, expecting processes carried out by the components of a given entity to be central to *any* explanation, at least in biology. For example, Connolly et al. (2017) suggest that ecology needs to focus exclusively on component- and process-based models, which depict the causal roles of components of a system or the processes that precipitate some outcome. These authors claim that the value of such models is that they can capture causal structure of a system. Philosophers who emphasize the explanatory value of mechanisms tend to equate a lack of detail about causal processes with a failure to explain (see, e.g., Craver, 2006). This is related to McGill and Nekola's (2010) characterization of ecologists sometimes justifying the value of their work by appealing to it being more mechanistic, resulting in "ideological squabbles" about what qualifies as a mechanism.

I urge a much broader interpretation of the call to identify causes. Not all explanatory causal information regards processes carried out by components. Some explanations feature causal patterns regarding the environmental context, such as optimal foraging models for evolved food preferences, which cite ecological factors like patterns of food distribution that give rise to certain selection pressures. These cite structural causes, by which I mean contextual factors that may not have changed to precipitate the phenomenon. Other explanations cite large-scale causes that are distant in space or time from the phenomenon, such as evolutionary or phylogenetic explanations for traits (temporally distant causes) and some ecological explanations, like wetlands suffering due to decreased snowpack in the mountains (spatially distant cause). Finally, still other explanations describe highly general causal patterns to which focal phenomena cohere, like appealing to the second law of thermodynamics to explain ice melting, cooling a beverage in the process; indicating that some trait is a product of natural selection; or indicating how scarlet ibis coloration is an instance of carotenoid pigmentation in birds. All of these are causal pattern explanations—explanations that feature information about causal dependence and information about the scope of that dependence—but none are naturally described as processes carried out by the components of the system. (Of course, as I have already suggested, other causal pattern explanations *are* naturally characterized as such.)

Philosophers who advocate mechanistic explanation disagree with me on this. For any of these cases of structural or large-scale causes or highly general causal patterns, most mechanists will either claim that the causal pattern is aptly characterized as a mechanism or call into question whether there is a genuine causal explanation. But I think causal patterns featuring contextual factors, large-scale causes, and highly general regularities significantly shape the phenomena of our world. This leads to their explanatory significance.

The expectation that all explanatory causes are local, component-based processes thus inhibits our recognition of a range of important causal patterns. These include, among many others, how ecological features shape selection pressures, phylogenetic influences on traits, and the highly general pattern of carotenoid pigmentation in birds. In my view, focusing on a narrow sense of mechanism both results from and contributes to an inaccurately reductionist view of the world, where causal significance is expected to be local and component-based. Such an expectation renders large-scale causal patterns less visible or even “spooky” seeming.

In this section, I have suggested that the call in biology for causes, process, or mechanism should be interpreted as a call for information about causal patterns, wherever they are found. This is a broader interpretation than that of philosophers of science who emphasize the significance of mechanisms, understood roughly as processes carried out by components. Yet this broader interpretation of the call for mechanism goes beyond establishing correlation, or the existence of a "mere" pattern. Causal patterns are more than just patterns: they are regularities in how causes exert their effects. This gives information about what to expect in different circumstances and about how to intervene on a phenomenon to bring about a desired effect. And this is so whether the causal pattern in question is local and component-based or large-scale. In the next section, I give reason to think that the very same phenomena will sometimes be explained by citing local, mechanistic causes and other times large-scale causes.

Much more argument would be needed for me to provide full support for this broad conception of explanatory causal patterns. But I hope this brief discussion is sufficient for two purposes. First, to provide some initial motivation for the idea that biologists should look beyond the local components of a system in their hunt for causes, explicitly including consideration of the significance of large-scale causal factors. And, second, simply to highlight that a philosophical question about scientific explanation is the degree to which explanations must be component- and process-based.

4. A Variety of Explanations Without Conflict

Scientists are regularly in the position of trying to discern whether a proffered explanation is right. This is a challenging task, and the details of how those decisions are made are, for the most part, beyond the scope of this chapter. (That said, philosophy of science does have significant resources to offer on this issue as well; see, for instance, the following chapter on knowledge.) But, the third point I want to make about scientific explanation regards a related issue. Alongside the need to discern whether a proffered explanation is right, scientists are often in the position of adjudicating between two different explanations of the same phenomenon. For instance, biologists may ask whether some trait is the product of natural selection or phenotypic plasticity, or whether an evolutionary game theory model or quantitative genetics model is more apt. If I am right that causal patterns explain, including broad causal patterns, this has an interesting consequence for the task of adjudicating between different potential explanations of the same phenomenon. At least sometimes, multiple explanations of a phenomenon *all* may be right.

