Biological Explanation

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Abstract One of the central aims of science is explanation: scientists seek to uncover *why* things happen the way they do. This chapter addresses what kinds of explanations are formulated in biology, how explanatory aims influence other features of the field of biology, and the implications of all of this for biology education. Philosophical treatments of scientific explanation have been both complicated and enriched by attention to explanatory strategies in biology. Most basically, whereas traditional philosophy of science based explanation on derivation from scientific laws, there are many biological explanations in which laws play little or no role. Instead, the field of biology is a natural place to turn for support for the idea that causal information is explanatory. Biology has also been used to motivate mechanistic accounts of explanation, as well as criticisms of that approach. Ultimately, the most pressing issue about explanation in biology may be how to account for the wide range of explanatory styles encountered in the field. This issue is crucial, for the aims of biological explanation influence a variety of other features of the field of biology. Explanatory aims account for the continued neglect of some central causal factors, a neglect that would otherwise be mysterious. This is linked to the persistent use of models like evolutionary game theory and population genetic models, models that are simplified to the point of unreality. These explanatory aims also offer a way to interpret many biologists' total commitment to one or another methodological approach, and the intense disagreements that result. In my view, such debates are better understood as arising not from different theoretical commitments, but commitments to different explanatory projects. Biology education would thus be enriched by attending to approaches to biological explanation, as well as the unexpected ways that these explanatory aims influence other features of biology. I suggest five lessons for teaching about explanation in biology that follow from the considerations of this chapter.

1 Introduction

One of the central aims of science is explanation: scientists seek to uncover *why* things happen the way they do. In biology, explanations have been sought for why offspring generally have the same traits as their parents; for why one area has a greater variety of species than another; for why the patterns on land snails' shells show the type of variation they do; for why shark populations increased in the Adriatic Sea during World War I. Biologists have also sought to understand the process by which plant cells convert sunlight into nutrients; the particular genetic influences on human smoking behavior; and why male seahorses, not females, gestate seahorse embryos. All of these—and many, many more besides—are attempts to explain biological phenomena, phenomena ranging from generalized to highly specific and from subcellular to encompassing vast swaths of the Earth.

Accordingly, a primary project in philosophy of science is providing an account of the nature of explanation, of what it takes to explain something. For over a hundred years, philosophers of science have been generating competing accounts of explanation. These accounts provide criteria that are supposed to be essential to explanation, such that any successful explanation will meet those criteria. Accounts are motivated with reference to examples of successful scientific explanations. In the early to mid twentieth century, much of philosophy of science largely focused on physics. Since then, philosophical treatments of explanation have been both complicated and enriched by attention to explanatory strategies in biology.

In this chapter, I survey biology's influence on philosophical accounts of scientific explanation. This highlights important features of explanatory practice in biology (Section 2). I then discuss how the explanatory strategies utilized in biology are integral to making sense of other features of scientific practice, such as the continued neglect of some central causal factors (Section 3). Finally, I make explicit how these issues bear on biology education (Section 4).

2 Biology and Philosophical Accounts of Explanation

A traditional and historically influential view in philosophy of science is that scientific explanations are produced by deriving the phenomenon to be explained from laws of nature. This deductive-nomological (D-N) account suggests that explanations follow a simple pattern: a phenomenon is explained by a set of true sentences from which the phenomenon's description can be derived, and which contains at least one law of nature essential to the derivation (Hempel and

Oppenheim, 1948; Hempel, 1965).[1] For example, Mendel's law of independent assortment and the fact that two genes are located on different chromosomes explains why the different alleles for those two genes are paired with each other in approximately the same number of gametes: according to Mendel's law, each pairing is equally likely.

One feature of the D-N account of explanation that this example violates is that this strategy can only explain phenomena when scientific laws *guarantee* their occurrence. The phenomenon must follow deductively, as a matter of logic, from the law and conditions cited. A companion to the D-N account of explanation was thus developed to apply to statistical cases. This inductive-statistical (I-S) account holds that phenomena can also be explained using an applicable statistical law, so long as the law confers high probability on the phenomenon. Technically, my simple example of explaining using the law of independent assortment is an I-S explanation. Broadly, the idea behind the D-N and I-S approaches to explanation is that a phenomenon is explained by specifying how what we know about the world—our scientific laws—bears on the particular circumstances at hand, which renders the phenomenon expectable. Laws of nature and the circumstances guarantee or render highly probable the phenomenon to be explained.

