Introduction

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There are many different ways to do the philosophy of biology. At one end of a spectrum of possibilities would be works of general philosophical interest drawing on biological examples for illustration and support. At the other end would be works that deal only with conceptual and methodological issues that arise within the practice of biology. The strategy of this book is closer to the second way of approaching the subject. It aims to provide overviews of philosophical issues as they arise in a variety of areas of contemporary biology. Traditionally, evolution has been the focus of most philosophical attention. While it surely remains true that "nothing in biology makes sense except in light of evolution" (Dobzhansky, 1973), this tradition within the philosophy of biology is myopic insofar as it ignores much – if not most – of the work in contemporary biology. Intended primarily for students and beginning scholars, this book takes a wider perspective and addresses philosophical questions arising in molecular biology, developmental biology, immunology, ecology, and theories of mind and behavior. It also explores general themes in the philosophy of biology, for instance, the role of laws and theories, reductionism, and experimentation. In this respect, this book aims to break new ground in the philosophy of biology. Before we turn to what is new, let us briefly look at the background from which contemporary philosophy of biology emerged.

1. Background

When the logical empiricists reoriented the direction of philosophy of science in the 1920s and 1930s, the loci of their attention were mathematics (and within it, almost entirely mathematical logic) and physics (initially relativity theory, later also quantum mechanics). This not only set the agenda, but also the tone, for the philosophy of science. The relatively simple axiomatic structures of relativity theory and quantum mechanics – or, at least, how professional philosophers conceived those fields – became the yardstick of comparison for other disciplines. If these other disciplines were found to be less general in their intended domain, to be using different criteria of rigor (that is, using techniques different from the type of mathematics used in mathematical logic), or simply different, they were presumed to be wanting. This applied not only to biology

or chemistry (or, for that matter, the social sciences) but even to other areas of physics. Biology thus suffered from a not always benign neglect throughout this period.

Yet, in spite of this limited attention, if the sophistication of the discussion is used as a standard, biology fared much better during the early decades of the logical empiricist regime (that is, from 1925 to 1945) than during the next 20 years. This is not only because many biologists – including Driesch (1929), J. S. Haldane (1929, 1931), Hogben (1930), and J. B. S. Haldane (1936, 1939) – explicitly debated philosophical positions, in particular, the relative roles of reductionism and holism in biology, during those decades. These debates within the biological community helped the development of philosophy of biology, but there were also significant attempts by philosophers to come to terms with the exciting developments that had taken place in biology, particularly in genetics and evolution, during the first three decades of the twentieth century. Woodger (1929) produced an exploration of traditional philosophical problems in biology, such as vitalism and mechanism, as well as a theory of biological explanation. In 1937 he went on to attempt to axiomatize parts of genetics.[1] By 1952 Woodger (1952) had clearly articulated what, after independent formulation and elaboration by Nagel (1949, 1951, 1961), became the standard model of theory reduction.[2] Nagel used this model in an attempt to explicate mechanistic explanation in biology. Less successfully, he attempted to provide a deflationary account of teleological explanation in biology (Nagel, 1961, 1977).

Arguably, until at least the 1960s, philosophers provided less philosophical insight about biology than theoretically oriented biologists. In the case of mechanistic explanation, for instance, as far as substantive biological questions are concerned, Nagel achieved little more than Hogben (1930). All he did was translate the simplest biological questions into the logical empiricists' framework and presumed that the result showed what was philosophically interesting about biology. Following the standard twentieth-century philosophical tradition, Nagel's writings on biology contributed little that scientists, even philosophically oriented biologists, found valuable. Nagel also displayed a strange refusal to follow contemporary developments in biology: between 1949 and 1961 he saw no reason to temper his bleak assessment of the state of mechanistic/reductionist explanation in biology – the events of 1953 either completely slipped by him, or failed to impress him. *The Structure of Science* from 1961 has several sections devoted to reductionism in biology but makes no mention of the double helix or, for that matter, any other development in molecular biology that had raised the potential for successful reduction in biology to an entirely different level (Nagel, 1961).

In the philosophy of biology, during the late 1950s and early 1960s only two notable exceptions stand out, Beckner's *The Biological Way of Thought* and, especially, Goudge's *The Ascent of Life*, the latter being a scientifically fairly sophisticated philosophical exploration of evolutionary theory (Beckner, 1959; Goudge, 1961; see also

1 Woodger (1937), under the sway of operationalism and skepticism about theoretical entities, attempted an axiomatization of genetics without "gene" as a term; Carnap (1958) developed some of Woodger's formal treatment in more interesting ways.