The thought here is that the same phenomenon is influenced by lots of different causal factors, and thus may be explained by a number of different causal patterns. A good illustration of this is Mayr's (1961) proximate and ultimate causes of traits: physiological or developmental influences on the one hand and evolutionary influences on the other. Patterns exist in how proximate causes exert their influence, and patterns exist in how ultimate causes exert their influence. There's no immediate reason to think that either pattern impinges on the other. Rather, some trait—let's say, scarlet ibis feather color—has a physiological explanation about the production of feathers with carotenoid pigmentation, as well as an evolutionary explanation about why this species of birds evolved to have feathers of this color.

What is more, feather color (and other traits) don't just have a proximate and an ultimate explanation. For scarlet ibis plumage coloration, for example, there may be an explanation focused on the role of selection—such as this coloration's role in mate attraction, as well as an explanation focused on the steps by which gene complexes supporting the necessary enzymes and selective transport of carotenoids evolved in birds. Or an explanation may detail the specific carotenoid-carrier protein in the blood of scarlet ibises but lacking from white ibises. There may also be something to say about how parasite load influences carotenoid metabolism and transport. Each of these explanations addresses why the scarlet ibis has the feather color(s) it does, but each does so by depicting different causal patterns, all of which may play a role in scarlet ibis coloration.

In this way, I think scientific explanations proliferate. There can be multiple different explanations of a given phenomenon without conflict—Mayr's proximate and ultimate explanations are just the tip of the iceberg. And, in my view, some disputes in biology over which kind of explanation is more successful—evolutionary game theory or quantitative genetic, evolutionary or evo-devo, etc.—are pursued in error. The question is often (not always, but often) not which explanation is correct, but simply which kind of causal pattern is sought. (See Potochnik, 2013, for a fuller development this point.)

The list I sketched above of different explanations for scarlet ibis coloration vary in terms of which causes of the coloration they feature. This is one way in which different causal pattern explanations, even of the same phenomenon, vary. Causal pattern explanations also may be more general, say, focusing on carotenoid metabolism in birds in general, or more nuanced, like how several of these causal factors combine for the scarlet ibis in particular. Which of these causal patterns is explanatory depends on the research priorities. To generate explanatory knowledge, the question is not simply, "what caused this?," but instead, "which of the potential causes are we interested to explore?," and only then, "what role did those causes play?"

It is certainly possible for one explanation of a phenomenon to reveal that another proffered explanation for that phenomenon is wrong. If it is discovered that some population of flamingos is white due to a lack of beta-carotene in their diet, it would be mistaken to look for an natural selection explanation for why flamingos are white. White coloration in this population is not the product of natural selection, but was directly, and recently, caused by environmental change. Yet it is much more likely for different explanations of a phenomenon to be compatible than for them to conflict. Phenomena have many different causal influences, and there are many different patterns in how these influences play out.

In some circumstances, biologists may be interested to piece together as much as possible about all the causal influences on some phenomenon—say, all the phylogenetic, evolutionary, developmental, metabolic, and environmental influences on carotenoid pigmentation in the scarlet ibis, as well as the interplay among those influences. Other times—and much more often, I suspect—the investigation of a phenomenon occurs in the context of some broader research interests that occasion focus on a particular causal pattern to the exclusion of others. For the present example, such a focus may be the evolution of carotenoid metabolism and selective transport in birds, or whether and in what ways sexual selection is responsible for carotenoid coloration in the scarlet ibis, or how parasite load influences carotenoid metabolism and selective transport, or etc.

The relationship among multiple explanations of a given phenomenon has come up in a few different contexts in philosophical discussions of scientific explanation. A handful of influential philosophers have suggested that any given explanation is partial, so there are inevitably multiple different explanations of any one phenomenon (Railton, 1981; Lewis, 1986). Philosophers have disagreed about whether and in what ways such multiple explanations should relate to one another, with some anticipating integration of these explanations (e.g. Mitchell, 2003) and others arguing, as I have also suggested here, that multiple different explanations of a phenomenon remain independent from one another. From my perspective, this explanatory independence, as I have called it elsewhere (Potochnik, 2010), arises due to varying research interests even among those investigating the same phenomenon and to different causal patterns being explanatory in light of those various interests.