The D-N and I-S approaches to explanation have largely fallen out of favor among philosophers in recent decades. One prominent criticism is that there seems to be an asymmetry in the explanatory value of derivations that satisfy the D-N conditions of explanation. Salmon (1989) employs the following example as an illustration. By deriving the length of a shadow from the height of a flagpole and the position of the sun, one explains the length of the shadow. But one can equally well derive the height of the flagpole from the length of the shadow and sun's position, and it seems this does nothing to explain the height of the flagpole. This and other criticisms are taken to show that derivation is not in itself sufficient for explanation.

Beyond the general difficulties with the D-N and I-S accounts, it seems that many biological explanations do not conform to this view of explanation. For one thing, some phenomena that are acknowledged to be improbable are nonetheless thought to be explained. For example, some genetic mutations are explained by oxidative damage, even though such mutations are rare and oxidants are frequently present. Additionally, there are many biological explanations in which laws, whether deterministic or statistical, seem to play little or no role (Hull, 1992). Why does sickle-cell disease result in anemia? The explanation will undoubtedly cite features of the abnormally rigid, sickled red blood cells found in those with sickle-cell disease. It would be at best strained to construe any element of the resulting explanation as a scientific law. Finally, there is plenty of uncertainty regarding even what should qualify as a biological law, and thus whether biology

[1] For the sake of simplicity, I use the word "phenomenon" throughout this chapter to stand in for various conceptions of the target of explanation: events or laws, propositions, explananda, etc. Such distinctions are not central to the aim of this chapter.

has many, or any, laws to offer (Ruse, 1970; Brandon, 1997; see Lange this volume). Whether Mendel's "law" of independent assortment, used in the example of D-N explanation above, would qualify as a scientific law is itself dubious (see Jamieson and Radick this volume; see Burian this volume).

Setting aside the difficulties with the requirement that any explanation cite a scientific law, as well as the requirement that any explanation confer a high probability on the explained phenomenon, the D-N and I-S approaches do align with some intuitions about what explanations should accomplish. This point was made by Friedman (1974) and Kitcher (1981; 1989). Friedman and Kitcher both argue that an explanation of a phenomenon "unifies" that phenomenon with other scientific beliefs in virtue of providing a pattern of argument from which all can be derived. According to this unification account, an explanation's value stems from its generality, simplicity, and cohesion, as these features together generate the power to unify disparate phenomena. Explanations that cite Mendel's law of independent assortment fare better on this account than the D-N account. Positing the independent assortment of genes (on different chromosomes) is a simple, cohesive explanation that is general enough to explain a variety of phenomena, ranging from a pea plant inheriting a parent's wrinkled peas but not the yellowness of its peas, to there being a 50% chance that a woman who carries the x-linked recessive gene for Duchenne muscular dystrophy has a son with the disease, regardless of what other traits he does or does not inherit (not on the X chromosome).

In contrast to the troubles encountered by the D-N and I-S accounts, explanatory practice in biology offers support for a different philosophical view of explanation, namely the causal account. On this view, a phenomenon is explained by the causal factors that brought it about (Scriven, 1962; Salmon, 1989, 1998; Woodward, 2003). This is a natural interpretation of, for example, evolutionary explanations that feature natural selection. The redshank sandpiper (*Tringatotanus*), a bird that feeds on worms in mudflats, exhibits a preference for eating large worms over small worms. This preference is explained by the fact that natural selection favors foraging habits that maximize energy intake; if large worms and small worms are both readily available, then a redshank sandpiper's energy intake is maximized when large worms are chosen, since they yield more ingested biomass (Goss-Custard, 1977). Notice, however, that although natural selection is an important cause of the sandpiper's evolved preference, selection does not *guarantee* that the preference will evolve. It is not the sole determiner, but one influence among many (Potochnik, 2010a).

Biology has also been used to motivate mechanistic accounts of explanation (Glennan, 1996; Machamer et al., 2000; Bechtel, 2005; 2006; see Laubichler this volume; see Bechtel this volume). Mechanisms are "entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions" (Machamer et al., 2000, p. 3). Explaining by citing a mechanism thus provides both causal and organizational information. A familiar mechanistic explanation in biology can be given for the organic compounds created via photosynthesis. This style of explanation would cite the initial presence of carbon dioxide and sunlight, then detail the successive reactions among the chemical compounds that eventuate in organic compounds and, as a byproduct, oxygen. Significant debate surrounds the question of how broadly this conception of explanation should be employed, for instance, whether natural selection should be considered a mechanism (Skipper and Millstein, 2005; Barros, 2008).

