

Philosophy of Biology

Ingo Brigandt

Philosophical questions about biology have been addressed by philosophers and scientists for centuries. Yet as a genuine discipline within philosophy, philosophy of biology started to emerge in the 1970s (Byron, 2007). One motivation for this was the fact that much of traditional philosophy of science—growing out of logical positivism—focused on physics as the exemplar of science. Thereby past philosophy of science simply assumed that accounts of confirmation, theory structure, laws, and explanation would apply to biology as well, creating biased or inadequate views about the nature of science. But rather than directly addressing issues in general philosophy of science in the context of biology, philosophers of biology have for the most part engaged in questions that originate from within biology, pertaining to concepts from a specific biological field or to phenomena from a particular biological domain. Some of these questions have been raised by biologists, resulting in debate and fruitful interaction among scientists and philosophers. This interdisciplinary practice of contemporary philosophy of biology is illustrated by the International Society for the History, Philosophy, and the Social Studies of Biology, and by philosophical journals to which many scientists contribute. Most questions in philosophy of biology are epistemological questions, e.g., about the character of particular biological explanations, models, and concepts, and are sometimes combined with issues about scientific method and practice. Yet these issues also tap into metaphysical considerations, at least insofar as they hinge on facts about the biological world.

Originally, most discussions in philosophy of biology centred on issues in evolutionary biology and systematics. For instance, the units of selection debate ponders which kind of entity

is the fundamental player driving evolutionary change—the individual, the group of individuals, the gene, or even the species. Arising out of disputes among evolutionary biologists, the epistemological question is how genuine explanations in terms of natural selection actually work. The related metaphysical issue is at what level of biological organization evolutionary causation by selection takes place, and philosophers have offered several clarifications to these biological questions. Given the many statistical models of evolutionary theory, philosophical interpretations of the nature and role of probabilistic factors (e.g. genetic drift) are put forward. The adaptationism debate concerns the circumstances in which phenotypic traits of species are best explained with exclusive reference to natural selection. In this context, attempts by sociobiologists and evolutionary psychologists at explaining the evolution of human behavioural and cognitive traits have been criticized by philosophers as falling short of the standards for acceptable evolutionary explanations. Philosophical studies of the meaning of ‘biological function’ discuss what the ascription of functions to biological traits involves (occasionally, but not always a reference to a trait’s selection history), and whether functional and teleological explanations are distinct from causal explanations.

In addition to the traditional philosophical questions pertaining to evolution (which are still live issues), nowadays molecular and experimental biology are of increasing philosophical focus. This philosophical trend is largely due to the rise of genetics and molecular biology, with such biological advances prompting the philosophical debate as to whether classical genetics and possibly other biological disciplines can be reduced to molecular biology. It has also been argued that the notion of ‘genetic information’ is empirically misguided or of no explanatory relevance in biology. Apart from the role of genes and non-genetic factors in explanations of the development of organismal traits, developmental biology has recently become a biological field subject to philosophical interest, as a link to evolutionary issues has been created by the recent

emergence of evolutionary developmental biology. With the scientific advance and societal importance of the life sciences and modern biomedical sciences, contemporary philosophers of biology also address issues in philosophy of medicine. Whereas views about the biological world have traditionally been based on higher animals (and plants), very recent scientific findings about microorganisms (largely driven by their now recognized medical relevance) may soon lead to challenges for philosophical views of biological individuality, social organization, the notion of species, and the idea of a universal tree of life.

It is beyond the scope of any single article to provide a review of the major issues and positions in philosophy of biology (for overviews see Hull, 1974; Sober, 1993; Griffiths and Sterelny, 1999; Hull and Ruse, 2007). Instead, the aim of this chapter is to lay out what implications biology has for some issues in general philosophy of science, including natural kinds, conceptual change, discovery and confirmation, explanation and reduction, and naturalism. Some of these offer additions and corrections to general metaphysical, semantic and epistemological views, and illustrate fruitful ways of conducting philosophical investigations that go beyond the practice of most of general philosophy (as the section on ‘Naturalism’ discusses).

Natural kinds

A few decades ago, the notion of natural kinds gained prominence in philosophy, in particular in the context of the causal theory of reference (Putnam, 1975) and rigid designation across possible world (Kripke, 1980). Ever since, it has enjoyed widespread acceptance, particularly in metaphysics. However, while philosophers not acquainted with the philosophy of biology still take species and higher taxa (e.g. vertebrates) to be a prime example of natural kinds, in the 1970s the biologist Michael Ghiselin (1974) and the philosopher David Hull (1978) argued that

species are not natural kinds. Instead, a particular species is an individual, a whole having the organisms of that species as its parts. This position has been extremely influential among biologists and philosophers of biology. Recently, following Richard Boyd (1999), some philosophers have put forward a revised notion of natural kinds that is claimed to apply to species. As a result, in contemporary philosophy of biology there are diverging views about which of the various biological things are natural kinds, what notion of 'natural kind' is appropriate for biological kinds, and how biological kinds relate to kinds studied by other sciences.