In some cases, these different interests are obvious. Other times, biologists may take themselves to disagree about causal facts, but the disagreement is also motivated by different research priorities and thus different aims for the explanations they are developing. To illustrate this point, let's return to Mayr's proximate-ultimate distinction but this time for a different purpose. Laland et al. (2011) challenge an implication this distinction has often been taken to have, namely, that developmental processes are evolutionarily unimportant (one might say, merely proximate). These researchers emphasize that, to the contrary, feedback loops exist by which developmental processes influence evolution. They conclude: "It is now vital to recognize that developmental processes frequently play some role in explaining why characters possess the properties that they do, as well as in accounts of the historical processes that explain their current state" (1516). This is an important observation that has significant implications for evolutionary theory. But, I do not think the significance of developmental processes to evolution is a reason to replace evolutionary explanations of traits with evolutionary-developmental explanations. Rather, in my view, this is better interpreted as the identification of a neglected kind of causal pattern, namely, patterns in how development influences evolutionary possibilities. These different causal patterns are explanatory in light of different research questions. Sometimes a classic evolutionary explanation suffices, and the influence of development on evolution can be ignored; other times the latter is central to what biologists aim to understand.

I have suggested that there can be multiple non-competing causal pattern explanations for any given phenomenon. In light of this idea, I urge biologists to take seriously the possibility that apparent conflict among different research programs arises not due to different competing explanations of the same phenomenon, but rather due to different research agendas that lead to emphasizing different causal patterns. Sometimes a breakthrough in understanding warrants revisiting what we thought we knew, including the nature of the causal patterns we had posited in our explanations. It may be that, for some traits, there is no evolutionary explanation—no causal patterns to be found—without taking development into account. Other times, breakthroughs in understanding bring to light new causal patterns but do not undermine our existing explanations.

5. Conclusion

Explanation is taken to be an important aim, if not the central aim, of science. In this chapter, I have motivated three ideas about the nature of scientific explanations. These ideas are grounded in philosophical debates about explanation, even as they also reflect my particular views. First, I have suggested that philosophical debates about the definitive features of explanation support the idea that both causal dependence and the scope of that dependence—that is, causal patterns—are important to explanation. If this is so, biologists might explicitly think about both the causal content and the generality or scope of the explanations they develop. It is not always more explanatory to build in more detail. When scarlet ibis coloration is investigated in the context of explaining carotenoid metabolism and selective transport in birds, any reference to, say, sexual selection for the ibis's coloration is mere distraction. Omissions and simplifying assumptions are ways of signaling that those details don't matter given the present research aims—that the pattern in question is independent of them.

Second, I have suggested that while some explanations focus on components and processes, others focus on large-scale causes, including contextual features, distant causes, and highly general patterns. I urge biologists to look beyond the local components of a system in their hunt for causes, and to explicitly include consideration of the significance of large-scale causal factors. I am inclined to think that all of us, scientists, philosophers, and the public alike, share certain reductionist tendencies. Among these is a tendency to consider the large-scale to be a fixed background and the local and tiny to be where the causal action is. Across science, again and again, this expectation has been revealed to be incorrect. And yet the tendency persists.

Third and finally, I have suggested that phenomena of interest in biology may have multiple explanations, each occasioned by different research agendas and featuring different causal patterns. In my view, some disputes about research strategies and methods are, at root, disagreements about which explanations are most interesting—which causal patterns enlightening—rather than disagreements about which explanations are accurate. This idea also relates to the idea I motivated about the explanatory value of large-scale causal patterns. One way in which large-scale causes have been rendered invisible is by pointing out that there is already an explanation in terms of components or other local factors. But if phenomena have multiple explanations, the recognition of local, small-scale influences shouldn't lead us to expect the absence of large-scale explanations. Cancer has genomic causes, but it also has developmental, environmental, and socioeconomic causes. And yet our research dollars seem to go disproportionately to the tiny molecular bits residing inside us.

This reveals the error in what I take to be another reductionist tendency: an implicit expectation that events have just one or a few causes. To the contrary, complex causal relations abound, with any event bearing the influence of many causes, and causal interaction and feedback common (Love, 2017). Recognizing and emphasizing that biological phenomena embody multiple causal patterns, and that different causal patterns can figure into explanations tailored to different questions, is one step toward counteracting these reductionist tendencies.

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