Chapter 1
Explanation in Biology: An Introduction

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Abstract Explanation in biology has long been characterized as being different from explanation in other scientific disciplines, in particular from explanation in physics. One of the reasons was the existence in biology of explanation types that were unheard of in the physical sciences: teleological and functional explanations, historical and evolutionary explanations. More recently, owing in part to the rise of molecular biology, biological explanations have been depicted as mechanisms. This profusion of explanatory patterns is typical of biology. The aim of the present volume *Explanation in Biology. An Enquiry into the Diversity of Explanatory Patterns in the Life Sciences* is to shed some new light on the diversity of explanation models in biology. In this introductory chapter, we recall the general philosophical context of scientific explanation as it has unfolded in the past seven decades, and highlight the specific issues that models of explanation have faced in biology. We then show how the different essays gathered in this collective volume tackle aspects of this important debate.

Keywords Scientific explanation • Biological explanation • Nomological explanation • Causal explanation • Mathematic explanation • Mechanistic explanation • Explanatory pluralism

1 Introduction

Among the different achievements of science – such as prediction, control or simply description – explanation is generally understood as occupying a very central and special location on the epistemic chessboard. Yet, explanation has also

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raised numerous questions and controversies among scientists and philosophers, especially since the development of the deductive-nomological model (Hempel and Oppenheim 1948; Hempel 1965). Though not everybody agrees, it is largely assumed that it is part of the task of science to *explain* natural phenomena, and that its methods enable it to do so incomparably better than common sense. But then what *is* a scientific explanation? What distinguishes an *explanation* from something that is not an explanation? And what distinguishes an explanation that is *scientific* from one that is not? Understanding what scientific explanations consist of has been one of the most central issues in the philosophy of science as it has developed throughout the twentieth century, and more recently as analyzed in the realm of biology. Part of the agenda has been to identify necessary and sufficient criteria that would enable distinguishing genuine scientific explanations from pseudo-explanations. Hence the issue is not only a matter of descriptive adequacy (accounting for the practice of science), but also has normative ambitions. Another strongly debated topic is whether there exists a single model of scientific explanation or several different ones, possibly depending on specific explanatory practices across disciplines. If what is accepted as an explanation varies across disciplines, if what is sought after in elaborating an explanation also varies, as well as the reasons why one pursues such an explanatory quest, then wouldn't all of this be good reasons to be skeptical about the existence of a single model of explanation? This debated issue has proven to be of much relevance in biology, both in light of the specificities of this multifaceted discipline compared to physics – the latter being often taken as a discipline of reference in philosophy of science – and in light of the heterogeneity of explanatory practices within biology itself. In this seventh decade since Hempel and Oppenheim's "Studies in the Logic of Explanation", the present volume *Explanation in Biology. An Enquiry into the Diversity of Explanatory Patterns in the Life Sciences* proposes a collection of essays that discuss some of the most recent philosophical perspectives of scientific explanation in light of the specificities of modern biology, including such a broad range of sub-disciplines as molecular biology, systems biology, evolutionary biology or developmental biology. In this introductory chapter, our objective is to set the context within which these latest developments on philosophical models of explanation have taken place. The chapter is organized as follows. We first provide a brief overview of the major models of scientific explanation that have been developed in the past six decades, and their "universalist" aspirations (Sect. 2). We then review the key issues that these models generally face in biology (Sect. 3). These issues are often taken as good reasons for developing philosophical models of explanation that are more narrowly tailored to the claimed specificity of biology and of its sub-disciplines; incidentally, they are also taken as good reasons against any universalist model of explanation. They therefore shape the debate – which is notably salient in biology – between "universalists" who argue in favor of a unified account of explanation, and "pluralists" who argue in favor of a profusion of explanatory patterns. We then show (Sect. 4) how the different contributions of the volume address facets of this important debate, be it by documenting a profusion of explanatory patterns, analyzing the specific heuristics at work in biology, or critically assessing mechanistic-type explanations and exploring alternative approaches.

2 Six Decades of Scientific Explanation

Elaborating a model of scientific explanation is a long-lasting aim of philosophy of science. However, accounting for what a scientific explanation really is has turned out to be much more difficult than one might have initially expected. As reviewed by Salmon in his *Four Decades of Scientific Explanation* (Salmon 1989), the literature on the topic is vast, triggered in one way or another by Hempel and Oppenheim's (1948) essay. Two decades later, scientific explanation is still a matter of much debate. Since Hempel's *DN* model, the general question of characterizing scientific explanation has branched out to address three types of problems that have structured the debate in the past six decades, and still structure it today: (1) Are there unique characteristics to scientific explanations? Can we define a set of necessary and sufficient conditions for scientific explanations? (2) Is causation a primitive notion for scientific explanation? (or should causation be construed on the basis of explanation?) And if yes, which account of causation is suitable? (3) Which role does context play in explanation, if any? The debate also concerns the ways models can or cannot address canonical counter-examples that range from flagpole shadows (as an illustration of explanatory asymmetry) to hexed table salt (explanatory relevance), syphilitic mayors (low probability explanations) and storms and barometers (correlations). The current debate about explanation in biology has inherited from all of these questions. Our aim here is to map the general context within which this debate arose, and to survey some of the most salient models of scientific explanation.

Typically addressing problems of type (1) above, the model of scientific explanation that has been the most discussed and that has influenced nearly almost all subsequent work is the deductive-nomological (*DN*) model, mainly developed by Carl Hempel (Hempel and Oppenheim 1948; Hempel 1965). As is well known, the *DN* model construes explanation as consisting of a deductive argument, the premises of which must contain at least one law-like generalization. According to this model, scientific explanation involves two epistemic elements: an *explanandum* – the phenomenon to be explained – that appears as the conclusion of the argument, and an *explanans* that consists of the set of premises that do the explaining. Several criteria constrain the *explanandum* and the *explanans*. In particular, the *explanans* must deductively entail the *explanandum*, and the deduction must make essential use of general laws; the *explanans* must also have empirical content. The decision to define explanation as a logical argument involving laws (or law-like generalizations) originated in part from empiricist worries about other concepts such as causation, found to be metaphysically too loaded. But of course, the whole approach depends on the ability to properly define what a law is, and this has proven to be far from straightforward (e.g., Ayer 1956; Dretske 1977; Cartwright 1980). We will see how this question is especially problematic in biology. Because many cases involving statistical generalizations are not covered by the *DN* model (and most special sciences are not based on deterministic laws), Hempel added an account of what he called inductive-statistical (*IS*) explanations (Hempel 1965). Similarly to a *DN* explanation, an *IS* explanation takes the form of an argument. Yet contrary to a *DN* explanation where the argument is deductive, the argument of an *IS* explanation is inductive. Explanation of the *IS* type thereby works by showing that the *explanans* confers a high probability onto the *explanandum*. This, however, has somehow proved to be a weakness of the model, as there happen to be many cases where explanation is deemed satisfactory despite involving statistical generalizations that only confer a low probability to the *explanandum* (e.g., Salmon 1965). The *DN* and the *IS* models share one essential feature: the general idea that explaining is showing that the occurrence of a phenomenon is to be expected on the basis of lawful generalizations.