Further disagreements regard the proper scope and purpose of biology explanations. Some argue that many or all biology explanations will soon be replaced by explanations that feature molecular biology; this is a form of explanatory reductionism. In large part, this argument and its rebuttal have focused on whether explanations that feature molecular genetics will entirely replace classical genetics (Waters, 1990). One of the main arguments employed in defense of the explanatory value of classical genetics is that the explanations it provides are *general* in the right way to be maximally explanatory (Kitcher, 1984; Sterelny, 1996). Sober (1999) suggests a middle ground, according to which some explanations benefit from generality—they explain by lumping together all similar phenomena—whereas other explanations are designed to be highly specific—they explain by showing what exactly brought about the specific phenomenon, in this particular case.

This distinction between generally applicable explanations and those that track the exact process that brought about a particular instance of a phenomenon evokes another distinction that has been made in the philosophical literature on explanation. Some philosophers distinguish how-possibly explanations from how-actually explanations (Dray, 1957; Brandon, 1990). As the terminology suggests, a how-actually explanation tracks the actual causal process that brought about a phenomenon, whereas a how-possibly explanation outlines a process that *could have* (but may not in fact have) brought about a phenomenon. How-possibly explanation is one way to conceive of the role of explanations that involve claims not fully supported by evidence (Forber, 2010).

To summarize, it seems that some patterns of explanation in biology corroborate a causal understanding of explanation, while other patterns of explanation suggest that mechanisms, where they exist, are explanatory. Also, though the traditional philosophical idea that all explanations cite laws of nature is undermined by biology, some biology explanations nonetheless corroborate the idea that citing general law-like patterns is indeed explanatory. This is further complicated, however, to the extent that biology explanations vary in their portrayal of a pattern shared by many phenomena versus the specific details of a single phenomenon, and relatedly, how closely an explanation is supposed to mirror actual reality.

This variety suggests that it is not a simple matter to find a single principle underlying all explanations that fall within the purview of biology (let alone all explanations in all of science). This introduces the question of how to reconcile the different points that have been made about biological explanation, if indeed they should be reconciled. There are at least two types of responses one could have to this question. One response is to simply acknowledge that a broad range of explanatory styles is present in biology, and then to focus on accurately characterizing that range of styles and the relationships among them. This would be a pluralist approach to scientific explanation, for it would not attempt to reconcile divergent points about explanation in biology. The end result would be a catalogue of different approaches to explanation, with the hope that the approaches described together capture all of explanatory practice (Brigandt, 2012).

The habit in philosophy is to consider this sort of pluralism a position of last resort. Simply declaring that there are several approaches without rhyme or reason governing the selection among them should be avoided until all avenues of discovering common principles have been exhausted. The alternative is to try to accommodate the variety of explanatory practices found in biology, features currently captured by different accounts of scientific explanation. This may create the groundwork for a unitary account of biological explanation, in spite of the seeming diversity.

Indeed, various attempts to reconcile different insights into explanation have been made. The unification account is presented by Kitcher (1981, 1989) as a successor view to the D-N account, the basis of which is supposed to be in Hempel's own observations. Strevens (2004) articulates an account of explanation that assimilates the insights of a causal approach to explanation and a unification approach. In Strevens' view, an explanation cites causal information at a sufficiently general, yet cohesive, level of description. There is an array of views regarding the relationship between mechanistic explanation and causal explanation; Skipper and Millstein (2005) view them as competing options, whereas Craver (2007) suggests the mechanistic approach as a way to make sense of the explanatory role of causal relationships.

I will conclude this section with some of my own ideas regarding how to create a unitary account of biological explanation. In my view, a promising start is to base a unitary account of biological explanation on the idea that causal information is explanatory. A causal understanding of explanation, in one version or another, seems to have gained dominance in philosophy of science, especially in philosophy of biology. Yet research in biology amply demonstrates that most biological phenomena result from complex causal processes, with many factors combining and interacting at each step in the process. This renders impractical a simple causal approach to explanation, whereby to explain you simply cite all the causes. It also creates an opportunity to fill out a broadly causal approach to explanation in a way that accommodates other intuitions about biological explanation.

I suggest adopting an insight advocated by the unification account, Strevens' (2004, 2009) causal account, and many other philosophical accounts of explanation. This is the idea that *generality* benefits an explanation. Though proper laws of nature may be few and far between in biology, depicting causal patterns—that is, how certain types of causes tend to bring about certain types of effects, given other conditions—is a more modest way to generate explanations that showcase lawlike behavior. This motivates explanations that ignore some details in order to depict broad causal patterns (Potochnik, 2011).