2 For a history, see Sarkar (1989).

Scriven, 1959). The situation changed for the better in the late 1960s and 1970s. Hull (1965, 1967, 1968) began to explore the conceptual structure of evolutionary biology. Wimsatt (1971, 1972) provided a detailed analysis of teleological explanation (and biological "feedback"), drawing extensively on contemporary work in theoretical biology. In a series of papers, Schaffner (1967a, b, 1969, 1976) began to argue the case for reductionism in molecular genetics while Hull (1972, 1974, 1976, 1981) questioned Schaffner's assessment. Ruse (1976) and Wimsatt (1976) were among those who joined this debate. A consensus emerged against reductionism (provided that reduction was construed in the fashion inherited from Nagel and the logical empiricists). Philosophy of biology also played its part, though rather late, in the rejection of logical empiricism in the 1960s and 1970s.

Since the early 1970s, the philosophy of biology has had a continuous and increasingly prominent presence in the philosophy of science. Occasional abuse of biology by philosophers has continued – as late as 1974, Popper would claim that Darwinism is not a scientific enterprise (Popper, 1974). Over the years, however, philosophy of biology has contributed to the development of the various alternatives to logical empiricism, including scientific realism, the semantic view of theories, and, in particular, naturalistic epistemology. Within the general context of the philosophy of biology, the last of these programs has been particularly natural and fecund presumably because philosophers of biology, because of their engagement with biology, are more likely than other philosophers to analyze how humans are evolutionarily produced, constrained, and challenged, as biological organisms. In fact, barring a very few exceptions, there is consensus among philosophers of biology of the great value of the naturalized perspective in philosophy where "naturalism" is very narrowly construed purely in evolutionary terms. Moreover, philosophers of biology have quite routinely begun to practice biology. If philosophy is to be done in continuity with science, as Quine once urged, no area in philosophy has followed that dictum more systematically than the philosophy of biology.

In the late 1970s, philosophy of biology became almost exclusively concerned with evolutionary theory. In some ways, this focus was productive; core philosophical questions were addressed about the foundations of evolutionary theory. For instance, Hull (1965a, b; see also Sober, 1988), advanced a discussion of different schools of phylogenetic analyses that has subsequently developed a rich literature on the methodological commitments of different schools of thought in systematics and phylogenetics. Philosophers including Wimsatt (1980), Brandon (1982), and Sober (1984) produced useful analyses of what constitutes the units of selection, while several prominent biologists, including Lewontin (1970) and Maynard Smith (1976), made important philosophical contributions. Sober's 1984 book, *The Nature of Selection*, advanced a clear analysis of the nature of laws and the structure of evolutionary theory, and particularly clarified related questions about the units-of-selection debate. Another 1984 book of equal merit was Flew's (1984) *Darwinian Evolution*. However, the almost exclusive focus on evolution in much of the literature of the late 1970s and 80s arguably hurt the development of the discipline. Many of the philosophical writings on biology from this period remained inattentive to molecular biology where, for better or for worse, most of biological research had become concentrated. Kitcher (1982, 1984) and Rosenberg (1985), however, are notable exceptions. Kitcher (1982) gave a thoughtful

analysis of the transformation of biology after 1953, as well as a critical discussion of gene concepts (Kitcher, 1984), and Rosenberg (1985) advanced a perspective that treated genetics and molecular biology as being central to biology.

Given this state of the field, it is easy to understand the molecular biologists' lack of concern for philosophical critiques of their enterprise. This lack of concern was particularly noticeable during the debates over the initiation of the Human Genome Project in the late 1980s and early 1990s, a debate on which philosophers, unlike historians and social scientists, had no perceptible influence. (A notable exception to these generalizations is neurobiology which has always received considerable philosophical attention though usually in the context of the philosophy of mind.)

Since the early 1990s, in a very welcome development, philosophical writing on biology has extended its scope to cover many areas within biology beyond evolutionary theory.[3] There has been much recent interest in ecology, molecular and developmental biology. There has also finally been some attention to the role of experimentation in biology. In particular, Rheinberger (1993, 1997) has pioneered the use of techniques from the continental tradition of philosophy in the analysis of experimentation in molecular biology. Philosophers of biology have usually also paid ample attention to the history of biology. With intellectual and technical history gradually falling out of fashion in the professional history of science, philosophers of biology have done much to keep the history of the *science* of biology alive in contemporary research. This book reflects all these trends.