As is well-known, the *DN* and *IS* models of scientific explanation have faced many counterexamples, which have suggested that they do not properly capture what a scientific explanation really is (see Salmon 1989 for a review). Two of the more salient problems are the problem of explanatory asymmetry and the problem of explanatory relevance. The first problem refers to cases where it is possible to switch the *explanandum* and a premise of the *explanans* while still fulfilling the formal criteria of the *DN* model, thereby leading a counter-intuitive explanatory argument. This is illustrated, among others, by the famous example of the flagpole and its shadow: the height of the flagpole and the laws of optics and trigonometry explain the length of its shadow, but one would not say that the length of the shadow and the laws of optics and trigonometry explain the height of the flagpole, despite the fact that this argument also fulfills the *DN* criteria (e.g., Bromberger 1966; van Fraassen 1980). This suggests that the *DN* model lacks criteria to capture the directionality we see in many explanations. The second problem refers to arguments that are valid according to the *DN* criteria despite the fact that the *explanans* includes factors that are totally non-relevant to the *explanandum*, thereby leading to counter-intuitive explanations. For instance, the dissolving of a sample of table salt would be explained by the fact that it has been hexed and that all samples of hexed salt dissolve in water (Kyburg 1965). What these examples seem to suggest is that the *DN* model is at best incomplete. As we will see below, for several philosophers, the problems faced by the *DN* and *IS* models come from a very foundational issue: the fact that these models do not make causation a central feature of explanation (e.g., Scriven 1962; Salmon 1978). Much of subsequent work on explanation can be seen as addressing these type (2) questions.

A first answer to this problem has been the statistical-relevance (*SR*) model, chiefly developed by Wesley Salmon (1971). The idea behind the *SR* model of explanation is to include a condition that captures the causal relevance of a factor, causation being understood in probabilistic terms. According to the model, explanation is a matter of identifying the set of factors that are statistically-relevant to the explanandum. Generally stated, the criterion of statistical relevance offered by Salmon is the following: given some class or population characterized by A, an attribute C will be statistically relevant to another attribute B if and only if the probability of B conditional on A and C is different from the probability of B conditional on A alone. This is meant to capture the fact that C makes a difference with regards to elements of the population characterized by A having the property

B. In other words, *C* causally explains why elements characterized by *A* have *B*. The obvious advantage of this model of explanation is to solve the problem of explanatory relevance that affects the *DN* model. To cite another famous example, taking birth control pills is non-relevant when it comes to explaining a man's failure to get pregnant, because it is statistically non-relevant to a person becoming pregnant if this person is a man (but it is statistically relevant if this person is a woman). Similarly, the *SR* model solves the problem of explanatory asymmetry that affects the *DN* model (see Salmon 1971 for details). Another advantage of the *SR* model is that, unlike the *IS* model, it can account for explanations of low probability events.

The *SR* model however also faces a number of problems. One of the consequences of the SR model that Salmon endorses but that many take to be counter-intuitive is the fact that, in some cases, a set of statistically relevant factors can be used to explain both an event and its opposite (take the simple example of why someone catches a cold or why he/she does not, given that there is a certain probability of catching a cold in given circumstances). More fundamentally, there is the question whether causal relationships can indeed be captured by statistical relevance relationships (Cartwright 1979; Salmon 1984; Spirtes et al. 1983). Indeed, it appears that causal relationships are greatly underdetermined by statistical relevance relationships. This can happen, for instance, when the causal relata are characterized as too coarsely grained. And it has also been shown that the same statistical relevance relationships can account for different sets of causal relationships. These deficiencies have led Salmon to develop another type of causal model of explanation: the causal-mechanical model.

The central idea of the causal-mechanical (*CM*) model of explanation is to construe explanation in terms of causation, and causation in terms of interactions of causal processes (Salmon 1978, 1984). Within this framework, explaining an event is showing how it fits into a causal nexus, this causal nexus being constituted by causal processes that interact at certain points. According to Salmon, causal processes are physical processes that are capable of propagating marks or modifications imposed upon them (see Reichenbach's mark criterion in his 1958). This characteristic makes it possible to distinguish them from pseudo-processes, such as moving shadows, that cannot transmit a mark and are hence explanatorily irrelevant. A car traveling along a road with a scraped fender is a paradigmatic example of a causal process. Causal interactions are then construed as spatio-temporal intersections of causal processes that produce modifications in the very causal processes that intersect. And a car accident is just such a causal interaction. According to the *CM* model, explaining an event consists of tracing the causal processes and interactions leading to that event.

The *CM* model certainly has several merits, including the fact of fitting quite nicely with intuitive ideas about what explains an event. It also proposes a satisfying criterion for distinguishing causal processes from pseudo-processes. However, it has been markedly criticized for not providing a precise enough characterization of the very causal processes and interactions that do the explaining, as opposed to those that carry little or no explanatory force (the bug hitting the car fender a few seconds before the accident certainly constitutes a causal interaction, but one that has no explanatory import with regards to the accident itself). In short, the fact that a causal process can transmit a mark says nothing about its explanatory relevance. This general problem of sorting out the explanatorily relevant processes and interactions from the irrelevant ones has been identified as one of the major flaws of the *CM* model (e.g., Hitchcock 1995).

In more recent work, and in order to counter some of the problems identified above, Salmon developed a modified version of the *CM* model in which he replaced the mark-transmission characterization of causal processes by a conserved-quantity characterization (e.g., Salmon 1994; see also Dowe 2000). In this modified version, a causal process is a physical process that propagates a non-zero amount of a physical conserved quantity (such as momentum, charge, energy etc.). And a causal interaction is a spatio-temporal intersection of physical processes during which there is an exchange of a conserved quantity. This modified version of the *CM* model, however, has been shown to face the same problem of explanatory relevance as the previous one (Hitchcock 1995).

Another worry that is especially salient for explanation in biology is that the *CM* model locates explanation at the level of the physical causal nexus. A consequence is that explaining higher-level phenomena with higher-level processes, for instance biological, is not an option since these processes do not correspond to spatio-temporally continuous causal processes in Salmon's sense (e.g., Woodward 1989). This is, of course, particularly important for biology, because what seem to be explanatorily relevant factors in many cases do not fulfill the *CM* model.

On the other hand, this is no argument against any general theory of causal explanation. Though it might be the case that the theory of causation that Salmon's *CM* model builds upon is not adequate, this is not to say that no theory of causation can serve as a basis for developing other causal models of explanation. Indeed, the topic of causation has seen several key developments lately, including Woodward's influential interventionist account (2003), upon which novel models of explanation are being elaborated.

While both the *SR* and the *CM* models of explanation have been developed to counter the problems faced by Hempel's *DN-IS* model, and do so by making the notion causation central to that of explanation, an alternative route has been explored by Kitcher (1981, 1989 – see also Friedman 1974) who has proposed construing explanation in terms of unification. It is argued that, of the most central virtues of science, is its ability to unify phenomena that look completely unrelated at first, and thereby providing some understanding of the workings of nature. In biology for instance, Darwin's theory of natural selection unifies phenomena as diverse as fossil records, animal development and animal instinct, and it gives a general explanatory scheme able to account for all these various features of the living world. The unificationist model of explanation thereby defines explanation on the basis of the epistemic notion of unification.

More specifically, whereas, for Hempel, explaining is deriving the *explanandum* from an *explanans* (that includes laws of nature), for Kitcher explaining consists in showing that the derivation that leads to the *explanandum* is made according to an argument pattern that belongs to a very specific set of patterns: the "explanatory store". The key characteristic of this explanatory store – and the reason why, according to Kitcher, argument patterns that belong to it have explanatory force – is that it consists solely of argument patterns that maximally unify the set of beliefs that are accepted at a particular time in science. In other words, explaining is a matter of deriving as many *explananda* as possible from as few argument patterns as possible, these argument patterns belonging to the explanatory store.