Whereas in a nominal kind several objects are grouped together by mere human convention, the idea of a natural kind is that there are groupings of objects that conform to the objective structure of the world (Bird and Tobin, 2009). The traditional notion of natural kinds was closely tied to kinds in physics and chemistry. It assumes that a kind is defined by a property called an 'essence', which has two functions. First, the essence determines the metaphysical identity of the kind. An object belongs to the kind if and only if the object possesses the essence. Second, the essence causally brings about the various properties characteristic of that kind, grounding the explanatory importance of natural kinds. For instance, the essence of oxygen is its atomic structure (including having eight protons and electrons). This atomic structure explains various physical and chemical properties of oxygen, in particular which compounds it can form and how it behaves in chemical reactions. Typically, essences have been taken to be intrinsic (internal) properties, as the example of chemical elements illustrates.

But it is easy to see that on this construal species cannot be natural kinds. For species are able to undergo unlimited evolutionary change. Whatever intrinsic property of an organism one chooses, be it a particular phenotypic feature or a genetic property, while many organisms existing at a point in time may share this internal property, future members of this species may

not. Likewise, applying the traditional view of natural kinds to species does not do justice to biological variation. While acknowledging differences among species members, the so-called essentialism still assumes that there is a natural biological state of the species governing all its members (Sober, 1980). The deviation of individuals from this alleged natural state is seen as being due to unusual intervening factors (e.g. environmental influences), so that the natural state (species essence) is seen as real, and any variation is explained away as an accident. The empirically adequate picture, in contrast, is that variation across individuals is maintained and created by biological mechanisms and is a feature of major scientific importance.

Arguing that species are not natural kinds, Ghiselin (1974) and Hull (1978) suggested that every species is an individual. Just like an organism is composed of cells, a species is an individual made up of organisms. A species does not have members as a set, class or kind does; instead, a species is a whole that has various organisms as its mereological parts. The motivation for this position is that an individual is precisely the metaphysical thing that is able to undergo change. An individual exists in a certain period of time only, being present at specific spatial locations at any point in time. An individual can substantially change across time; and similarity among its mereological parts is not required of an individual, in contrast to the view that the members of natural kinds are identical in many properties. In analogy to this, a species comes into being at a specific point in time, inhabits concrete locations, undergoes evolutionary modification, and goes extinct.

The view that species are individuals became the dominant view among philosophers of biology and in particular biologists (Ereshefsky, 2007). But recently Richard Boyd (1999) developed a revised notion of natural kinds that is designed to capture kinds as found in biology and the social sciences; and several philosophers and handful of biologists have picked up on it (Wilson *et al.*, in press; Rieppel, 2008). On this approach, a natural kind is a so-called

homeostatic property cluster (HPC). First, the major assumption is that a natural kind is not defined by a simple property that all kind members share (an essence). Instead, a kind is characterized by a cluster of many properties that are more or less correlated, where a kind member need not possess all of these properties, and none of the properties is shared by all kind members. In fact, exhibiting a certain kind of variation can be characteristic for being a certain biological kind, and such a correlation and variation structure is in need of explanation (Wilson *et al.*, in press). The correlation of properties is not accidental, but due to some causal features (dubbed ‘homeostatic mechanisms’). For this reason, the grouping of the members into a kind answers to features existing in nature, so it is a natural rather than a nominal kind. The statistical correlations or causal relations among the properties of the cluster make it possible for the kind to figure in scientific induction and explanation.

Second, the HPC construal of kinds explicitly maintains that properties of the cluster characterizing a natural kind need not be intrinsic, but may well be relational properties. For instance, a higher taxon (e.g. mammals) includes those species that are descended from a founding species, and having a certain ancestry is an extrinsic property of a species. Several species can share this relational property of having the same ancestry while differing in various (intrinsic) properties. Apart from common ancestry, the identity of a species may be defined by the ability of individuals to interbreed, which is also a relational property (of an individual) consistent with evolutionary change. As a result, historical entities such as species and higher taxa can be natural kinds, assuming that the identity of the latter is at least partially characterized by relational properties (Griffiths, 1999).

These developments in philosophy of biology have several implications for theorizing about natural kinds in general. First, accounts that species are individuals pointed to serious drawbacks of traditional, essentialist conceptions of natural kinds, and have offered a whole new way of

thinking about biological entities. In addition, the HPC construal of kinds developed a revised and novel notion of natural kinds, motivated by a naturalism according to which philosophical notions should be tied to scientific practice, in this case kinds as they occur in biology. While the individuals vs. kinds debate focused on species and higher taxa, the HPC approach has broadened this scope by considering and attempting to capture many other putative biological kinds. In fact, Boyd developed the HPC account to likewise include kinds from the social sciences. Kinds are studied by different scientific disciplines, and there may well be different types of natural kinds, a diversity to which philosophical theories should be sensitive. It has also been suggested that some things (e.g. species) can at the same time be an individual and a natural kind (Dupré, 1999; LaPorte, 2004; Brigandt, 2009), offering new metaphysical possibilities and pointing to problematic philosophical dichotomies.