2. Structure of the *Companion*

Most of biology today is molecular biology, and the *Companion* begins with a section on molecular biology and genetics ("Molecular Biology and Genetics"). Rheinberger and Müller-Wille ("Gene Concepts") provide a historical review the various ways in which genes have been conceptualized, and how these have changed from the period of classical genetics to the post-genomic era in which we now find ourselves. Artmann ("Biological Information") explores the troubled question of whether and how biological information is susceptible to precise, quantitative measurement, an issue that has been hotly debated by philosophers (Godfrey-Smith, 2004; Sarkar, 2005). Contrary to many philosophers (Sarkar, 1996), he argues that there is more to informational talk in biology than mere metaphor.

Lewontin ("Heredity and Heritability") provides a philosophically sophisticated account of how classical genetics views heredity and adds a critique of the much-abused concept of heritability. Sarkar ("Genomics, Proteomics, and Beyond") speculates on where the study of heredity and development is going in the wake of the massive whole-genome sequencing projects. Both Lewontin and Sarkar emphasize the limitations of a gene-centered view of biology and argue for a more developmentally oriented approach to understanding the emergence of phenotypes.

The next section ("Evolution") turns to a number of classic issues addressed in the philosophy of biology, as well as some issues that have not perhaps received the atten-

3 The textbook by Sterelny and Griffiths (1999) is indicative of this trend.

tion they deserved. Reconciling Darwin's own views with the various ways in which "Darwinism" has been understood during the last 130 years has been a challenge for biologists, historians, and philosophers of biology. Lennox ("Darwinism and Neo-Darwinism") identifies the core principles of Darwin's original theory, and traces their empirical and conceptual development through the evolutionary synthesis, arguing that there is a meaningful set of commitments one can identify as "Darwinian." A further classic problem in evolutionary biology is how species should be defined and classified. Ereshefsky ("Systematics and Taxonomy") analyzes a variety of controversies that have arisen among biologists and philosophers of biology about the nature of species and their classification, ultimately defending a pluralist view of how species should be defined.

Population genetics has typically been viewed as the theoretical core of evolutionary biology. Stephens ("Population Genetics") recounts the history of the origins of population genetics, and reviews central debates in the history of the theory. He also considers a number of conceptual issues about representation and explanation that arise in the context of theoretical population genetics. Okasha ("Units and Levels of Selection") reviews the conceptual as well as empirical issues at stake in the debate over the units and levels of selection and gives a history of the debate from Darwin to the present day. He shows how this debate is tied to concerns about the evolution of altruism, the plausibility of group and kin selection, species selection and macroevolution, and concludes with a review of multilevel selection theory. Dietrich ("Molecular Evolution") describes the rise of the neutral theory of molecular evolution, and discusses how debates over drift versus selection in molecular evolution are exemplary of relative significance debates in biology.

One area that has received relatively little attention in philosophy of biology is the relationship between micro- and macro-evolution, and in particular, issues surrounding how hypotheses about change at and above the species level are tested. Plutynski ("Speciation and Macroevolution") addresses this question, and reviews recent empirical and theoretical work on speciation, the punctuated equilibrium debate, and questions about the disparity and evolvability. Finally, Godfrey-Smith and Wilkins ("Adaptationism") trace the history of the debate over "adaptationist" thinking, nicely demarcating different senses of adaptationism: empirical, explanatory, and methodological. In conclusion, they suggest a resolution to some of the controversy by illustrating how various alternatives might be resolved through careful attention to the grain at which evolutionary processes are being described.

The section on "Developmental Biology" contains three important contributions. Kaplan ("Phenotypic Plasticity and Reaction Norms") returns to the question of the relation between genotype and phenotype, already explored earlier by Lewontin. Once again the emphasis is on the complexity of this relation, which was largely ignored in classical genetics. Much of modern evolutionary theory was formulated at the genotypic level, ignoring the complexities of organismic development. The received view is that development can be put in a "black box" and phenotypic change tracked by recording changes at the genotypic level. However, it has long been recognized that, eventually, to understand the evolution of phenotypes, we must understand how developmental mechanisms have evolved. The past decade has seen a lot of excitement in evolutionary developmental biology, which many biologists now hold as finally

successfully integrating evolutionary biology and studies of development. Amundson ("Development and Evolution") puts these studies in historical perspective, analyzing the long, sometimes idiosyncratic, and largely unsuccessful past attempts to integrate the two disciplines. It is an open question whether the near future will be much different from the past. In "Explaining the Ontogeny of Form: Philosophical Issues," Love provides a survey of issues surrounding the explanation of the ontogeny of form. He provides a philosophical framework for approaching different kinds of explanations in developmental biology, and addresses a variety of related epistemological and ontological issues; among them: representation, explanation, typology, individuality, model systems, and research heuristics.

