Contemporary Debates in the Philosophy of Biology : A Historical Review

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Abstract

The philosophy of biology has existed as a distinct sub-discipline within the philosophy of science for about thirty years. The rapid growth of the field has mirrored that of the biological sciences in the same period. Today the discipline is well represented in the leading journals in philosophy of science, as well as in several specialist journals. There have been two generations of textbooks and the subject is regularly taught at undergraduate as well as graduate level. The current high profile of the biological sciences and the obvious philosophical issues that arise in fields as diverse as molecular genetics and conservation biology suggest that the philosophy of biology will remain an exciting field of enquiry for the foreseeable future.

Keywords: *philosophy of biology, systematic biology, philosophy of science, molecular biology, developmental biology, ecology and conservation biology.*

Three Kinds of Philosophy of Biology

Philosophers have engaged with biological science in three quite distinct ways. Some have looked to biology to test general theses in philosophy of science. Others have engaged with conceptual puzzles that arise within biology itself. Finally, philosophers have looked to biological science for answers to distinctively philosophical questions in such fields as ethics, the philosophy of mind, and epistemology.

The debate which marked the beginning of contemporary philosophy of biology exemplified the first of these three approaches, the use of biological science as a testing ground for claims in general philosophy of science. In the late 1960s, Kenneth C. Schaffner applied the logical empiricist model of theory reduction to the relationship between classical, Mendelian genetics and the new molecular genetics (Schaffner 1967; 1969; Hull 1974). While the failure of this attempt in its initial form reinforced the near-consensus in the 1970s and 1980s that the special sciences are autonomous from the more fundamental sciences, it also led the formulation of increasingly more adequate models of theory reduction (Schaffner 1993; Sarkar 1998).

Another important early debate showed philosophy engaging biology in the second way, by confronting a conceptual puzzle within biology itself. The concept of reproductive fitness is at the heart of evolutionary theory, but its status always been problematic. It has proved surprisingly hard for biologists to avoid the criticism that natural selection explains the reproductive success of organisms by citing their fitness, while defining their fitness in terms of their reproductive success (the so-called 'tautology problem'). Philosophical analysis of this problem begins by noting that fitness is a supervenient property of organisms: the fitness of each particular organism is a consequence of some specific set of physical characteristics of the organism and its particular environment, but two organisms that have identical levels of fitness may do so in virtue very different sets of physical characteristics (Rosenberg 1978). The most common solution to the 'tautology problem' is to argue that this supervenient property is a propensity -a probability distribution over possible numbers of offspring (Mills and Beatty 1979). Thus, although fitness is defined in terms of reproductive success, it is not a tautology that the fittest organisms have the most offspring. Fitness merely allows us to make fallible predictions about numbers of offspring, predictions that become more reliable as the size of the population tends to infinity. It remains unclear, however, whether it is possible to specify a probability distribution or set of distributions that can play all the roles actually played by fitnesses in population biology (Rosenberg and Bouchard 2002).

The third way in which philosophy has engaged with biology is by tracing out the wider ethical, epistemological, and metaphysical implications of biological findings. This has sometimes occurred in response to philosophical claims issuing from within biology itself. For example, some proponents of sociobiology -the application to humans of the models

developed in behavioral ecology in the 1960s – suggested that the conventional
social sciences could be reduced to or replaced by behavioral biology. Others claimed that certain aspects of human behavior result from strongly entrenched aspects of human biology and thus that public policy must be designed to work with and around such behavior rather than seeking to eradicate it. These claims were evaluated by leading philosophers of biology like Michael Ruse (1979), Alexander Rosenberg (1980), and Philip Kitcher (1985).
Query: is this part of the third way? Unclear how this fits in. On other occasions, rather than responding to philosophical claims issuing from within biology, philosophers have actively sought from biology answers to questions arising in their own discipline, questions that may not be of particular interest to working biologists. The extensive literature on biological teleology is a case in point. After a brief flurry of interest around the time of the modern synthesis, during which the term 'teleonomy' was introduced to denote the specifically evolutionary interpretation of teleological language (Pittendrigh 1958), the ideas of function and goal directedness were regarded as relatively unproblematic by evolutionary biologists and there was little felt need for any further theoretical elaboration of these notions. In the 1970s, however, philosophers started to look to biology to provide a solid, scientific basis for normative concepts, such as illness or malfunction (Wimsatt 1972; Wright 1973). These discussions eventually converged on an analysis of teleological language fundamentally similar to the view associated with the modern synthesis, although elaborated in far greater detail. According to the 'etiological theory of function', the functions of a trait are those activities in virtue of which the trait was selected (Brandon 1981; Millikan 1984; Neander 1995, 1991). Despite continued disputes over the scope and power of the etiological theory amongst philosophers of biology (Ariew, Cummins, and Perlman 2002), the idea of 'etiological' or 'proper' function has become part of the conceptual toolkit of philosophy in general and of the philosophy of language and the philosophy of mind in particular. These three approaches to doing philosophy of biology are exemplified in different

combinations in philosophical discussion of the several biological disciplines.