Second, the HPC approach has highlighted the relevance of relational properties. Samir Okasha (2002) acknowledges that relational properties often individuate biological kinds (individuation being one function of traditional essences), but he claims that relational properties do not support biological explanations (in contrast to the second function of traditional essences). However, relational properties are in fact an important ingredient in explanations in biology and the social sciences (Brigandt, 2009). Equations in ecology and economics explain dynamic change based on the existence of stable relations among some entities. More generally, while the causal capacities of biological entities (including molecular entities such as genes) are partially based on their internal structure, these causal capacities obtain only in certain biological contexts or given a suitable relation with other biological entities. Many causal capacities being non-intrinsic properties, biological explanations have to appeal to relational properties as well. (Biologists arguing against some versions of reductionism have always emphasized the

explanatory relevance of the structured contexts in which some entities occur [Brigandt and Love, 2008].)

Finally, while proponents of the view that species are individuals have defended it by metaphysical arguments (Hull, 1978; Ereshefsky, 2007), the HPC approach highlights epistemological considerations. For a natural kind is a grouping of objects that—despite the heterogeneity among the members of a biological kind—underwrites scientific generalization and explanation (thereby ‘accommodating’ scientific demands, as put by Boyd, 1999). More generally, any kind of representation scheme used by scientists (be it grouping objects into kinds, be it considering objects as part of an enduring individual) is used to meet certain epistemic purposes such as making particular inductive inferences or putting forward certain explanations. Philosophical accounts of the metaphysical nature of scientific entities have to pay attention to the epistemological reasons that make scientists refer to these (rather than other) entities and use them successfully in their theorizing by representing them in a certain way (Brigandt, 2009; Love, 2009). Different representations and classifications are used in different scientific contexts, resulting in the philosophically relevant fact that the totality of kind concepts and classification schemes used by biologists cross-classify nature (Dupré, 1993).

Conceptual change

Recent philosophical accounts of conceptual change have often been developed as a reply to the incommensurability challenge. Thomas Kuhn (1962) argued that the same term can be used with radically different (incommensurable) meanings in two paradigms (different theoretical frameworks), so that effective communication across paradigms and a rational choice of one such theory over the other is impossible. Paul Feyerabend (1970) claimed that the content of two

theories containing incommensurable concepts cannot be compared. The standard reply to the incommensurability challenge has been to focus on the reference of scientific terms (Putnam, 1975; Fine, 1975; Devitt, 1979). For even if a term is used with different meanings in two theories, the term may nonetheless refer to the same entity across these theories, so that the theories can potentially make conflicting claims about this common referent and are thus comparable. The causal theory of reference provided an explanation of how stable reference despite substantially different theoretical views about the referent is possible (Sankey, 1994). According to this theory, a term's reference is not fixed by (potentially false) descriptions of the referent, but a term is introduced by causal interaction with the referent and refers to that natural kind thusly picked out (so that the structure of the world plays a part in reference determination).

Some cases from the philosophy of biology offer a broader perspective for general discussions of conceptual change. With the advent of evolutionary theory, biological views about the nature of species clearly changed. However, given that Darwin could communicate his arguments to his contemporaries, philosophers have questioned whether the pre-evolutionary and the Darwinian conception of species are incommensurable concepts and whether they are even different concepts at all (Beatty, 1986). Thus, the question is how these two conceptions of species are related, whether they are distinct concepts, and in either case how to make room for some conceptual continuity despite theoretical change. Moreover, nowadays different species definitions are used by biologists (Mayden, 1997 lists 22 major definitions), and philosophers typically assume that many of them are indeed distinct concepts. One species concept considers those organisms that can interbreed with each other to be of the same species. Other species concepts focus on considerations of common ancestry and phylogenetic lineages, and still other use ecological criteria to delineate species. Not only do these concepts offer different criteria of what a species is, but they also lead to different classifications of individuals into species, so that

these concepts differ in their extensions / reference. Most philosophers and biologists endorse a pluralism about species concepts, i.e., the idea that there is not one single true species concepts (yet to be found or agreed upon), but that biology needs a multitude of different species concepts (Dupré, 1999; Ereshefsky, 1992; Kitcher, 1984b; Wheeler and Meier, 2000). The justification is that each species concept picks out some causal factors that influence the formation of partially distinct groups of organisms and that different species concepts are needed for different scientific purposes or in different biological disciplines. This situation raises several philosophical questions. How are these different definitions of species related? Arguably the fact that the term ‘species’ is used in many different ways does not lead to substantial problems in communication among scientists (Kitcher, 1984b), but a philosophical analysis of this issue is needed. Does the context of use determine which particular species concept is referred to on a certain use of ‘species’ (so that no ambiguity arises), or is there some ambiguity that does not matter much as some of the species concepts overlap in their intension and extension?