The next section ("Medicine") takes up the relatively underexplored field of health and disease. One area that has received relatively little attention among philosophers of biology is immunology. Howes ("Self and Nonself") considers how philosophers can play a critical role in analyzing the conceptual foundations and empirical justifications of different models of self and nonself deployed in immunology. Murphy ("Health and Disease") considers "objectivist," "constructivist," and "revisionist" perspectives on health and disease, and focuses his discussion on the role of norms in judgments concerning mental illness.

The "Ecology" section summarizes much of the recent work on the philosophy of ecology, another area of the philosophy of biology that is receiving increased attention in recent years. Perhaps the most theoretically mature part of ecology is population ecology, and Colyvan ("Population Ecology") summarizes the philosophical work on the subject, showing how this is a fertile area to explore questions such as the role of laws and theories in biology. Justus ("Complexity, Diversity, and Stability") turns to a central issue in community ecology, whether there is any relation between diversity and stability. He shows how the concepts of diversity and stability (and, also, though to a lesser extent, complexity) can be interpreted in a variety of inconsistent ways, making it almost impossible to answer this question.

In the context of our increasing concern for the environment, Peacock ("Ecosystems") describes recent thinking on ecosystems, including work done within science, and philosophically intriguing ideas at the fringe of science such as the Gaia hypothesis. Turning to conservation biology, Norton ("Biodiversity and Conservation") shows how the concept of biodiversity is both descriptive (capturing some feature of habitats) and normative (reflecting the values people have which make them want to preserve nature). He also embeds philosophical discussions of biodiversity in the context of environmental policy.

The next section turns to mental and cultural life ("Mind and Behavior"), about which there is perhaps more scientific controversy than in any other area explored in depth by philosophers of biology. Griffiths ("Ethology, Sociobiology, and Evolutionary Psychology") gives a historical analysis that shows the deep connection between mid-twentieth-century ethology, human sociobiology, and contemporary Evolutionary Psychology. He notes that, while there is no reason to doubt that mental features are results of biological and cultural evolution, the research program of contemporary "Evolutionary Psychology" makes many controversial assumptions that should be scrutinized carefully. Alexander ("Cooperation") takes up recent approaches to the evolution of cooperative behavior including the many applications of game theory.

Finally, Bickerton ("Communication and Language") explores what we do and do not know about the emergence and evolution of human language and notes both the analogies and disanalogies between language and animal communication systems.

The final section ("Experimentation, Theory, and Themes") takes up a variety of general issues in the philosophy of biology, ranging from metaphysical issues about how to define life, or whether there are biological laws, to epistemological issues about how biologists investigate the living world. Bedau ("What is Life?") explores the variety of attempts to set out conditions for "life," and discusses how and why this question has become especially pressing with recent research into artificial life. Weber ("Experimentation") analyzes the special difficulties and characteristics of experimental work in biology. He considers the roles of model organisms, the limitations and advantages of laboratory work in biology, and the nature of evidence and objectivity in the biological sciences.

Many philosophers hold that biology is not at all like physics insofar as there are no "laws" of biology; however, Lange ("Is Biology Like Physics?") argues to the contrary. He considers the objection that laws of biology are not exceptionless and non-accidental, and argues, using a number of different examples, that lawful generalizations are an integral part of evolutionary biology. While it is uncontroversial that models and modeling are central to empirical and theoretical work in all branches of biology, philosophers do not agree on what a "model" is. Odenbaugh ("Models") reviews philosophical work on models, starting with the logical empiricists, explaining the subtle differences between the syntactic and semantic view of theories, and discusses a variety of historical and recent work on models and metaphors, and models as "mediators" between theory and data in the biological sciences.

It is hard to imagine biology without talk of functions but there is little philosophical agreement on what a function is. Garson ("Function and Teleology") gives a comprehensive review of the philosophical literature on functions, from etiological to consequentialist theories of function, and concludes with a defense of pluralist and context-dependent approaches to assignments of function. Yet another contentious issue in philosophy of biology has been the claim whether biological facts are reducible to molecular chemical or physical facts. Rosenberg ("Reductionism in Biology") takes a radical stance on this question, arguing that while the reducibility of theories, as the logical empiricists understood it, is implausible, generalizations in functional biology can and should be reduced, in the sense of being "completed, corrected, made more precise or otherwise deepened" by "fundamental explanations in molecular biology."

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