One example of this feature of explanation is the difference between explanations for short-term and long-term evolutionary change. An evolutionary modeling approach termed optimality or optimization modeling accounts for the prevalence of a trait in a population by showing how that trait led to selective advantage (in the environment at hand). Several biologists have shown that this modeling approach can be expected to succeed only with *long-term* evolutionary change, that is, over a large number of generations (Hammerstein, 1996; Eshel et al., 1998), whereas a population genetic approach is required for generational evolutionary change. One might thus anticipate that, in virtue of the different causal patterns involved in short-term and long-term evolution, different explanations are warranted. I explore this difference between optimality explanations and population genetic explanations in (Potochnik, 2010a).

A similar contrast can be drawn between *microevolutionary* and *macroevolutionary* explanations. Microevolution is the evolutionary change within a population, whereas macroevolution is the evolution of species (or even larger clades). Sterelny (1996) argues that this is another instance where different types of phenomena warrant different types of explanations, explanations that vary as to their degree of generality. In his view, whether macroevolution requires a distinct type of explanation comes down to whether it is due to distinct causal influences acting on whole species or clades. This version of explanatory pluralism once again suggests attending to the sort of causal pattern embodied by a phenomenon.

Yet a complication is introduced by the point I made just above, that many biological phenomena result from exceedingly complex causal processes. Consider, for example, the causal processes involved in bringing about the long necks of giraffes. In no particular order, these include, at least, features of ancestral giraffes' environment, including the presence of nutritious leaf matter high up in tall trees; various genetic influences on giraffe morphology; developmental processes, including additional regulator genes, involved in giraffe neck-development; certain genetic mutations arising; competition for resources such that giraffes with a greater reach enjoyed increased rates of survival; and changes in developmental processes resulting in longer necks. All of this causal complexity means that different explanations may focus on different causal patterns. For instance, there may be one explanation of giraffe neck development and a different explanation of selection for lengthened giraffe necks. What causal pattern is explanatory, and thus what parts of the causal process should be mentioned, depends on what one might generally call the *context of explanation*. This is determined by the goals of the research program for which the explanation is generated. Recall from above the debate over reductionism, including whether biological explanations will ultimately all feature molecular biology. The current view is antireductionist, for it suggests that multiple, different explanations will continue to be valuable, insofar as each captures a different causal pattern (Potochnik, 2010b).

To summarize, my attempt to integrate different insights into explanation results in the view that biological explanations (1) give causal information, (2) in a way that depicts a broad causal pattern that is (3) explanatory given the particular research goals at hand. I more fully articulate and defend this view in (Potochnik, unpublished). This approach accommodates much of the diversity of views about biology explanations surveyed in this section, but it unites them into a single view. It also disputes or neglects some claims, such as the idea that some explanations benefit by maximizing their specificity (Sober, 1999), or the idea that explanations generally depict mechanisms. Finally, I must emphasize that my suggested account of explanation is of course one view among many, and the debate surrounding different philosophical views of scientific explanation, and explanation in biology, will not end anytime soon.

3 Explanation and Scientific Practice

In the previous section, we surveyed the range of styles of explanation found in biology and considered a few approaches to making sense of that diversity. Let us now set aside questions surrounding how biological explanations are formulated and focus instead on how the aims of explanation influence other features of scientific practice in biology. This will demonstrate how an accurate understanding of explanatory practice in biology contributes to an understanding of other characteristics of the field. In this section I will focus primarily on evolutionary biology, but I will also indicate points of contact and resonances with other areas of biology.

In contemporary evolutionary biology, genes are important. From the discovery of DNA, to the Human Genome Project, and most recently the Thousand Genome project, genetics—and especially molecular genetics—has received much attention both in biology and society at large. And genes are, of course, absolutely central to the evolutionary process. Though epigenetic inheritance is well documented (see Uller this volume), genetic inheritance remains central to most evolutionary processes (see Avise this volume).

In spite of all of this, many well-regarded models of evolutionary change ignore genes entirely. A prime example of this is evolutionary game theory. This modeling approach is applicable to the long-term evolution of traits with frequency-dependent fitness, i.e., when the fitness of a phenotypic trait depends upon the traits of others in the population.[2] Different phenotypes are represented as different strategies to playing a game, and their fitness is represented as the "payoffs" of those strategies. Evolutionary game theory is used to calculate the equilibrium point for distribution of phenotypes that would result if natural selection acted unimpeded on the population; there may be one such equilibrium, multiple, or none. For example, the vampire bat's behavioral trait of sharing hunting spoils with oth-

[2] A trait's fitness is a measure of the trait's relative contribution to organisms' ability to survive and reproduce. However, the concept of fitness is vexed; see Rosenberg and Bouchard (2010) for an overview of the difficulties.

er vampire bats is conceived of as a strategy, as is the behavior of not sharing. The first trait has a higher payoff—a greater fitness value—when other bats share food in return. Thus one observes reciprocal altruism in the form of food-sharing among vampire bats (Wilkinson, 1984).