As with its predecessors, this model has not won general agreement, because it raises various problems. One of these problems is that it is not clear how causal relationships can be derived from the concept of explanatory unification. This problem shows especially in cases that hinge on the problem of explanatory asymmetry. For instance, it has been argued that retrodictive derivations might be done using as few argument patterns as predictive derivations, hence making retrodictions as explanatory as predictions (e.g., Barnes 1992). Most importantly, it seems that unification is a broader notion than explanation, thereby implying that not all unifications are explanatory. This is illustrated by the use of a common mathematical formalism to describe different kinds of unrelated systems, or by the elaboration of broader classificatory schemes: such formal unification that is achieved by using the same argument patterns is often observed in science, and yet does not have any explanatory import (e.g., Morrison 2000; Sober 2003).

Parallel to the development of these models of explanation, some have sought to investigate the way explanations are provided so to speak in real life. This has led to developments that take type (3) problems – about the role context plays in explanation – as central. A classical objection to the *DN* model is that actual explanations are rarely set as a formal deductive argument (e.g., Scriven 1962). For instance, we tend to accept some historical narratives as explanatory despite the fact that these narratives do not make it possible to elaborate an argument that would show that the *explanandum* follows from a set of premises. As a response, some have looked into explanatory acts and the pragmatics of explanation as another means to characterize scientific explanation (e.g., van Fraassen 1980; Achinstein 1983). For instance, for van Fraassen, solving the puzzles of explanation can only be done if we have a clear understanding of the why-questions that are at the origin of the requests for explanation. Van Fraassen therefore construes explanations as answers to why-questions that he defines as ordered triples of the form $<P_k, X, R>$, P_k being the topic of the why-question, X its contrast class, and R the relevance relation that the answer A to the why-question must bear to $<P_k, X>$. Modeling requests for explanation in this way highlights the contrastive nature of why-questions (why P_k rather than P_m or P_n). It also highlights the contextual nature, made apparent both in the contrast class and in the relevance relation.

This model, however, has been criticized for not offering enough constraints as to what should really count as a proper explanation. Because the relevance relation, in particular, is not strictly specified, van Fraassen's account of explanation suffers from a risk of trivialization that would make any statement count as a proper explanation of a well-chosen why-question (Kitcher and Salmon 1987). On the other hand, it has been proposed that van Fraassen's non-formal criteria as to what should count as a *good* explanation could be rendered more formal, thereby alleviating parts of Kitcher and Salmon's criticisms (e.g., Richardson 1995). In any case, van Fraassen's account is often viewed as a key contribution that takes into account the pragmatics of explanation by specifying how we elaborate requests for explanation, yet one that fails to appropriately characterize what is offered as explanation.

So, what are we left with, six decades after Hempel and Oppenheim's essay? The harsh reality is that there does not seem be much consensus on how best to characterize scientific explanation. Several models have been proposed. And yet, each one has been shown to be plagued with imperfections. As a response, at least two different strategies can be pursued.

The first is to continue searching for an even better model of scientific explanation, be it one developed on the basis of yet another theory of causation, or one that would combine several features of existing models, or that would even explore radically novel avenues. In a way, this is still trying to solve the three major types of problems identified above. A presupposition of this strategy is that scientific explanation comes in one sort. In turn, this presupposition makes it possible to envision a set of conditions that would be jointly necessary and sufficient to single out scientific explanations from things that do not deserve such labeling (recall that there is also a normative aspect in this philosophical project). However, it is not at all clear that what counts and/or should count as a scientific explanation in domains as different as fundamental physics, genetics, ecology, sociology or economics, can be accounted for by a single model of explanation.

Arguing that this is indeed not the case leads to a second strategy for pursuing the debate: the strategy of defending some form of pluralistic view about scientific explanation. In short, the idea is to say that accounting for scientific explanation requires different models, possibly depending on the scientific disciplines or the types of *explananda* or both. Explanatory pluralism raises several questions: Are there good reasons to endorse pluralism, beyond the fact that so far no unique model of scientific explanation has been found? If one accepts explanatory pluralism, how are the different models related to each other? Do they stand in competition with each other, possibly offering different *explanantia* to the same *explanandum*? Do they complement each other by targeting specific types of *explananda*, or by being linked to scientific disciplines or fields, for instance via their methodological components? Should they be considered components of a (yet to come) more unified model of explanation that would be capable of capturing all these points while avoiding fatal counterexamples? Or should we rather acknowledge that no universal model might be able to capture all the dimensions of what a scientific explanation is?

Investigating how scientific explanation works in biology is one way to tackle the questions that arise when one adopts either one of these two strategies. In particular, there is a general worry as to whether the models of scientific explanation that have been mostly developed with physics as paradigmatic source of inspiration are indeed applicable to the biological sciences. As it has often been noted by commentators, until recently contemporary philosophy of science has been very much influenced by the physical sciences and many discussions have been somehow biased and possibly non-transposable to biology. A relative lack of interest in the special sciences in general has led to the ignoring of their peculiarities, including when it comes to investigating models of scientific explanation. Yet, there are obvious differences between explanations in physics and in biology. After all, contrary to physics and to most of chemistry, biology is held by many to have few very general theories based on universal laws and that make fundamental use of mathematical language. So the worry is that even if one (or several) of these models of explanation were able to capture adequately how explanation works in the physical sciences, it is not clear that the same could be said when it comes to biology or other special sciences.

Furthermore, because of a profusion of different schools of thoughts and research traditions *within* biology, different types of explanations seem to be pervasive across all of biology, ranging from historical narratives in evolutionary biology, to functional explanations in anatomy or to causal-mechanisms in molecular biology. This situation can be taken as an argument in favor of explanatory pluralism, not just by making explanation models specific to scientific disciplines, but by making explanation models even vary within a discipline, and possibly depending on finer elements such as problem types, heuristics, methodologies, cognitive and epistemic context and so forth (e.g., Sterelny 1996; Plutynski 2004; Brigandt 2013). Of course, it might just turn out that what superficially looks like rather peculiar forms of biological explanations are in fact only particular cases that would all fit a more general model in the end. Nevertheless, biological explanatory practice requires specific attention in this respect, and has indeed started to become the focus of a rich array of work.

3 Thinking About Explanation in Biology

Thinking about explanation in biology with the background mentioned above raises several kinds of questions and suggests at least that all of the proposed models of explanation need some revision if they are to work properly in biology. We will outline four of the most salient problems in the current debate. These problems are related to (1) whether natural laws exist in biology, (2) whether causation plays a specific explanatory role in biology, (3) whether other forms of explanation – e.g., functional or teleological – are also needed, and (4) whether the recent mechanistic-type model of explanation that brings together some form of law-like generalizations and of causation fulfill all expectations.

A major potential problem for the application of nomological models of explanation in biology is indeed the rarity (or perhaps even the absence) of natural laws, at least as they have been often conceived in philosophy from the study of the physical sciences. Of course, we find many generalizations in biology that appear to be involved in explanation, but they do not meet most criteria of lawfulness. These generalizations usually admit exceptions; they are spatio-temporally limited, or do not support counterfactuals (e.g., Smart 1962; Ruse 1970; Rosenberg 1994; Brandon 1997). Even the few generalizations that are called laws in biology, such as Mendel's laws, are problematic for *DN* types of models of explanation.