A case that is currently subject to extensive philosophical debate is the gene concept. With the scientifically important advent of molecular genetics, semantic change resulted, with the classical gene concept and the molecular gene concept typically being considered different concepts. A philosophical question is how the molecular concept could rationally grow out of the classical gene concept (Kitcher, 1982), where it has to be taken into account that the molecular concept neither replaced nor reduced the classical concept, and both continue to be used in tandem (Weber, 2005). Moreover, even reference changed in this historical period (Burian *et al.*, 1996), as among other things both gene concepts individuate genes differently and thus differ in their extensions. Marcel Weber argues that geneticists have tracked not one but several (overlapping yet distinct) kinds by the term ‘gene’, and uses the notion of ‘floating reference’ for the idea that the reference of the gene concept has changed constantly, though in a gradual

fashion, suggesting that “this floating of the term’s reference seems not to have diminished its theoretical importance or practical usefulness” (Weber, 2005, p. 224).

In addition to conceptual change in the course of history, nowadays the molecular gene concept is used in quite different ways by different types of molecular biologists, resulting in the meaning and reference of the term ‘gene’ sometimes varying from context to context (Beurton *et al.*, 2000; Brigandt, *in press-b*; Falk, 1986; Stotz and Griffiths, 2004). This situation is due to findings in molecular genetics and recently in genomics. A gene is not a continuous stretch of DNA coding for one product, where all genes have the same structural features (which would permit a unique definition of what a gene is). Instead, it turned out that many different kinds of (structurally characterized) DNA segments are involved in the production of RNA and polypeptides. One genetic segment can code for many products, and several separate genetic segments may be needed for a single product. In the latter case some biologists consider these separate DNA segments as different genes and others as one gene physically spread out within the genome. As a result, philosophers discuss how to study and characterize the current semantic variation surrounding the molecular gene concept. While Moss (2003) argues that there are two distinct gene concepts used in molecular biology and Griffiths and Stotz (2007) opt for three basic gene concepts, Waters (2000) controversially maintains that one shared molecular gene concept underlies all varying uses. Since apart from ‘gene’ nowadays further terms are used to refer to DNA elements involved in the coding for gene products (e.g., ‘transcription unit’, ‘exon’), another possible, though very unconventional option is to suggest that in the future the term ‘gene’ will be or should be replaced by a plurality of other terms (Kitcher, 1992).

These considerations from recent philosophy of biology have implications for general philosophical theories of conceptual change. Many traditional accounts have focused on reference to rebut the incommensurability challenge. However, even if a theory of reference

ensures that a scientific term has the same referent in two theories (so that they can make conflicting claims), given that the term may be used with a different meaning in each of these theories the notion of reference alone does not solve Kuhn's original challenge—how communication across different approaches and rational theory choice is possible despite variation in meaning. Several accounts of conceptual change have already acknowledged that the historical change in the meaning of terms is to be philosophically understood (e.g., Kitcher, 1982; Nersessian, 1984). Cases from biology like the change of the gene concept show that scientists confidently discard previous definitions they used to put forward, and philosophical accounts have to explain why it can be rational for scientists to modify a term's definition. And even the very reference of a biological term can be subject to change, so that a philosophical approach that assumes stability of reference cannot account for this aspect of conceptual change.

Furthermore, in addition to diachronic change, terms such as 'species' and 'gene' show that even at one point in history both the meaning and the reference of a scientific term can vary across uses. (Other possible such cases are the homology concept [Brigandt, 2003] and the notion of a stem cell [Shostak, 2006].) Semantic variation raises several questions to be addressed (Brigandt, in press-b). What are the reasons for variation in a particular term's usage? How are different uses of a term related, and what structure does the semantic variation have—do different biological subdisciplines or approaches each favour a different use, can one and the same scientists use the term differently in different research contexts? To which extent does semantic variation hamper communication? While in his early work Kuhn assumed that differences in meaning are intrinsically problematic, some instances of semantic variation may in fact be beneficial to scientific practice, e.g., by promoting a division of semantic labour (Wilson, 2006). To the extent that semantic variation is compatible with successful communication, why is this possible and when and how does semantic variation support scientific practice?

Discovery and confirmation

Accounts of confirmation in general philosophy of science typically attempt to advance a theory that is as universal as possible and covers all scientific fields and empirical domains. Assuming that confirmation in science is inductive, such a logic of induction describes the form of the confirmation relation between evidence statements and theory, abstracting away from the particular empirical content involved in a particular instance of confirmation—just like deductive logic determines whether premisses entail the conclusion in terms of the form but not of the content of the statements involved. However, recently the philosopher of physics John Norton (2003) pointed out that the search for formal schemata of inductive inference has proven largely futile. Reviewing different kinds of inductive schemes and their known flaws (such as inductive generalization, hypothetico-deductive accounts including error statistics, abduction, and Bayesianism), he concludes that there is a strong trade off between generality and inductive strength: schemas of induction that are of universal scope are either unreliable (conclusion is not supported by premisses in too many instances) or circular (and thus useless for the purposes of inductive as ampliative inference). His diagnosis is that we have been misled by deductive logic in thinking that there are universal schemes of inductive inference.