Most evolutionary game theory models entirely ignore genetic inheritance. Some explicitly incorporate population genetics, featuring one- or at most two-locus inheritance, but this is uncommon, and even then the genetic dynamics are simplified to the point of unreality. This situation is puzzling: genes are acknowledged by all to be crucial causal influences on evolution, and yet they are ignored in many approaches to modeling evolution, with evolutionary game theory as a prime example.

This neglect of important influences is a feature of modeling approaches throughout biology. Population genetics and quantitative genetics both ignore the niceties of complex genetic influences on phenotypic traits, as well as ignoring the environmental sources of fitness upon which game theory focuses. Cutting-edge genetic research sets aside a host of non-genetic factors. For example, Amos et al. (2010) focus on the genetic influences on human smoking behavior, mentioning that of course there are many other causal influences on an individual's decision for or against smoking cigarettes. Models of development tend to ignore entirely evolutionary influences on traits. In recognition of this, Mayr (1961) distinguished between proximate (developmental) and ultimate (evolutionary) causes.[3]

This practice of continued neglect of central causal factors would be mysterious without attending to explanatory aims. Recall that in the previous section, I encouraged thinking of explanations as portraying causal patterns, and I pointed out that complex causal processes necessitate a choice of which causal pattern an explanation should feature. This offers a way to make sense of modeling approaches in biology continuing to neglect many causal influences, some of which are actually crucial to bringing about the phenomenon to be explained. A primary use of models in biology is to provide explanations. Causal factors, including some central ones, are neglected when those factors are not part of an explanation's focal causal pattern.

Neglecting causal factors makes a model more general in the following sense. A causal factor would be represented in a model by including an additional variable or parameter. By omitting that variable or parameter, the model simply says less about the world; it remains mute about that factor, including even whether it *is* a factor. Put another way, the model abstracts away from any causal factor it

[3] Mayr's distinction between proximate and ultimate causes can be construed as a distinction between explanations of *why* members of a population have some trait (evolutionary/ultimate causes) and explanations of *how* members of the population came to have that trait (proximate/developmental causes). This proximate/ultimate distinction has received a good amount of attention in philosophy of biology. Ariew (2003) reinterprets the distinction as distinguishing between dynamical versus statistical explanations. Laland et al. (2011) argue that Mayr's distinction fails because the types of causes distinguished are interrelated.

neglects; it does not represent anything with regard to the factor—not its presence, its value, nor its absence. For example, a population genetic model that does not employ a parameter for effective population size (N_e) is mute on whether and to what degree drift is a significant causal factor. This results in a model that is more abstract than if the neglected causal factor had been represented, and also more general, for the model applies to systems that vary with respect to the neglected causal factor. Continuing the example above, a population genetic model that does not represent drift is more abstract because of that omission. It is also more general, for it applies to genetic change in populations where the significance of drift varies. (Notice, however, that the fidelity of a model that omits N_e will be lower than that of a model that employs N_e whenever drift is a significant influence.)

Models of a phenomenon that represent just one applicable causal pattern and neglect other causal influences are sometimes simplified to the point of unreality. That is, sometimes a dummy variable or parameter is included in a model that no one expects to accurately represent the world. This is the strategic use of idealizations to ignore causal influences. For instance, population genetic models often assume that a population of organisms is infinite in size. This assumption allows the influence of genetic drift to be ignored. Similarly, evolutionary game theory models often simply assume that offspring resemble parents—that like begets like—thereby ignoring the complexities of systems of genetic inheritance. This is, then, an additional feature of biology that explanatory practice helps to make sense of. The aims of explanation account not only for the continued use of simplified, partial models, but even models that are *unrealistic* in many respects.

A variety of philosophers and biologists have appealed to the aims of explanations in order to account for the continued use of abstractions and idealizations in models. Levins (1966) introduced the idea that there are competing aims for models—accuracy, precision, and generality—and that some precision and accuracy may be traded off for a compensatory gain in generality. Weisberg (2006) argues that such a tradeoff is justified by the aim of using models to give explanations. Godfrey-Smith (2006) dubs the resulting way of doing science "model-based science". Finally, Wimsatt (1987) discusses the role of idealizations in particular (see Pennock this volume for considerations related to model-based reasoning).