One reason for the absence of strict laws in biology stems from the nature of the biological world. Biological entities are the product of a long history, partly driven by natural selection and dependent on historical contingencies. Although this is a very difficult question in evolutionary biology, it is arguable that evolutionary history could have been different and that, as a consequence, the biological generalizations we now have could have been different too. This argument, made forcefully by John Beatty (1995), highlights the fact that evolutionary contingency undermines the very possibility for biological laws. All generalizations that are distinctively biological describe contingent outcomes of evolution. And yet, natural laws must be more than just contingently true. For instance, it is a very general biological fact that genetic heredity is encoded in nucleic acids (DNA or RNA). However, this might be only one possible solution that has been retained at the beginning of evolutionary history and that has then become universal (at least on our planet). If we think about other possible forms of life that might exist elsewhere in the universe, heredity might be handled in different ways and it is not clear at all whether our most general biological models (about say heredity or metabolism) would apply to them. Contrary to physics, biological generalizations seem to lack nomic necessity.

Another way to describe the problem is to recognize that many biological explanations are historical in nature. Explanations are obviously possible in the historical sciences, but they have peculiar features and raise several issues (e.g., Dray 1977; Clayton 1996). Most notably, *explananda* consist of unique events situated in the past. This does not preclude their explanation, but likely requires a different style of explaining, typically based on narratives. Authors like David Hull (1992) have argued that historical narratives in biology have a strong explanatory force, that does not depend much on general laws but more on particular circumstances: they tell stories that describe causal sequences of events. Historical explanations are legitimate, yet the impossibility to have direct empirical access to these causal chains give them a problematic status, which has led some scientists and philosophers to deny them the status of proper scientific explanation or at least to give them a lower explanatory status (e.g., Schaffner 1993). A particular and much-discussed case of historical explanation in biology is the explanation of traits as adaptation, i.e., as the product of natural selection. Following Gould and Lewontin (1979) famous criticisms, many have come to consider them as unfalsifiable "just-so-stories", which do not satisfy the criteria for genuine scientific explanation. It is indeed easier to imagine possible adaptive scenarios than to test them. This is of course not a fatal flaw for these explanations, but a sign that historical explanations must be offered with caution.

Coming back to the role of laws in explanation, their apparent absence in biology has led to various answers. One possibility is to relax the criteria for lawfulness and accept that biological generalizations are laws, but different from what we know from physics or chemistry (e.g., Sober 1993; Lange 1995; Mitchell 1997). In other words, the concept of scientific law can be redefined so as to accommodate the generalizations found in biological explanations. This move can save conceptions in line with the *DN* model, that make explanations depend on laws. Another response is to propose to drop the requirement for laws and accept that other kinds of generalizations can support genuine explanations (e.g., Woodward 2000). According to Woodward's account, the important feature for a generalization to be used in an explanation is not its lawfulness but rather its invariance. Invariance of a generalization means that it would continue to hold under a relevant class of changes. Conceiving explanation in terms of invariant generalizations has the advantage of avoiding several problems, including the restricted validity of generalizations in biology and the existence of exceptions. By acknowledging different degrees of contingency between laws and accidents, this strategy offers a more nuanced account of how generalizations work in scientific explanation. Yet another line of response might still be to argue that the arguments against laws in biology are mistaken, and that there exist indeed distinctively biological laws (Elgin 2006). In any case, the debate is still open and all the more so as the very notion of 'law of nature' is a delicate one to tackle (e.g., DesAutels 2009; Haufe 2013).

The problems raised by nomological accounts in biology give strong reasons to turn to alternative models of explanation, and in particular to those that center on causation. Indeed, causal accounts of explanation have been offered as a solution to many of the problems traditionally encountered by nomological models. Furthermore, many explanations in biology do involve citing causes and causal regularities (e.g., Schaffner 1993; Waters 1998). The question then becomes whether existing causal models of explanation fit the explanatory practice as found in biology and in all its sub-disciplines.

Concerns have been raised as to the applicability of Salmon's causal-mechanical (*CM*) model, be it under its mark-transmission form or under its more recent conserved-quantity version. As noted above, the mark-transmission model faces serious difficulties, leaving the conserved-quantity model as the only likely contender. Yet, the conserved-quantity model focuses very heavily on the physical level, in particular by situating causation at the level of conserved physical quantities. In this respect, explanations that fit this model must include physical details that are usually not considered relevant in biological explanations. Of course, causal relations at higher biological levels should in principle be analyzable in terms of physical processes. Yet, this is almost always unmanageable in practice. Furthermore, explanations that would be so framed at the level of conserved physical quantities would differ notably from what is usually taken as explanatorily relevant in biology (e.g., Woodward 1989; Glennan 1996).

An alternative solution would be to turn to the recently developed interventionist model of causation (Woodward 2003) as a basis for construing a causal model of explanation that would suit the practice of most – if not all – domains of biology. On this conception, a causal explanation consists in the exhibition of patterns of dependency between the factors cited in the *explanans* (causal factors) and those cited in the *explanandum*. These patterns of dependency are revealed by means of interventions onto the different causal factors – variables in a causal model – and the identification of subsequent changes in the effect factors. The main idea behind the interventionist account of causation is that causal relationships are revealed by the fact that when one intervenes on a given factor – while holding fixed a proper set of background conditions – one witnesses changes in another factor. One of the key motivations for such an account is to capture the practice of experimental science, which is characterized by specific interventions onto systems that are placed in well controlled set-ups. Another advantage is that interventionism does not require causal relationships to be exclusively located at the physical level. Rather, causal relationships are possible at any level of investigation, provided the variables that enter the relevant causal models fulfill the formal conditions of interventionism. Furthermore, as Woodward argues by looking at specific biological explanations, causal relationships that fulfill additional conditions of stability, proportionality and specificity are those that are usually called upon in proper causal explanations (Woodward 2010; see also Waters 2007). While the interventionist account of causation has generally been well adopted by proponents of mechanistic explanations in biology (see below – yet see also Weber 2008), the feasibility of developing a satisfactory model of explanation on this basis hinges on the viability of interventionism in general as a theory of causation. This is a matter of intense debate, with such questions concerning the circularity of the account (causation is defined by means of interventions, that are themselves causal), the possibility of interventions in cases of supervenient properties or foundational assumptions that relate to modularity and the Causal Markov Condition (see for instance Cartwright 2006; Glymour 2008; Mitchell 2008; Strevens 2008; Baumgartner 2009).

Whatever the merits of various theories of causal explanation, one ought not assume that all explanations are necessarily causal. One example that has received much attention in the philosophy of biology is the case of equilibrium explanation (e.g., Sober 1983; Potochnik 2007). Equilibrium is a stable state of a system that has a domain of attraction larger than the state itself, so that when the system is perturbed it returns to this equilibrium state. Using Fisher's explanation of sex-ratio equilibria, Sober (1983) has argued that equilibrium explanations are not causal. They are explanatory because they show that many initial conditions lead to this state, but they are not causal because they do not cite the actual causes that have produced that state. Tracing the actual causal history is not explanatorily relevant here. It seems that the same could be argued about a number of mathematical explanations in biology and in science (e.g., Baker 2009). Among them, models of patterns and allometric scaling laws, which describe how processes scale with body size and with each other, seem to capture essential properties of living systems without appealing to causes. However, it is not exactly clear what explanatory work they actually perform. Moreover, rather than genuine explanations they might be considered as observations in need of explanation, for example by physical principles (West et al. 1997).