The philosophy of evolutionary biology Evolutionary theory has been used as a case study in support views of views of the structure of scientific theories in general, an approach that conforms to the 'testing ground' conception of philosophy of biology described above. The example is most often thought to favor the 'semantic view' of theories (Lloyd 1988). Most philosophical writing about evolutionary theory, however, is concerned with conceptual puzzles that arise inside the theory itself, and the work often resembles theoretical biology as much as pure philosophy of science. Elliott Sober's classic study The Nature of Selection: Evolutionary theory in philosophical focus (1984) marks the point at which most non-specialists became aware of the philosophy of biology as a major new field. In this work Sober analyzed the structure of selective explanations via an analogy with the composition of forces in dynamics, treating the actual change in gene frequencies over time as the result of several different 'forces', such as selection, drift, and mutation. Sober's book also introduced the widely used distinction between 'selection for' and 'selection of'. Traits that are causally connected to reproductive success, and which can therefore be used to explain reproductive success, are said to be 'selected for' (or to be 'targets' of selection). In contrast, there is 'selection of' traits which do not have this property but which nevertheless are statistically associated with reproductive success, usually because they are linked in some way to traits which do have the property. For example, when two DNA segments are 'linked' in the classical sense of being close to one another on the same chromosome, they have a high probability of being inherited together. If only one of the two segments has any effect on the phenotype, it is the presence of this segment alone that explains the success of both. There is selection for the causally active segment but only selection of its passive companion.

Robert Brandon's classic analysis of the concept of the environment is, similarly, of as much interest to biologists as to philosophers (Brandon 1990). Several biological authors have criticized the idea that the 'environment', in the sense in which organisms are adapted to their environments, can be described independently of the organisms themselves. Brandon defines three different notions of ‘environment’ all of which are needed to make sense of the role of environment in natural selection. All organisms in a particular region of space and time share the ‘external environment’, but to understand the particular selective forces acting on one lineage of organisms it is necessary to pick out a specific 'ecological environment'consisting of those environmental parameters whose value affects the reproductive output of members of the lineage. The ecological environment of a fly will be quite different from that of a tree, even if they occupy the same external environment. Finally, the 'selective environment'is that part of the ecological environment which differentially affects the reproductive output of variant forms in the evolving lineage. It is this last which contains the sources of adaptive evolutionary pressures on the lineage.

Part of the early philosophical interest in selective explanation arose due to philosophical interest in sociobiology. Sociobiology was widely criticized for its ‘adaptationism’ -an exclusive focus on selection to the exclusion of other evolutionary factors. This gave rise to several important papers on the concept of ‘optimality’ in evolutionary modeling (Dupré 1987). Philosophers have now distinguished several distinct strands of the adaptationism debate and many of the remaining issues are clearly empirical rather than conceptual, as is made clear in the latest collection of papers on this issue (Orzack and Sober 2001).

The sociobiology debate, and related discussion of the idea that the fundamental unit of evolution is the individual Mendelian allele (Dawkins 1976) also drove the explosion of philosophical work on the ‘units of selection’ question in the 1980s (Brandon and Burian 1984). Philosophical work on the units of selection question has tended to favor some form of pluralism, according to which there may be units of selection at several levels within the hierarchy of biological organization – DNA segments, chromosomes, cells, organisms, and groups of organisms. Arguably, philosophers made a significant contribution to the rehabilitation of some forms of ‘group selection’ in evolutionary biology itself, following two decades of neglect (Sober and Wilson 1998).

More recently, a heated debate has developed over the ontological status of the probabilities used in population biology. On the one hand, our best models of the evolutionary process assign organisms a certain probability of reproducing (fitness) and make probabilistic predictions about the evolutionary trajectory of populations. On the other hand, the actual process of evolution is the aggregation of the lives of many individual organisms, and those organisms lived, died, and reproduced in accordance with deterministic, macro-level physical laws. Hence, it has been argued, the evolutionary process itself is deterministic, a vast soap opera in which each member of the cast has an eventful history determined by particular causes, and the probabilities in evolutionary models are introduced because we cannot follow the process in all its detail (Rosenberg 1994; Walsh 2000). If correct, this argument has some interesting implications. It would seem to follow, for example, that there is no real distinction in nature between the process of drift and the process of natural selection. (At a technical level this does not follow, though the position is probably correct—just a passing note.)