Notice that, although generating explanations motivates the continuing importance of abstract and idealized models, this does not guarantee that all of biology functions this way. Though some precision and accuracy may be sacrificed to the end of building a general model, there may be situations where other tradeoffs are warranted. For instance, some explanations integrate more causal factors than others; an example is models that integrate both game theory and population genetics. Additionally, some models are used for purposes other than generating explanations of real-world phenomena; this is true of many models in theoretical population genetics. Finally, mathematical modeling may not be central to all fields of biology, for example, to physiology.

Setting aside the features of models, another feature of biological practice that explanatory practice helps account for is many biologists' total commitment to one or another methodological approach, and the intense disagreements that result. Proponents or critics of particular approaches are prone to making sweeping, ideologically loaded claims. Evolutionary game theory is a prime example here as well. The use of game theory in biology has been described as a "leap of faith" (Grafen, 1984) and a "worldview"(Brown, 2001) by its proponents, and criticized for the same reason by its detractors. Roughgarden (2009) criticizes sexual selection theory on the grounds that it is wrong about what is "basic to biological nature". Many similar sweeping claims can be found in other areas of biology.

That differences in approach are frequently construed as a matter of fundamentally opposed ideologies suggests that different research programs are incompatible, insofar as they are committed to different views of biological reality. But in my view, such debates are better understood as arising not from different theoretical commitments at all, but commitments to different explanatory projects. As we have discussed here, models employ abstractions and idealizations in order to focus on targeted features of a phenomenon, at the expense of ignoring or misrepresenting other features. Different modeling approaches thus can seem to be incompatible, for they employ different parameters/variables and opposed assumptions. However, the exact opposite is true. The limitations of such models make the use of multiple approaches essential. Thus, despite the ideologically laden rhetoric biologists often employ, the question to ask about apparently competing modeling approaches is not which grounds a more successful worldview, but which method better serves one's present research aims. And research aims are in large part determined by explanatory goals, that is, by what phenomena and causal patterns that influence them are of primary interest (Brigandt, forthcoming). To return to one of the examples above, evolutionary game theorists focus on the role of natural selection in evolution and set aside non-selective influences, either by ignoring them entirely or by accommodating their influence in model parameters. This need not be the result of a *worldview*—at this point, biologists agree that non-selective influences can crucially shape the evolutionary process. The use of evolutionary game theory is instead best defended on the basis of the aim of explaining selection's influence on evolutionary phenomena.

Though I have argued that ideological positions are not often warranted in biology, I also suspect that the tendency of biologists to adopt such ideological positions indicates something important about biological phenomena. Let us ask: what enables simple differences of explanatory focus to be interpreted as wholly different worldviews? That there are such entrenched proponents and opponents to different approaches indicates that a variety of approaches have some purchase on the evolutionary process. In my view, this reflects the complex causal processes at work in biological phenomena, and the endless variety in how causal factors combine and interact. This further corroborates the suggestion made in Section 2 that a philosophical account of biological explanation must accommodate variety in explanations that arise from focusing on different causal patterns.

Put most broadly, explanatory aims account for the continued diversity of approaches in biology, as well as biologists' tendencies to adopt one or a few approaches as their guiding principle/worldview/etc. Explanatory aims also account for why grappling with exceedingly complex causal processes often does not motivate increasingly complex models. Explanations focus on just one among many causal patterns that govern a phenomenon, and this is accomplished by models that abstract and idealize away from other causal factors in order to represent the focal causal pattern. Sometimes the resulting model is simplified to the point of unreality, yet it can still do its job of representing a causal pattern important to the occurrence of the phenomenon to be explained.

4 Conclusion: Teaching about Biological Explanation

So far in this chapter, we have considered what philosophical accounts of scientific explanation can tell us about biology explanation, and how explanatory practice in biology has influenced—and should influence—general accounts of explanation. We have also explored some features of the field of biology that only make sense in light of the aim of generating explanations and particular explanatory strategies. By means of all of this, I hope to have demonstrated that approaches to biological explanation and how they influence scientific practice are important to biology education. In this section I will develop five suggestions for particular ways in which biology education should attend to issues related to scientific explanation. Along the way I will suggest a few advantages that stand to be gained from implementing these suggestions.

4.1 *Suggestion 1: Do not overly emphasize laws when thinking about biology explanations*

It is to be expected that discussions in biology will include reference to "laws." Calling something a law is a way to express the idea that certain phenomena proceed according to a more-or-less lawlike pattern. For instance, Mendel's Laws capture some regularities pertaining to genetic transmission. Such references to laws may, for the most part, reasonably set aside the question raised in Section 2 regarding whether and to what degree there are laws of biology. In discussions focused on biological phenomena and not intended to describe the field of biology, the term "law" can simply be used loosely. Hence we continue to refer to Mendel's Laws, even though there are clear exceptions to these laws—exceptions that generate their own distinct lawlike patterns.