Another type of explanation that immediately comes to mind in biology is functional explanations. Indeed a central part of the explanation of an organism structure and of its parts (traits) features and organization involves the concept of function. Organs are explained by their function and this explanatory pattern is omnipresent down to the molecular level (genes and proteins). Some have argued that this is even part of what gives biology its explanatory autonomy, since more fundamental sciences such as physics and chemistry simply do not possess such explanatory concepts (e.g., Hull 1974; Mayr 1988). Though they seem indispensable in biology, functional explanations are problematic because they imply the notion of goal, hence of teleology. And teleologically describing the world is not acceptable since the rise of modern science. Of course, by showing that the apparent teleological nature of organisms can be explained by the action of natural selection, Darwin has offered a solution to this problem. And philosophers such as Nagel (1961) and Hempel (1965) have accordingly tried to define "function" in terms that make functional explanations unproblematic. However, things have turned out to be more complicated and competing views about how to best define biological function have been proposed. In particular, two main accounts have been defended. The etiological account (e.g., Wright 1973; Millikan 1989) defines the function of specific traits by referring to what those traits were selected for doing in the organisms' ancestors. Such a construal of function is thus fundamentally historical. On the other hand, the systemic account of function (e.g., Cummins 1975) defines the function of some trait in terms of what this trait does in the organism that possesses it (for instance the role it plays in maintaining the overall organization of the organism in its present state). These two accounts are not necessarily incompatible, but a unified theory of function and of functional explanation still is the focus of much debate. The corresponding literature needs not be reviewed here (but see Wouters 2005), but it shows that the nature of this central type of biological explanation still raises questions, in particular regarding its relation to other models of explanation.

We have noted above that explanation in biology is often claimed to incorporate a strong causal component. In some domains of biology – such as molecular biology, cell biology, or physiology just to name a few – these causal explanations often take the form of mechanistic models. This has led a growing number of philosophers in the last 20 years to develop mechanistic models of explanation (e.g., Bechtel and Richardson 1993; Glennan 1996; Machamer et al. 2000; Craver 2007; Bechtel and Abrahamsen 2012; Craver and Darden 2013).

One of the motivations was to bring philosophical analysis closer to the reality of scientific research. Examining the explanatory practices of biologists reveals that phenomena are often explained by identifying the mechanisms that produce these phenomena. Although several alternative definitions of mechanism (and of mechanistic explanation) have been offered in the recent literature, they tend to converge on their most critical features. A mechanism can be thought of as being composed of parts that interact causally (usually through chemical and mechanical interactions) and that are organized in a specific way. This organization determines largely the behavior of the mechanism and hence the phenomena that it produces. Explaining a phenomenon in a mechanistic way involves decomposing the system that is at the origin of that phenomenon into interacting parts, and giving a description of how the organization and activities of these parts produce the phenomenon to be explained. A key difference from nomological models of explanation is that neither laws of nature nor logical derivations play any significant role in mechanistic explanation. Mechanisms can be formalized in different ways, including with the help of diagrams and schemas, and are usually supplemented by causal narratives that describe how the mechanisms produce the very phenomena to be accounted for. Explaining results from rehearsing how the different parts of a mechanism causally produce the *explanandum*.

The interest for mechanistic explanation also corresponds to a broadening of the discussions on scientific explanation. While analyses have traditionally focused on the context of justification, a lot of recent work has been devoted to elucidating how mechanistic explanations are actually developed (but see also Schaffner 1993). Close attention to heuristics and experimental methods (manipulation of biological systems) has thus enriched the understanding of explanatory practices, and especially in biology.

Since causation plays a significant role in mechanistic explanation, a theory of causation is an implicit assumption of this model of explanation. As noted above, several mechanistic philosophers tend to endorse an interventionist account of causation (e.g., Woodward 2002; Craver 2007 – but see also Bogen 2005). It is debated however whether mechanistic explanation requires such an account of causation. It is also debated whether mechanistic explanation so construed fits the increasingly complex and dynamic systems that are now uncovered in many domains of biology, and whether the mechanistic model of explanation needs to be extended in some way or another (e.g., Kaplan and Bechtel 2011). As many of the contributions to this present volume show (see below), the topic of mechanistic explanation currently receives a lot of attention.

4 The Seventh Decade of Explanation: Insights from Biology

When we look back at research on scientific explanation in philosophy of science, we cannot help but see a gap between two lines of investigation. On the one hand, there is a very central objective that was and still is pursued in general philosophy of science that consists in characterizing *any* scientific explanation, be it by addressing type-1, type-2 or type-3 problems as outlined above in Sect. 2 (Are there necessary and sufficient conditions for any scientific explanation? What role does causation play in explanation? What role does context play in explanation?). Underlying most approaches is the assumption that there *must be* a general model of explanation, and that one of the goals of philosophy of science precisely is to find that model. On the other hand, most of the work on explanation that has been done in the philosophy of biology has followed a less ambitious path, mainly attempting to characterize particular types of explanations as found in the practice of biology at large, from evolutionary biology to molecular biology, including developmental biology, systems biology or synthetic biology to name a few, and somehow structuring itself around the four major questions identified above in Sect. 3 (Are there natural laws in biology or other forms of explanatorily relevant generalizations? Which role does causation play in biological explanation? Are other forms of explanation needed? What are the strengths and weaknesses of the recent mechanistic-type model of explanation in biology?). For instance, all proponents of the new mechanism-based model of explanation are cautious to emphasize that they do not claim that all explanations in biology, let alone in other scientific domains, ought to take the form of mechanisms. Similarly, the same caution characterizes the debate about functional and teleological explanations and other types of explanations identified in biology. The objective that is generally pursued is to propose models of explanation that capture the specificities of each important sub-class of explanation we find here or there across all of biology. Recent debates have shown that this objective is already difficult to reach. However, it also gives the impression that the original question about explanation pursued by general philosophy of science has been given up by philosophers looking at biology. For this reason, rethinking the relationships between the different models of biological explanation and of general scientific explanation is crucial.

There is another reason for extending further the recent lines of research about explanation in biology. As mentioned earlier, mechanistic analyses have come to dominate the scene in the last decade. Based on the intuition that many explanations we find in the biological sciences fulfill mechanism-based models, several authors have offered various accounts of how these models are characterized, how they get their explanatory force, how they are built, and so forth. Though probably no philosopher would seriously argue that all biological explanations are mechanistic, the frequency of such mechanistic explanations in biology makes it tempting to adopt a rather expansionist attitude and develop an extremely broad conception of mechanistic explanation that would apply to an extended domain of science. For instance, some authors wonder whether historical and evolutionary explanations, despite their characteristic contingency and their populational character, might be considered particular cases of mechanism-based explanation (Skipper and Millstein 2005; Barros 2008; Glennan 2009). Because not everyone agrees on this view, it is worth clarifying once again the core of the concept of mechanism-based explanation, and, most importantly, determining its specific application domain and limits. In other words, it is needed to have a clearer view of what mechanistic explanations can really explain and of what falls outside of their explanatory range. It is also crucial to identify the reasons why certain biological phenomena might resist mechanistic explanations, and by the same token, to investigate whether the mechanism-based model of explanation might be extended to handle such difficult cases. Another question that arises is whether mechanism-based explanations might not simply be also subsumed under a broader model of explanation, such as one of the more general models investigated in general philosophy of science.