Robert Brandon and Scott Carson have strongly rejected this view, insisting that evolution is a genuinely indeterministic process and that the probabilistic properties ascribed to organisms by evolutionary models should be accepted in the same light as the ineliminable explanatory posits of other highly successful theories (Brandon and Carson 1996).

The Philosophy of Systematic Biology

Philosophical discussion of systematics was a response to a ‘scientific revolution’ in that discipline in the 1960s and 1970s, a revolution which saw the discipline first transformed by the application of quantitative methods and then increasingly dominated by the ‘cladistic’ approach, which rejects the view that systematics should sort organisms into a hierarchy of groups representing a roughly similar amount of diversity, and argues that its sole aim should be to represent evolutionary relationships between groups of organisms (phylogeny). Ideas from the philosophy of science were used to argue for both transformations, and the philosopher David L. Hull was an active participant throughout this whole period (Hull 1988). Another major treatment of cladism is (Sober 1988).

The best known topic in philosophy of systematics was introduced by the biologist Michael Ghiselin, when he suggested that traditional systematics was fundamentally mistaken about the ontological status of biological species (Ghiselin 1974, see also Hull 1976). Species, it was argued, are not natural kinds of organisms in the way that chemical elements are natural kinds of matter. Instead, they are historical particulars like families or nations. However, the view that species are historical particulars leaves other important questions about species unsolved and raises new problems of its own. As many as twenty different so-called 'species concepts' are represented in the current biological literature, and the merits, interrelations, and mutual consistency or inconsistency of these concepts has been a major topic of philosophical discussion (the papers collected in Ereshefsky 1992 provide a good introduction to these debates).

The philosophy of systematics has influenced general philosophy of science, and indeed, metaphysics, through its challenge to one of the two classical examples of a 'natural kind' – biological species. The result has been a substantial re-evaluation of what is meant by a natural kind, whether there are natural kinds, and whether traditional views about the nature of science which rely on the idea of natural kinds must be rejected (Wilkerson 1993; Dupré 1993; Wilson 1999).

The Philosophy of Molecular Biology

As mentioned above, one of the first topics to be discussed in the philosophy of biology was the reduction of Mendelian to molecular genetics. The initial debate between Schaffner and Hull was followed by the so-called 'anti-reductionist consensus' embodied in Philip Kitcher's classic paper '1953 and All That: A Tale of Two Sciences' (1984). The reductionist position was revived in a series of important papers by Kenneth Waters (1990, 1994) and debate over the cognitive relationship between these two theories continues today, although the question is not now framed as a simple choice between reduction and irreducibility. For example, William Wimsatt has tried to understand ‘reduction’ not as a judgment on the fate of a theory, but as one amongst several strategies that scientists can deploy when trying to unravel complex systems. The philosophical interest lies in understanding the strengths and weaknesses of this strategy (Wimsatt 1976,1980). Lindley Darden, Schaffner and others have argued that explanations in molecular biology are not neatly confined to one ontological level, and hence that ideas of ‘reduction’ derived from classical examples like the reduction of the phenomenological gas laws to molecular kinematics in nineteenth century physics are simply inapplicable (Darden and Maull 1977; Schaffner 1993). Moreover, molecular biology does not have the kind of grand theory based around a set of laws or a set of mathematical models that is familiar from the physical sciences. Instead, highly specific mechanisms that have been uncovered in detail in one model organism seem to act as ‘exemplars’ allowing the investigation of similar, although not necessarily identical, mechanisms in other organisms that employ the same, or related, molecular interactants. Darden and collaborators have argued that these ‘mechanisms’ specific collections of entities and their distinctive activities – are the fundamental unit of scientific discovery and scientific explanation, not only in molecular biology, but in a wide range of special sciences (Machamer, Darden, and Craver 2000).

An important strand in the early debate over reduction concerned the different ways in which the gene itself is understood in Mendelian and molecular genetics. The gene of classical Mendelian genetics has been replaced by a variety of structural and functional units in contemporary molecular genetics. One response to this is pluralism about the gene (Falk 2000). Another is to identify a central tendency that unifies the various different ways in which the term ‘gene’ is used (Waters 1994, 2000). Identifying the different ways in which genes are conceived in different areas of molecular biology and their relations to one another is a major focus of current research (Beurton, Falk, and Rhineberger 2000; Moss 2002, Stotz, Griffiths, and Knight 2004). Another very active topic is the concept of genetic information, or developmental information more generally (Sarkar 1996a, 2004; Maynard Smith 2000; Griffiths 2001; Jablonka 2002).