What should be avoided is taking too seriously references to biological laws. From the fact that there are references to laws within biology, it should not be inferred that the field of biology progresses via the discovery of new laws (see Lange this volume for an examination of what would be required for there to be biological laws.) Similarly, it should not be inferred that finding a law is needed in order to explain a phenomenon. It has been thoroughly demonstrated in this chapter that many explanatory projects in biology do not rely on laws. This means that, in biology education, accepted explanations should not be portrayed as citing laws, especially when such a portrayal is somewhat forced. Encountering a range of biological explanations that resist simplification to laws will help prepare students for the vast range of work in biology to which laws are minimally relevant or not relevant at all.

4.2 *Suggestion 2: Explicitly motivate forms of explanation that are common in biology*

Following on the heels of the first suggestion, the idea here is that biology education is enriched by explicitly attending to features of biological explanations that may seem strange to outsiders, but are in fact quite common explanatory strategies in biology. This involves more than discussing particular explanations, and resisting the temptation to construe them as based on laws. The suggestion additionally involves inviting students to think—critically but openly—about *how* various explanations succeed. I will provide three brief illustrations here, though there are almost certainly additional forms of explanation across biology that deserve such focus.

Recall from above that traditional optimality explanations account for the prevalence of a trait in a population by showing how that trait led to selective advantage (in the environment at hand). Optimality explanations may be understood as a type of functional explanation: the presence of a trait is explained according to the role it plays for an organism. In evolutionary contexts, this style of explanation is made possible by the assumption that natural selection promotes traits that increase fitness. Thus the fitness-conferring role of a trait is a *causal influence* on the trait's propagation. This is a helpful lens through which to view optimality explanations, for it at once showcases what is fitting about this style of explanation, and also its limitations, or what may be problematic.

Evolutionary game theory models provide an explanatory strategy closely related to that of optimality models. However, the emphasis is shifted from the selective advantage of a trait to points of stability in the shifting proportions of a range of trait values. One prominent approach to evolutionary game theory is fruitfully considered as a type of equilibrium explanation.[4] Equilibrium explanations are, in my view, a type of broadly causal explanations, for they capture some features of causal patterns (cf. Kuorikoski, 2007). Yet equilibrium explanations differ from traditional causal explanations, for they entirely omit any information about the causal process that led to the equilibrium point.

Another, very different type of explanation is mechanistic explanation, viz., explaining a phenomenon as the result of a structured series of causal steps. An example is the molecular explanation of photosynthesis, which traces the series of chemical transformations among macromolecules by which carbon dioxide and sunlight are converted into sugars and other organic compounds. In some regards, this form of explanation is the complete opposite of functional and equilibrium forms of explanation. Whereas equilibrium and functional explanations cite endpoints and neglect processes, mechanistic explanations instead detail the exact steps by which a phenomenon proceeds.

There are, of course, many unresolved questions about the relationship among these forms of explanation and the relative value of each. Some considerations were introduced in Section 2, including one possible way to assimilate all forms of biological explanation. Regardless of the theoretical questions about their relationship, though, each form of explanation deserves explicit attention in biology education. Implementing this suggestion will facilitate a broad education in the range of explanatory projects in biology. It will also help spur students to explicitly consider what form of explanation is generated—or attempted—in different and novel research programs. This is facilitated by introducing forms of explanation as tentative, susceptible to reinterpretation or the revision of methodology (see the next suggestion for more on this idea).

4.3 *Suggestion 3: Resist the temptation to simplify the diversity of approaches in biology and their apparent incompatibility*

This chapter has only surveyed a small part of the astounding variety of explanatory projects in biology. This variety of explanatory projects is not surprising, given the vast array of types of phenomena under investigation in different subfields of biology. Some considerations from Section 2, and subsequently suggestion 2 above, suggest that there may even be different *strategies* of explanations in biology, viz., explanations with wholly different aims and attributes.

One might be tempted to simplify this picture in the classroom. Introducing a large variety of explanatory projects can undermine generalizations that can be es-

[4] This approach analyzes games for points of stability, e.g., evolutionary stable strategies (Maynard Smith and Price, 1973). A different approach to evolutionary game theory instead specifies population dynamics, e.g., replicator dynamics, and thus results in dynamical models.