In contrast, Norton proposes what he calls a ‘material theory’ of induction, according to which induction is grounded not in universal schemas but rather in empirical matters of fact. To illustrate this with a simple example (of mine), formal accounts of analogical reasoning as a type of induction construe an inference from an object a having property P to object b having this property as justified in case objects a and b are similar in that they share properties Q₁, Q₂, ... Such a formal account has to acknowledge that the inductive inference Pa |— Pb is justified only insofar as the degree of similarity between objects a and b is significant and the properties Q_i are

relevant for the property P to be projected (Salmon, 2002). However, what is relevant or significant crucially depends on features of the particular case, and thus the plausibility of the inference is essentially contingent on empirical information (matters of fact), while the inference's logical form is actually quite insignificant for its justification. On Norton's account, new empirical knowledge generates new inferential power (by providing additional matters of fact), but not by yielding novel abstract schemes of inference. As matters of fact relevant for an induction hold only in certain scientific domains, scientific induction is local. Individual instances of induction may be too domain-specific to be categorized together with other inductions under a general type of induction.

While Norton's proposal is motivated by unsuccessful attempts to put forward formal schemata of induction in general philosophy of science, recent philosophy of biology provides more direct support for the idea that confirmation in science is not based on universal schemes, but domain-restricted and contingent upon specific empirical content. For instance, Marcel Weber (2005, Ch. 4-5) offers a detailed discussion of confirmation in experimental biology. He scrutinizes the oxidative phosphorylation controversy, a debate in biochemistry that started in 1961 with two rival accounts but could not be settled until 1977. Weber rejects Bayesian confirmation theory, arguing that in this scientific case it would have made erroneous normative suggestions about theory acceptance. (On a Bayesian analysis the true biochemical theory should have been accepted too early—in 1966, at a point where the total evidence did not favour one hypothesis over the other.) Deborah Mayo's (1996) error-statistical theory aligns with experimental biology better than Bayesianism, as her approach does not assume that scientific inference solely consists of a confirmation relation between theory and evidence and it instead captures the piecemeal production of evidence and scientists' attempts to control for error. However, Weber argues that a statistical notion of error cannot apply to experimental biology, as

the relevant reference class for an experiment is unclear, so that no error frequencies can be assigned. Based on the practice of experimental biology, he concludes that epistemic norms used by biologists are not universal rules (as in Bayesianism and error statistics), but domain-specific, empirical considerations. In the context of evolutionary biology, Elliott Sober (2008) argues for a pluralism about scientific inference, where different inference methods are appropriate in different situations. He emphasizes that scientific inference methods are not a priori and valid for every case, but presuppose specific empirical assumptions and thus are legitimate only in a certain range of empirical cases.

A similar picture applies to discovery in biology. Originally, philosophy of science—growing out of logical positivism—did not view scientific discovery as a philosophical issue at all. Back then the distinction between the context of discovery and the context of justification was such construed that while scientists may come up with hypotheses by any possible means (including non-rational psychological processes), the subsequent justification of a hypothesis always has to follow standards of rationality. Consequently, only confirmation was viewed as a subject for philosophy, while the process of discovery may be studied by psychology or sociology. Due to more recent developments in philosophy of science such as the New Experimentalism movement (Hacking, 1983) and naturalism, discovery in experimental and theoretical science is nowadays viewed as a rational process—in the sense that scientists use reasoning strategies and discovery heuristics that are reliable at yielding plausible hypotheses, or at least more likely to yield to fruitful hypotheses than other strategies (Nickles, 1980; Wimsatt, 2007). Thus, discovery is in need of philosophical analysis.

However, given the traditional philosophical ideal according to which rationality consists in formal logic and the use of universal principles, early accounts of discovery in biology have followed this philosophical model. For instance, Ken Schaffner (1974) initially argued that

discovery (just like justification) is reasoning using deductive logic, though he himself came to abandon this idea. In his reanalysis of the biological case addressed by Schaffner (the lac operon model of gene regulation), Weber (2005, Ch. 3) argues that this instance of discovery involved a variety of analogical reasoning, in a form that is prohibited in the context of justification.

Another prominent account of discovery in biology was put forward by Lindley Darden (1991) in the context of Mendelian genetics. Her account is influenced by artificial intelligence modelling, and she lays out a set of general strategies of discovery. She acknowledges that it is historically impossible to tell whether these strategies have actually been used, but argues that they could have been used to arrive at the hypotheses put forward in the history of Mendelian genetics. However, Weber (2005) rightly objects that this does not settle one important philosophical issue—whether general and domain-unspecific rules actually are or have been used by scientists in instances of discovery. Based on his study of experimental biology, Weber is sceptical about this, and prefers the interpretation that reasoning in discovery involves strategies that are limited to certain domains and cannot be universal as they are based on specific empirical considerations.