Such questions about the unity vs. diversity of explanation are particularly pressing in biology for several reasons. Although biology is certainly not completely unique from that point of view, it does offer a striking variety of explanatory practices and can be seen as the locus where very different explanatory patterns are indeed put to work, sometimes jointly, sometimes independently of each other. This specificity of biology with regards to the concept of scientific explanation originates from at least three sets of reasons.

First, the biological sciences cover a huge variety of phenomena studied at broad range of levels, from molecular entities all the way up to ecosystems. Models of explanation must therefore be able to adapt to the different scales at which these phenomena unfold. Note that these variations of scales are also temporal, as biology encompasses phenomena that span over billion of years, such as the evolution of unicellular organisms, as well as phenomena that unfold in much less than a second, as is the case, for instance, of a synaptic neuro-transmission.

Second, biology is a scientific discipline in which numerous diverse approaches to science coexist. Some may advocate reductionist methodologies, as is often said to be the case in molecular biology, while others favor more holistic views, as is the case in some approaches to developmental biology. Analysis is said to drive most of the research done in general biology, while at the same time synthesis is claimed as major methodological approach in some novel branches such as synthetic biology. The diversity of methodologies or heuristics in biology is also visible in the diversity of complementary disciplines that contribute to the development of biological knowledge, and that range from applied mathematics and computer science to engineering and complex systems science. Because such heuristics determine how biological phenomena are approached, it is important to understand also to which extent they might in turn determine shifts in what is taken to be explanatory.

Third, biology is also characterized by a lack of theoretical unifying principles or laws, except perhaps for the principle of evolution by natural selection. As a result, explanation takes the form of a patchwork of different explanatory practices that are related to each other in complex ways that require clarification. Moreover, as sub-disciplines within biology appear and disappear, reorganize, merge or split, these relationships between explanatory practices often change rapidly. Recently for instance, two interesting cases have attracted much attention: on the one hand, evo-devo considers as central the question of articulating evolutionary and developmental explanations; on the other hand, systems biology pursues the explanatory integration of mathematical and computational modeling with biologically relevant considerations.

The present volume *Explanation in Biology. An Enquiry into the Diversity of Explanatory Patterns in the Life Sciences* aims at addressing parts of these complex questions. Though some issues are tackled in several essays across the volume – for instance, the limitations of mechanistic explanation – we have organized the essays into five parts that echo the broad range of questions that the notion of explanation addresses in biology today, in this seventh decade of philosophical investigations about scientific explanation. The ordering could have been done otherwise, but we have tried to sort out the essays according to their main philosophical theses (e.g., explanatory pluralism, emendations of mechanistic explanation, role of mathematics and of heuristics in explanation, new theories of explanation) as opposed to the biological sub-disciplines from which they borrow examples (e.g., molecular biology, evolutionary biology, systems biology, environmental biology etc.).

Part I of the volume explores explanatory pluralism in biology, be it by looking at research traditions in biology or by investigating some of the explanatory specificities of particular branches of biology, such as systems biology, evolutionary biology, or developmental and molecular biology.

Michel Morange (Chap. 2) argues that explanations are plural in biology and often compete against each other. This has been amply documented, for instance, in the field of evo-devo, but the situation is common to all branches of biology. For Morange, this multiplicity of explanations has three sources. First, many of the explanation-seeking questions raised in biology are ambiguous and can be interpreted in different ways. This leads unavoidably to the search for different answers, hence different explanations. Second, the objects investigated by biology – e.g., biomolecular processes, cells, organisms, ecosystems etc. – are the product of a historical evolutionary process. As a result, and despite similarities, these different objects exhibit unique features that require unique explanations, hence resulting in a plurality of explanations of apparently similar phenomena. Third, biology is a discipline in which long lasting explanatory traditions compete against each other, such as the reductionist tradition versus the holistic one. This leads to a multiplicity of approaches when it comes to explaining biological phenomena.

By reflecting on case studies borrowed from systems biology, Constantinos Mekios (Chap. 3) argues that this biological sub-discipline is the locus of a rich plurality of types of explanations. These types of explanations include a profusion of mechanistic explanations that target specific minute domains of enquiry, but also of more systemic explanations that aim at providing a broader integrative view, as well as of explanation patterns borrowed from other sciences, physics in particular as well as mathematics. While mechanisms do play an important explanatory role, they are not sufficient to capture the richness of the explanatory endeavor in systems biology, be they bottom-up or top-down. As Mekios argues, integrating or patching together many explanatory schemes of different nature, some of them of ambiguous status, is the only method of reaching intelligibility in systems biology. Mekios also shows that explanatory pluralism is not just a matter of abstract theoretical considerations, but is driven by real practical problems that arise in the actual practice of systems biology.

As Derek Turner reminds us (Chap. 4), many explanations in evolutionary biology are of historical nature. These have received some attention from philosophers in the past, but Turner takes a fresh look at paleontology and macroevolutionary theory in order to clarify the explanatory relation between two central issues, the contingency of evolutionary history and the passive vs. driven nature of large-scale evolutionary trends. These issues are important when we think about explanation in biology because the role of contingency in evolution has direct consequences for our ability to predict evolutionary outcomes and for the possibility to make generalizations, and also because the existence of trends has been accounted for very differently, both in adaptive and non-adaptive terms. Turner explores the hypothesis that the contingency of evolutionary history explains why some evolutionary trends are passive. He also discusses what sense of contingency is adequate in this context. According to Turner, the relation between these two issues reveals a deeper unity in macroevolutionary theory than it is usually recognized. This is important for the potential explanatory contribution of macroevolutionary models and concepts in evolutionary biology, a question that has been much debated since the 1970s. Turner's argument thus supports the view that macroevolutionary theory has a genuine and irreducible explanatory role to play.

In her contribution to this volume, Francesca Merlin (Chap. 5) examines how explanation is a matter of linking an *explanandum* to an *explanans*. Interestingly, specific phenomena sometimes act as *explanandum* and sometimes as *explanans*. Merlin points at the particular case of developmental noise as studied by developmental biology. Sometimes, developmental noise is considered an *explanans*, for instance when it comes to explaining the particular physical characteristics of individual organisms. And at other times, Merlin argues, developmental noise is considered an *explanandum* that is addressed typically from a selective-evolutionary history, but also from a physico-chemical perspective in terms of noise-reducing constraints. Such a case study highlights in particular the plurality of possible explanations linked to a same phenomenon.

Part II of the volume gathers contributions that investigate the applications of the mechanism-based model of explanation in biology, while also looking at some possible emendations. These limits are apparent, for instance, in molecular biology when faced with the tantamount complexity of the systems that are analyzed, but also in other areas of biology such as developmental biology where classic mechanisms are supplemented with other models when used to formulate explanations. Such situations can in turn be used as stepping-stones to elaborate extensions of the mechanism-based model of explanation.

Molecular biology, one of the most successful biological domains of the last century, has provided philosophers with numerous examples of how explanations work in biology and has been interpreted as supporting the mechanistic framework. However, by looking at recent research on genetic regulation by microRNA, Frédérique Théry (Chap. 6) argues that explanation in molecular biology (and functional biology in general) cannot be reduced to mechanistic explanation, as it has been characterized in recent philosophical discussions. Biologists are increasingly interested in properties of living systems that the concept of mechanism fails to capture. Théry describes two alternative types of explanation involved in microRNA research that go beyond the limits of mechanistic explanations. First, quantitative explanations fully take into account the fact that molecules are present in cells as populations. Mechanistic explanations primarily deal with the qualitative component of causal relations and largely ignore that the function of many molecular components depends on the relative cellular concentrations of the different molecules involved in the process. Second, systemic explanations go beyond the idealization of mechanisms producing a function autonomously and show how different causal processes are interconnected at the cellular level. These alternative explanations do not contradict classical mechanistic models, but are rather meant to complement them. By recognizing the specificities of the various explanatory schemes in functional biology Théry thus invites us to embrace a more pluralistic perspective.