pecially useful as heuristics for students. It also takes up additional class time that could be used in other valuable ways. Yet ignoring—or not focusing upon—the immense variety of explanatory projects and explanatory strategies in biology trains students to expect the field of biology to proceed in lockstep, and may result in later suspicion regarding unfamiliar projects or opposed methodology. Exposure to variety should have the opposite effect. This instead facilitates a more nuanced appreciation for the vast range of causal influences and interactions within the purview of biology, and the diverse routes to understanding found throughout the field. For example, recall from above Mayr's distinction between proximate (developmental) and ultimate (evolutionary) explanations. Kampourakis and Zogza (2009) employed that distinction to help students clarify for themselves the elements of evolutionary explanations. In this case, emphasizing the distinction between *why* members of a population have some trait and *how* they came to have the trait leads students to the recognition that evolutionary explanations and developmental explanations contain distinct elements, that they play distinct roles—that is, that one does not preclude the other, and that there are patterns in what sort of causal information is provided by each. Notice that this educational role can be played by Mayr's distinction in spite of criticisms of that distinction, viz., regardless of whether the types of causes in question are in fact often interrelated or the precise construal of the type of explanatory difference.

Teaching the diversity of explanatory projects and strategies and how those have changed over time should also engender in students an expectation that accepted explanatory strategies change alongside accepted knowledge in the field. For instance, optimal foraging theory was initially met with suspicion, for it was thought that this required too much psychological sophistication of cognitively simple animals. Since, it has been clarified that optimal foraging explanations are evolutionary explanations, with no assumptions made about the means by which organisms' foraging behavior develops. Such shifts in accepted explanatory strategies are a central example of how methodological norms, and not just stores of knowledge, progress in biology. As such, it helps prepare students to think explicitly and critically about methodology, and to see explanatory practice as a central component of the field of biology.

4.4 *Suggestion 4: Explicitly consider the role of models—partial, unrealistic representation*

Another move that facilitates the explicit and critical analysis of methodology is a teaching focus on the role of models in biology and how that role varies among subfields and research programs. I suggested above that there is no reason to assume that laws are central to biology. In contrast to the circumstances regarding laws, it is clear that constructing models—whether mathematical, physical, or computer—is an important component of many projects in biology. Evolutionary game theory and population genetic models, predator-prey models, species abundance models, model organisms, agent-based models... the list could go on much longer.

Explicitly addressing the role of models in biology should involve, at least, considering the purposes to which models are put, and how those purposes and the features of models vary among different subfields and research programs. There may or may not be much found to be common among mathematical models, physical models, and computer simulations. Another prime emphasis should be the mechanics of abstraction and idealization, and the purposes to which these are put. As we saw in Section 3, the continued importance of simplified models of complex phenomena is due, at least in part, to aims of biological explanations. An investigation of the prominent methodological role of models will thus both necessitate and further investigations of the role of explanation in biology.

4.5 *Suggestion 5: Emphasize methodological differences over seemingly ideological differences; teach that a plurality of approaches is here to stay*

This suggestion takes off from the considerations introduced toward the end of Section 3. There I argued that a range of issues on which biologists have taken ideological positions—declaring that a research program is the basis of a successful "worldview," or should be taken on faith (or avoided for that reason), etc.—are more profitably considered to be methodological differences. Commitments to different explanatory projects can lead to the endorsement of different background assumptions, abstractions, and idealizations, and hence differing views about the well-foundedness of various modeling approaches. For instance, advocates of evolutionary developmental biology (or "evo-devo"), the subfield of biology devoted to the evolution of developmental processes, view the field as a corrective to traditional evolutionary biology. Yet some statements of evo-devo's role go too far in the opposite direction. According to Müller (2007), the "explanatory weight" belongs to development, not evolution, for evolving developmental systems are "*the* causal basis for phenotypic form" (emphasis added). Evo-devo draws attention to one set of causal influences, and how they interact with selection. This likely is an important, even crucial, part of the evolutionary story, but it does not undermine the importance of evolution. Emphasis in biology education on how methodological differences arise in the field of biology would help the next generation of biologists avoid such arguments over the primacy of one or another approach, refocusing attention on careful development and critique of methodology, etc.

The suggestion to emphasize methodological differences instead of ideological positions is an outgrowth of the first four suggestions made here. Those suggestions began with the idea that a monolithic picture of law-based explanation should be avoided (Suggestion 1), substituting in its place a critical analysis of the range of common forms of explanation in biology (Suggestion 2). That analysis should resist the temptation to simplify the diversity of approaches to explanations or to minimize differences or seeming incompatibilities (Suggestion 3). Careful attention to the features of biological explanations benefits from and reinforces consideration of the role of models in biology and their relationship to explanations (Suggestion 4). All of this arms the student of biology to interpret debates among biologists with an eye to the diversity of projects, and the diversity of methods they motivate (Suggestion 5). A consequence of implementing these components in biology education is the lesson that a plurality of methods in biology is here to stay.

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