The Philosophy of Developmental Biology

Developmental biology has received growing attention from philosophers in recent years. The debate over ‘adaptationism’ introduced philosophers to the idea that explanations of traits in terms of natural selection have time and time again in the history of Darwinism found themselves in competition with explanations of the same traits from developmental biology. Developmental biology throws light on the kinds of variation that are likely to be available for selection, posing the question of how far the results of evolution can be understood in terms of the options that were available (‘developmental constraints’) rather that the natural selection of those options (Maynard Smith et al. 1985). The question of when these explanations compete and when they complement one another is of obvious philosophical interest. The debate over developmental constraints looked at developmental biology solely from the perspective of whether it could provide answers to evolutionary questions. However, as Ron Amundson pointed out, developmental biologists are addressing questions of their own, and, he argued, a different concept of ‘constraint’ is needed to address those questions (Amundson 1994). In the last decade several other debates in the philosophy of biology have taken on a novel aspect by being viewed from the standpoint of developmental biology. These include the analysis of biological teleology (Amundson and Lauder 1994), the units of selection debate (Griffiths and Gray 1994), and the nature of biological classification, which from the perspective of development is as much a debate about classifying the parts of organisms as about classifying the organisms themselves (Wagner 2001). The vibrant new field of evolutionary developmental biology is transforming many evolutionary questions within biology itself and hence causing philosophers to revisit existing positions in the philosophy of evolutionary biology (Brandon and Sansom 2005).

Increasing philosophical attention to developmental biology has also led philosophers of biology to become involved in debates over the concept of innateness, the long tradition of philosophical literature on this topic having previously treated innateness primarily as a psychological concept (Ariew 1996, Griffiths 2002)

The Philosophy of Ecology and Conservation Biology

Until recently this was a severely underdeveloped field in the philosophy of biology. This situation was surprising, because there is obvious potential for all three of the approaches to philosophy of biology discussed above. First, ecology is a demanding 'testing ground' for more general ideas about science, for reasons explained below. Second, there is a substantial quantity of philosophical work in environmental ethics, and it seems reasonable to suppose that answering the questions that arise there would require a critical methodological examination of ecology and conservation biology. Finally, ecology contains a number of deep conceptual puzzles, which ecologists themselves have recognized and discussed extensively.

The most substantial contributions to the field to date include Kristin Schrader-Frechette and Earl McCoy's Method in Ecology: Strategies for conservation (1993), Gregory Cooper's The Science of the Struggle for Existence: On the foundations of ecology (2003), and Lev Ginzburg, L. and Mark Colyvan's. Ecological Orbits: How planets move and populations grow (2004). Cooper focuses on the particular methodological problems that confront ecology as a result of its subject matter – massively complex, and often unique, systems operating on scales that frequently make controlled experiment impractical -- and on the consequent lack of connection between the sophisticated mathematical modeling tradition in ecology and ecological field work. Schrader-Frechette and McCoy's book, as its title suggests, is primarily concerned with how practical conservation activity can be informed by ecological theory despite the problems addressed by Cooper (for a related discussion, see Sarkar 1996b). Ginzburg and Colyvan, in contrast, argue forcefully that ecology may still produce simple, general theories that will account for the data generated by ecological field work in as satisfactory a manner as Newtonian dynamics accounted for the motion of the planets.

The concept of the niche stands in a marked contrast to other ecological concepts for having been widely discussed by philosophers of biology (summarized in Sterelny and Griffiths 1999, 268-79). This, however, reflects the importance of the niche concept in evolutionary biology. Topics that merit much more attention than the little they have received to date include the concept of biodiversity and that of stability (or, in its popular guise, the ‘balance of nature’). A recent extended philosophical discussion of these concepts, integrating themes from the philosophy of ecology and conservation biology with more traditional environmental philosophy is (Sarkar 2005).

Conclusion

The philosophy of biology is a flourishing field, partly because it encompasses all three of the very different ways in which philosophy makes intellectual contact with the biological sciences, as discussed above. The scope of philosophical discussion has extended from its starting points in evolutionary biology to encompass systematics, molecular biology, developmental biology and, increasingly, ecology and conservation biology. For those who wish to explore the field beyond this article and the related articles in this volume, recent textbooks include Elliot Sober’s Philosophy of Biology (Sober 1993) and Kim Sterelny and Paul Griffiths’ Sex and Death: An Introduction to Philosophy of Biology (Sterelny and Griffiths 1999). Two valuable edited collections designed to supplement such a text are Elliot Sober’s Conceptual Issues in Evolutionary Biology (2nd Ed.), which collects the classic papers on core debates (Sober 1994), and David Hull and Michael Ruses’ The Philosophy of Biology which aims at a comprehensive survey using recent paper (Hull and Ruse 1998). Evelyn Fox Keller and Elizabeth Lloyd have edited an excellent Keywords in Evolutionary Biology, aimed primarily at philosophers of biology (Keller and Lloyd 1992).

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