Ingo Brigandt (Chap. 7) explores in turn the limits of philosophical accounts of mechanistic explanation in evolutionary developmental biology. Contrary to the classical account that distinguishes explanatory from phenomenological models, and that classifies mathematical models among the latter, Brigandt argues that mathematical models are often indispensable components of mechanistic explanations, and therefore have specific explanatory value. In particular, Brigandt argues that quantitative models are required as a complement to mechanisms to provide proper explanations not only of quantitative features but also of qualitative features of mechanisms. To support his case, Brigandt draws on the scientific literature of the evo-devo field. For instance, he shows that mechanistic explanations – when conceived in the classical fashion – cannot account for the evolutionary origin of morphological features like the cusp number and shape of the teeth in mammals, or the development of segments in vertebrates: indeed, explanations of such phenomena cannot be achieved by rehearsing the causal roles of the entities of the underlying mechanisms, but do require mathematical models that make it possible to understand the emergence of the spatio-temporal behaviors that constitute the explananda. Brigandt extends his case to other evo-devo phenomena, like the explanation of robustness, of plasticity and of modularity.

As Fridolin Gross recalls (Chap. 8), the mechanistic explanatory framework is often taken to consist of entities and activities characterized by change-relating relationships construed along a manipulationist account of causation. These change-relating relationships occupy a central role in explaining why the mechanisms behave the way they do, and this picture of mechanistic explanation assumes that only relationships of dependence have explanatory value. But, as Gross points out, relationships of *non*-dependence may sometimes also play a crucial explanatory role in systems biology. Gross argues that this is typically the case when it comes to explaining such behaviors as stability at an equilibrium point, transition from one stable equilibrium to another, or robustness in the face of perturbations. In this contribution, Gross argues that non-dependence relationships cannot be deemed explanatorily irrelevant simply on the basis of not being change-relating relationships (as the classic account of mechanism would require). Rather, depending on contexts, non-dependence relationships also play an explanatory role alongside change-relating relationships.

A peculiarity of mechanistic explanation is its apparently restricted scope. Biologists study particular mechanisms in particular model organisms, which makes generalization difficult and always uncertain. However, generality seems to be an important explanatory virtue. William Bechtel (Chap. 9) shows how the use of new tools, in particular graph-theoretic representations of mechanisms, provides a basis for developing more general accounts of mechanisms organization and behaviour. Bechtel focuses on two strands of research, the first concerns the broad topological organization of large networks, while the second is interested in the structure of small network motifs, which are specialized for specific types of processing. By enabling the formalization of organization patterns, these tools facilitate the identification of a common abstract graph structure in different mechanisms and hence allow generalizing knowledge gained on particular mechanisms.

Because of the complexity of many biological phenomena, explanations in biology often make ample use of mathematics and mathematical tools, and, hence, the question whether mathematics play a specific role in explanation arises. Part III consists of a set of essays that investigate this question through different angles. Biology appears to be an interesting discipline to carry out such investigations: the types of mathematical problems are highly diverse; these problems are also complex but not too complex, and they trigger tools and solutions from several branches of mathematics. Biology therefore is a most relevant place to ask the question whether there exist or not distinctly mathematical explanations in science, but also to investigate the relationships between "abstract" mathematical theorems and derivations on the one hand, and "empirical" biological explanations on the other, be they of the causal-mechanical type or otherwise.

Alan Baker (Chap. 10) focuses on the explanatory role of mathematical objects, especially when mobilized in the context of biological phenomena. This is for instance the case when mathematics play a critical role in explaining the periodical life-cycle of certain North American species of cicada, or the hexagonal shape of bee honeycombs. More generally, Baker proposes to distinguish three types of genuine mathematical explanations in science (*MES*): (1) *Constraint MES* that explain why some physical outcomes are impossible by showing that they are mathematically impossible, (2) *Equilibrium MES* that explain why some physical outcomes occur by showing that they are mathematically inevitable across a range of starting conditions, and (3) *Optimization MES* that explain why some physical outcomes occur by showing that they are mathematically optimal. Baker argues that the crucial role that mathematics play in some recent and controversial explanations of puzzling biological phenomena calls for an even finer characterization of these different types of genuine mathematical explanations that permeate science.

By looking at the case of systems biology, Tobias Breidenmoser and Olaf Wolkenhauer (Chap. 11) argue that *organizing principles* – which typically take the form of specific mathematical theorems – are an indispensable complement to mechanistic explanation when it comes to explaining key behavioral features of biological systems. Breidenmoser and Wolkenhauer distinguish phenomenological models –that only "save the phenomena" by providing curve fitting of some sort – from mechanistic models – that explain by describing underlying molecular and cellular processes. Yet they argue that mechanistic models are limited in that they fail to account for specific *explananda* that are of major interest in systems biology, such as the origin of robustness. Breidenmoser and Wolkenhauer argue that explanation of such features must appeal to analytic theorems, such as the "robustness theorem". More broadly, they propose that certain types of *explananda* require the use of organizing principles as a complement to mechanistic models.

For Tarik Issad and Christophe Malaterre (Chap. 12), the plurality of explanatory patterns should reflect in the ways these explanatory patterns get their explanatory force. Issad and Malaterre investigate the explanatory force of (classically construed) mechanistic explanations (e.g., Machamer et al. 2000; Glennan 2002) and of dynamic mechanistic explanations (e.g., Bechtel and Abrahamsen 2012). They argue that, whereas mechanistic explanations get their explanatory force from rehearsing a causal story, dynamic mechanistic explanations are explanatory in virtue of displaying mathematical warrants that show how the explanandum follows from a mathematical model. Dynamic mechanistic explanations therefore are not causal explanations, even if elements of the models they rely on may receive causal interpretations. Despite this apparent difference in explanatory force, Issad and Malaterre argue that mechanistic explanations and dynamic mechanistic explanations can be construed as limit cases of a more general pattern of explanation that they name "Causally Interpreted Model Explanations" and in which the explanatory force of causation and of mathematical derivation are redistributed. Such pattern of explanation draws its explanatory force from a model, a causal interpretation that links the model to biological reality (but does not necessarily extend into a causal story), and a mathematical derivation that links the model to the explanandum phenomenon (and that may, in simple cases but not in complex ones, be reformulated as a causal story).

Several essays stress the role that different heuristic strategies in biology play when it comes to formulating explanations. We have gathered them in Part IV of the volume. The debate concerns the question whether current models of explanations are sufficient or not to account for how explanations are developed in science, and particularly in biology. In also concerns the question whether heuristic strategies impact or not the ways explanations are formulated. These questions arise in the context of the discovery of more and more complex systems in biology that require novel conceptual tools for their investigation, be they from mathematics, computer science or engineering.

Carlos Zednik (Chap. 13) recalls that much of the philosophical debate about mechanisms has focused on heuristic strategies used to build mechanistic explanations. Bechtel and Richardson's analysis in terms of decomposition and localization has been particularly influential. However, Zednik argues that the classical examples on which most discussions have been based offer only a limited view on the strategies actually used by scientists. In particular, the application of mathematical and computational modelling has deeply changed heuristic methods and explanatory practices. Using examples from contemporary research in neurobiology and evolutionary robotics, Zednik shows that the discovery and description of mechanisms involve more than the principles of decomposition, localization and diagrammatic representation. He focuses in particular on the use of tools from graph theory and dynamical systems theory, which have been recently, increasingly put to work in different domains of biology. An important consequence of these new heuristic strategies is that they increase the scope and power of mechanistic explanation, by enabling the discovery and description of very complex mechanisms that were beyond the reach of classical models.