In sum, many accounts of discovery and confirmation in general philosophy of science have focussed on formal rules of inference, which by abstracting away from particular empirical content apply to any scientific field and domain. But “to show that a kind of reasoning can be rational ... is not the same as showing that it employs general rules or procedures” (Weber, 2005, p. 86). A look at biological practice suggests that scientists’ reasoning in discovery and confirmation is contingent upon empirical content specific to a particular case and thereby conforms at best to local and domain-specific principles. This is not to say that a philosophical study of confirmation or discovery is impossible. While overarching philosophical theories may be of limited use, more insightful studies reveal the particular scientific principles and

considerations used in certain cases, highlighting the concrete empirical content (in addition to formal structure) that justifies the effectiveness and rationality of this kind of reasoning in the respective empirical domain. This aligns to a large extent with the practice of contemporary philosophy of biology. Philosophers of biology rarely address ‘confirmation’ and ‘discovery’ in a direct fashion—at least they often do not phrase their studies in these terms from general philosophy of science. But their many case studies and discussions pertaining to biological issues shed light on scientific method and reasoning as used in different parts of biology.

Explanation and reduction

Just like the precise nature of discovery and confirmation in biology can vary with the empirical domain, biological explanations can take different shapes in different cases and what counts as an adequate explanation depends on empirical considerations tied to a particular case. Different accounts of explanation have been put forward in general philosophy of science. The deductive-nomological model assumes that an explanation is a logical deduction from law statements, which presupposes that a certain scientific discipline contains laws in the first place (Hempel and Oppenheim, 1948). Statistical relevance models argue that explanations are not logical arguments at all (neither deductive nor inductive), and take instead statistical relevance relations among quantitative variables to be explanatory (Salmon, 1971). Causal-mechanistic models contend that explanations exhibit causal structures as they occur in physical processes (Salmon, 1984) or biological mechanisms (Machamer et al., 2000). While sometimes these accounts have been seen as rival approaches, at least from the point of view of many philosophers of biology there is no need to choose one of them as the correct theory of explanation. For different such types of explanations occur in different parts of biology, and can even be used in one discipline.

For instance, explanations in evolutionary biology often combine quantitative models (in line with deductive-nomological, unification, or possibly statistical relevance accounts) with their application to concrete populations that exhibit the material features accounting e.g. for fitness differences (in line with causal-mechanistic models). Furthermore, following the logical positivist ideal, early accounts attempted to capture what a good explanation is in purely formal terms, so that for instance the deductive-nomological approach had to offer a syntactic construal of when a statement is a law of nature (attempts to do so failed). In contrast, what makes a particular explanation in biology a scientifically acceptable explanation is likely to depend on empirical considerations that cannot be characterized in a formal-syntactic fashion.

A related philosophical issue is reduction. In the philosophy of mind, accounts of reduction have centred on ontological issues (emergence, supervenience, how to construe physicalism). In contrast, while taking some notion of ontological reduction for granted (e.g. that every particular biological system is constituted by nothing but molecules and their interactions), the reductionism debate in philosophy of biology has turned on epistemological and methodological issues. In a nutshell, epistemic reduction is that idea the knowledge about one scientific domain (typically about higher level processes) can be reduced to another body of scientific knowledge (typically concerning a lower level). This broad idea can be spelled out in different (stronger and weaker) ways, so that the reductionism debate concerned not only the question of whether reduction is possible, but which notion of reduction is the appropriate one for biology—leading to a diversity of philosophical accounts of reduction.

One basic notion of reduction is theory reduction. Originally developed by Ernest Nagel (1961) as a general framework for science, it is the idea that one theory (construed as a formal system) can be logically deduced from a more fundamental theory. Inspired by the rise of molecular biology, Ken Schaffner (1976) applied it to biology by claiming that the theory of

classical genetics can be deduced from the theory of biochemistry. However, the notion of theory reduction was immediately criticized (Hull, 1976; Kitcher, 1984a). The proponents of theory reduction acknowledged that a reduction of classical genetics to molecular biology has not been achieved yet (and that theory reduction is not an aim of scientists), while arguing that theory reduction is in principle possible. Yet the critics wondered why such a notion of reduction is relevant for understanding biological research in practice, including reductionistic methods and explanations (Wimsatt, 2007). As a result, the notion of theory reduction was largely abandoned in favour of another class of models, which may be called accounts of explanatory reduction (Brigandt and Love, 2008). There are different such models, but they differ from the earlier approach (which assumes that whole theories are reduced) by assuming that generalizations of varying scope, mechanisms, or even individual facts are the features reductively explained. A reductive explanation need not be a logical deduction from a theory containing laws; and while it proceeds by explaining a complex whole in terms of its (lower-level) parts, the explanans need not exclusively contain terms referring to lower-level entities (in contrast to the logical premisses in theory reduction consisting of statements of the reducing theory only). Due to these differences, models of explanatory reduction are much better able to capture the piecemeal nature of research progress and explanation in molecular biology. Furthermore, an individual philosopher may be inclined to focus on one notion of reduction and use it as an overarching model of ‘reduction in biology’. However, when biologists discuss the possibility or impossibility of reductions they typically mean very specific explanatory or methodological issues about their particular empirical cases, so that ‘reduction’ as used across different research contexts may express different scientifically relevant claims.