Pierre-Alain Braillard (Chap. 14) explores how transfer of methods, models and concepts from engineering in the context of the emergence of systems biology, has influenced biologists' explanatory practices. In particular, mathematical modelling methods developed by engineers have been increasingly put to use in order to capture biological systems complex dynamic properties that are difficult or even impossible to analyze and represent with traditional mechanistic approaches. But more than simple mathematical tools, Braillard shows that it is a whole view of how to best decompose and explain complex systems that engineering-oriented scientists have brought to biology. Based on the assumption that biological systems are modular in the same way that many complex engineered systems are, this heuristic and explanatory framework offers promising solutions to deal with the complexity biologists are facing. However, part of the validity of these approaches depends on important assumptions made about biological systems structure, which remain hypothetic.

Tudor Baetu (Chap. 15) argues that models of mechanisms and mathematical models, rather than being antagonistic, play a complementary role in explaining biological phenomena such as those stemming from molecular networks in systems biology. Baetu's thesis can be understood as mediating the positions of Craver who argues that mathematical models are explanatory only to the extent that they identify the physico-chemical entities that causally produce the phenomena (e.g., Craver 2007), and of Weber who argues that explanation requires the derivation of the phenomena from mathematically formulated law-like regularities (e.g., Weber 2005). As Baetu explains, (quantitative) mathematical models cannot replace (qualitative) mechanistic models, but rather complement them in so far as they are required for formulating a broad range of predictions that mechanistic models alone cannot formulate, and as they offer insights into the temporal dynamics of certain systemic parameters. This complementarity, Baetu explains, also shows when considering the development of biological explanations over time and the associated heuristics: because molecular networks are abstract representations of molecular mechanisms, revisions of the latter entail revisions of the former. But the converse is also true in that mathematical models may reveal unsuspected anomalies or holes in previously accepted mechanisms, thus prompting also their revision. For Baetu, the molecular networks studied in systems biology show that a mixed approach to explanation is needed, one that associates models of mechanisms with mathematical derivation from law-like regularities.

An alternative path to probing the limits of mechanistic explanation and elaborating emendations to this model is to explore models of explanation within which mechanisms are not central. Part V of the volume gathers several essays that propose to think anew some of the classical models of explanation – such as Hempel's covering law model – in light of biological specificities, or that investigate, for instance, how causation is mobilized in explanation, in particular when several causal factors act together.

Despite the apparent heterogeneity of explanations in biology, especially when compared to physics, Joel Press (Chap. 16) argues that an underlying unity in all scientific explanations can be found in the form of a "cursory covering law" model of explanation. As the name suggests, the cursory covering law model builds upon Hempel's covering law – or deductive-nomological – model of explanation, and the criticisms this latter model received when it was tentatively applied to biology. Because biology lacks generalizations of the sort required by laws of nature, it has often been argued that the covering law model cannot account for the types of explanations that one finds in biology, thereby prompting either a revision of what laws are in biology (e.g., Brandon 1997; Mitchell 1997), or a dismissal of laws as explanatorily relevant in biology (e.g., Machamer et al. 2000). Press proposes to reconsider the covering law model and relax some of the constraints that bear on the *explanans* so as to include approximating statements about laws, somehow extending Hempel's idea of partial explanations. The proposed "cursory covering law" model subsumes, Press argues, alternative accounts of explanation in biology, be they based on modified accounts of what laws are or articulated without appeal to the notion of laws of nature.

For Melinda Bonnie Fagan (Chap. 17), the analysis of research on stem cells provides illuminating examples of explanations-in-progress linked to developmental processes. Stem cell research broadly construed aims at explaining the branching process of cell development, from a single initiating "stem", through intermediate stages, to one or more termini. By looking more specifically at the case of stem cell reprogramming, Fagan investigates how explanations are constructed in this domain of biology. In light of this analysis, she reviews three major accounts of explanation: a broad interventionist account (based on Woodward 2003), a more focused gene-centered account (based on Waters 2007), and a mechanistic account (based on Craver 2007). She argues that all three accounts encounter limitations when it comes to explaining stem cell reprogramming in so far as the *explananda* typically require the *joint* action of several causal factors, and not just their separate listing as causal contributors. She proposes that explanation – at least in the case of stem cell reprogramming – requires appeal to a notion of *jointness* which appears to be key in explaining how experimental interventions onto already differentiated cells result in pluripotent cells, through the joint action of several factors.

Laura R. Franklin-Hall (Chap. 18) also takes causation to be a central feature of explanation, and in particular of explanation in biology, but she tackles a different issue: she addresses the question of how we select *some* causal factors as being explanatory relevant rather than others. This causal selection problem has two facets: a horizontal one that concerns the omission of background conditions, and a vertical one that concerns the omission of low-level details. Franklin-Hall proposes a Causal Economy account according to which explaining an event is citing precisely the causal factors that "cost less" in virtue of being more abstract, and "deliver more" in virtue of making the event to be explained more stable under variations of other causal influences. While applying her account to the explanation of biological phenomena such as signalling systems and biological development, she also suggests that the Causal Economy account could offer a single principle that would guide explanation construction across the sciences, and in particular across the sub-disciplines of biology, thereby subsuming their apparent heterogeneity and plurality.

5 Beyond the Seventh Decade

As a collection of essays, *Explanation in Biology. An Enquiry into the Diversity of Explanatory Patterns in the Life Sciences* is bound to be exploratory. It would be unrealistic to ask that all problems raised by such a rich question as that of "explanation in biology" be solved. Nevertheless it is our hope that the volume addresses at least some of these problems and contributes interesting and challenging ideas about how to tackle them. There is, no doubt, much more to be said about explanation in biology, and each one of the volume's essays branches out further to novel research directions. The plurality of explanatory patterns and practices in biology remains puzzling. We see it as a springboard for future investigations about whether such pluralism reveals something deeper about the notion of scientific explanation. If this is so, then the quest for a unified account of scientific explanation is likely to be ill grounded. If not, such a unified account might still be possible, yet the role of pragmatics in shaping the explanatory context would certainly deserve further studying. One possible way to go is to continue investigating the limitations of the mechanistic model of explanation and, by so doing, to possibly identify means of extending this model beyond its current limitations. Some may prefer going the route of exploring alternative models, either in the direction of nomological models (hence focusing on the role law-like generalizations may play in explanation), or in the direction of causal models (thereby addressing questions about the necessity of causation in any model of explanation as well as about the modalities of its explanatory force). Others still may opt for investigating the heuristics of explanation as a means to a deeper analysis of explanation itself, and in this respect, looking at the actual practice of science and how this practice currently evolves under the pressure of more and more complex objects of investigation might very well also generate radically novel insights about how science now explains nature. The complexity of biological objects may also point to the need for better articulation of explanation and understanding, and all the more so as some phenomena – say the behavior of complex molecular networks – may somehow challenge our capacity for understanding nature despite being amenable to some form of explanation or another. In any case, scientific explanation remains a key target for philosophical analysis, and its study from the biological angle continues to uncover issues that were previously not considered.

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