Many arguments against epistemic reduction fall into one of two categories (Brigandt and Love, 2008). One type of consideration is that the effects of a biological system, especially of

lower-level molecular processes, depends on the overall biological context in which it occurs. One molecular kind can correspond to many higher levels kinds, if this molecular kind is part of different overall systems. As a result, reductions must usually be able take the context of and relations among molecular entities and processes into account. The second argument proceeds from the fact that many molecular kinds correspond to one higher level kinds, due to the fact that a higher level biological structure or process can be instantiated by different kinds of molecular processes (in line with multiple realization arguments known from the philosophy of mind). As a result, explanations in terms of such higher level kinds can have a higher generality (encompassing several different lower level accounts) or point to causally more robust features (picking out entities that are stable across time while their underlying molecular constitution changes). These arguments are effective against accounts of theory reduction, and possibly also against some models of explanatory reduction. In addition to developing alternative notions of reduction, the rejection of theory reduction led many philosophers of biology to endorse pluralism, i.e., the idea that biology needs a diversity of methods, models, and modes of theoretical reasoning (Mitchell, 2003). Sometimes this was phrased in a bold anti-reductionist stance as an argument for the disunity of biology (Dupré, 1993; Rosenberg, 1994).

Theory reduction as a model assuming the reduction of various biological fields to one theory does not do justice to the diversity of different biological approaches. At the same time, the mere endorsement of pluralism or a disunity of science fails to study the intellectual relations that exist across disciplines. For this reason, arguably the most promising philosophical approaches in the last few decades concern the coordination and integration of different concepts, models, and explanations. For instance, Lindley Darden and Nancy Maull (1977) developed a model (of ‘non-reductive unification’, as they put it) that argues that integration proceeds by two fields coming to be linked by so-called interfield theories. For example, the

chromosome theory of inheritance is an interfield theory that in the early 20th century came to connect Mendelian genetics (the study of phenotypic inheritance across generations) and cytology (the study of the material contents of cells). This was a non-reductive integration because neither did genetics reduce cytology, nor did cytology reduce genetics. In contrast to the possibility of unification in virtue of several theories reducing to a new, more fundamental theory, an interfield theory connects theories without reducing them.

Philosophical studies on integration in biology have often been conducted in the context of molecular, cellular, and experimental biology, with related attention to disciplinary change and institutional factors (Bechtel, 1986). Accounts of biological mechanisms in these biological domains have shown that mechanistic explanations often appeal to entities on several levels of biological organization at the same time (Craver, 2005; Darden, 2005). In a similar vein, the units of selection debate in evolutionary biology led to some agreement that units of selection can be found on different levels, so that there is no single level that would a priori be the most fundamental one in evolutionary explanations, but in each case it is an empirical question at which level(s) selection takes place (Brandon, 1988). Studies of the emerging integration of evolutionary biology and developmental biology suggest the epistemological importance of problems addressed by biologists (Love, 2008). A complex scientific problem such as the explanation of the evolutionary origin of novel structures necessitates the integration of different ideas and approaches. Apart from motivating integration, a problem also structures integration by determining which disciplines, methods, concepts, and models are to be integrated. Integration (or unification) is not a regulative ideal or aim in itself for biologists, but may be needed to solve a particular biological problem (Brigandt, in press-a).

Naturalism

Naturalism is a characteristic feature of contemporary philosophy of science, and even major strands of philosophy in general. Yet ‘naturalism’ as used by different philosophers can denote different ideas (Papineau, 2009). It can express certain metaphysical tenets, such as the commitment to a purely physicalist ontology or the idea that humans (including their intellectual and moral capacities) are a part of nature as well. A methodological variety of naturalism is particularly germane to the practice of philosophy of biology (Wimsatt, 2007). Here the idea is first that given philosophy of science’s task to understand science and its success, philosophical accounts have to do justice to and reflect actual science. Second, the practice of philosophy of science is continuous with scientific practice, and empirical methods of science can be useful tools for philosophers in their attempts to form philosophical notions. This was illustrated by several themes from this chapter’s earlier sections. Given the plurality of kinds of explanation used in biology and the fact that ‘reduction’ as used by biologists expresses different specific commitments in different contexts, naturalistic philosophy has to capture this diversity. If biologists’ reasoning involved in discovery and confirmation is dependent on empirical considerations and the particular shape of discovery and confirmation (and what makes it justified) can vary across biological domains, philosophical accounts of discovery and confirmation must accommodate this. In the case of conceptual change, sometimes the notion of reference and the existence of stable reference across theoretical change were considered a satisfactory reply to the incommensurability challenge. While some discussions in general philosophy of science have taken place under these assumptions and within these limits, we saw that the notion of reference alone does not explain how rational theory choice is possible in the face of meaning differences, and that the reference of biological terms can be far from stable, prompting the need to philosophically address this.

In philosophy as a whole, concepts are often put forward and debated by the use of intuitions. Various possible scenarios are considered and it is determined whether the concept applies to a scenario (according to one's intuitions). However, the practice of philosophers of biology suggests that a more fruitful approach is to view philosophical concepts as technical terms that—just like scientific terms—are introduced for certain theoretical tasks. Any philosophical account is to be defended in terms of its fruitfulness and adequacy of performing this task (an a posteriori question), rather than conforming to a priori intuitions. For instance, according to widespread intuitions, the identity of a natural kind is determined by an internal essence. Yet an actual justification for the traditional notion of a natural kind is that it captures features of physical and chemical kinds and how they figure in scientific explanation (which can in principle be empirically contested). A novel notion of natural kinds such as the notion of homeostatic property clusters is needed to the extent that it is necessary to deal with biological kinds. Above I indicated that different notions and models of epistemic reduction have been put forward. It is not sufficient to simply motivate one definition of 'reduction' and then argue that classical genetics can be (or cannot be) reduced to molecular biology on this definition, but the philosophical relevance of this notion of reduction has to be defended, which also involves reference to scientific practice. Indeed, the notion of theory reduction (defended by the mere in principle possibility of theory reduction) was challenged for failing to shed light on reductionistic research in practice.

To give another example, metaphysicians have attempted to analyze the concept of causation. Any such definition of 'cause' is subject to counterexamples (i.e., a scenario that intuitively is an instance of x causing y but not according to the definition, or vice versa). This has led to philosophical debates, where the method of conceptual analysis by intuitions does not even suggest how such a controversy can be settled. On a naturalistic approach, in contrast, a

look at physics shows that the term ‘cause’ is not used there at all, suggesting that different terms altogether may be more suitable to philosophically understand the properties of physical systems and how they make explanations possible. The notion of causation is used in biology (and the social sciences), but causal talk there can be diverse, so that a philosophical account of causation and causal explanation in biology has to capture this and cannot assume that a simple definition of ‘cause’ in terms of necessary and sufficient conditions will be adequate to understand explanatory practice.

In philosophy of mind and several other fields, providing a naturalistic account is often understood as giving a reductive definition of a philosophical concept in terms of an alleged ‘scientific’ vocabulary. For instance, the aim is to offer a naturalistic reduction of semantic and intentional notions (e.g., ‘reference’, ‘meaning’, ‘mental representation’), in particular to reduce the normativity associated with correct vs. incorrect representation. (Some such attempts are causal theories of reference, teleosemantic accounts of representation, or Fodor’s asymmetric dependency account of representation.) However, such a naturalistic vocabulary is somewhat of a philosopher’s fiction. For as we saw in the section on ‘Explanation and reduction’, scientists use concepts referring to entities on many levels of organization and do not attempt to reductively define their concepts in terms of the vocabulary of a particular field such as molecular biology. Biologists provide reductive explanations only when it is empirically beneficial to do so. As a result, a methodologically naturalistic approach in philosophy of science—attempting to do philosophy in analogy to scientific practice—is not committed to settle a priori on a specific vocabulary and attempt to reduce philosophical concepts to it. (To mention another way of using biological practice as a guideline for philosophical method, Burian *et al.* [1996] argue that there is probably no unique philosophical account of meaning and reference. Just like biological concepts are often used in varying ways—with there being several

gene concepts—philosophical concepts require local analyses and are best employed in different versions for different purposes.)

When philosophers talk about ‘explanation’ (e.g. ‘explaining reference’), they often mean a definition of a philosophical term by means of necessary and sufficient conditions. Explanation in biology (e.g. ‘explaining life’) involves something different. Biologists do not aim at giving a definition of life. Instead, the aim is to gain partial but ever increasing insights into the causal workings of various life processes. Likewise, naturalistic philosophy of science is not so much concerned with defining ‘knows that p’ in terms of necessary and sufficient conditions, but to understand the various aspects of knowledge production. This includes empirical issues such as the cognitive factors involved in belief formation. Various social aspects of the organization of scientific research are a major reason for the success of modern science, so that many philosophers of biology pay attention to the sociology of science and history of science (Hull, 1988; Downes, 1993). This use of social and other empirical factors is not inconsistent with philosophy of science dealing with normative concerns such as the rationality of discovery and the justified endorsement of theories, as certain social factors can be precisely those that underlie the rational and effective generation of knowledge (Longino, 2002). Ron Giere (1988) assumes that naturalistic philosophy of science consists in an empirical-descriptive approach, but cannot be concerned with normative considerations. However, biologists freely use normative notions, for instance when talking about proper method, adequate representations, justified hypotheses, relevant problems, and the proper intellectual aims of their discipline. In a similar vein, naturalistic philosophers may arguably engage in normative considerations in their subject matter, the study of science (Laudan, 1990). Just like biologists fruitfully study the causal interactions of entities on several levels of organization, the aim for philosophers of science should be to shed light on the relations among phenomena referred to by philosophical (including

normative) concepts and the phenomena studied by the cognitive, natural and social sciences. Rather than being reduced or eliminated, normativity is thereby one out of many factors. Due to its methodological construal of naturalism and its interaction with biologists, historians, and sociologists, philosophy of biology has become an interdisciplinary approach.

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