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Philosophy of Biology

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LAST MODIFIED: 27 APRIL 2017
DOI: 10.1093/OBO/9780195396577-0341

Introduction

Philosophy of biology is a branch of philosophy of science that centers on philosophical issues concerning biology. While philosophical interest in biology has a long history, philosophy of biology as semi-autonomous discipline originated in the 1970s, with an international society (the International Society for the History, Philosophy, and Social Studies of Biology) and dedicated academic journals from the 1980s onward. One of the original motivations for pursuing a philosophy of biology was in reaction to the dominant focus on physics in philosophy of science, where the treatment of topics such as “explanation” and “laws” was felt to be unsatisfactory in the context of biology. For example, many explanations in physics involve general laws, but biology involves few if any basic laws. Thus, philosophy of biology informs and provides a context for larger questions in the philosophy of science. However, a lot of work in the philosophy of biology is pursued independently of problems in the general philosophy of science. Such work concerns issues specific to biology, and such accounts are not always generalizable. From its inception, philosophy of biology has been heavily focused on philosophy of evolutionary biology. This, among other reasons, reflects both the central place of evolution within biology, and the implications that evolution has for traditional philosophical topics, such as morality and human nature. However, over the decades, philosophy of biology has branched out to other domains, such as microbiology and ecology. A development that has run in parallel to this growth has been the increasing collaboration between philosophers and biologists. Such collaboration has become increasingly common in areas at the frontier of research, such as the topics concerning the extended synthesis. As a consequence, philosophical work has often become more focused on specific conceptual problems directly relevant for empirical practice, producing more tailor-made accounts that are not easily generalizable.

General Overviews

Given the wide range and depth of the field of philosophy of biology, general overviews invariably involve a selection of topics. The following offer overviews of the field, or of a specific subfield, and are particularly useful for those new to the philosophy of biology. Sterelny and Griffiths 1999 offers one of the broadest introductions and could be a good place to start for those new to the field. Sober 2000 is less broad and has less biological detail than Sterelny and Griffiths 1999, but it is philosophically rich and serves as a good window into philosophy of biology—especially for readers without a substantial biology background. Rosenberg and McShea 2008 and Godfrey-Smith 2014 focus on some central and cutting-edge topics in the discipline and allow one to see what direction research in the field is taking.

Godfrey-Smith, Peter. *Philosophy of Biology*. Princeton, NJ: Princeton University Press, 2014.

Includes discussion of biological laws, information, social behavior, genes, and evolutionary biology.

Greene, Marjorie, and David Depew. *The Philosophy of Biology: An Episodic History*. Cambridge, UK: Cambridge University Press, 2004.

An overview with an historical focus, this book explores philosophical topics in the history of biology and the history of philosophical treatments of biology from Aristotle onward.

Lloyd, Elisabeth Anne. *The Structure and Confirmation of Evolutionary Theory*. Princeton, NJ: Princeton University Press, 1994.

Analyzes structure and semantics of evolutionary theory. Especially focused on population genetics and the levels of selection debate.

Mayr, Ernst. *Toward a New Philosophy of Biology: Observations of an Evolutionist*. Cambridge, MA: Harvard University Press, 1988.

Written by one of the most important evolutionary biologists of the 20th century, this explores many of the central topics in the philosophy of evolutionary biology.

Pigliucci, Massimo, and Jonathan Kaplan. *Making Sense of Evolution: The Conceptual Foundations of Evolutionary Biology*. Chicago: University of Chicago Press, 2006.

A discussion of the basic evolutionary concepts, with special attention for the levels of selection, adaptationism, adaptive landscapes, and the species problem.

Rosenberg, Alexander, and Daniel W. McShea. *Philosophy of Biology: A Contemporary Introduction*. New York: Routledge, 2008.

Covers biological laws, reductionism, complexity, progress, the levels of selection, human nature, and related topics.

Sober, Elliott. *Philosophy of Biology*. Boulder, CO: Westview, 2000.

Overview mainly focused on fundamental conceptual issues in the philosophy of evolutionary biology.

Sterelny, Kim, and Paul E. Griffiths. *Sex and Death: An Introduction to Philosophy of Biology*. Chicago: University of Chicago Press, 1999.

Classic overview of philosophy of biology with a wide range of topics, from evolutionary biology and development to genetics and human nature.

Reference Works

The *Stanford Encyclopedia of Philosophy* contains a number of excellent general overviews of philosophy of biology, as well as overviews of entire subdomains within philosophy of biology (e.g., conservation biology, developmental biology, molecular biology). The *Wiley Encyclopedia of Life Sciences* has seventy-seven contributions on “Philosophy and the Life Sciences.” Griffiths 2008 and Hull

2001 are the most general articles from each of these two sources. Another resource that focuses on current research in philosophy is the journal *Philosophy Compass*. It does not provide general overviews of philosophy of biology but instead offers insight into the state of some recent debates.

Griffiths, Paul. "Philosophy of Biology." In *The Stanford Encyclopedia of Philosophy*. Edited by Edward N. Zalta, 2008.

Offers a brief general overview of core areas of research in the philosophy of biology—and a starting point for other *Stanford Encyclopedia of Philosophy* articles in the philosophy of biology.

Hall, Brian K. *Keywords and Concepts in Evolutionary Developmental Biology*. Cambridge, MA: Harvard University Press, 2006.

Includes a discussion of fifty key concepts in evolutionary developmental biology.

Hull, David L. "Philosophy of the Life Sciences." Wiley Online Library, 2001.

An overview of philosophy of biology centering on evolutionary biology, development, and sociobiology.

Keller, Evelyn Fox, and Elisabeth A. Lloyd. *Keywords in Evolutionary Biology*. Cambridge, MA: Harvard University Press, 1994.

Offers extended discussions by biologists and philosophers of key concepts in evolutionary biology.

Anthologies

There are a number of excellent anthologies that are helpful both as introductions to philosophy of biology and as teaching resources. Ruse 2008, Hull and Ruse 2008, and Sarkar and Plutynski 2008 are collections of contributed essays, while Rosenberg and Arp 2010 and Sober 2006 are anthologies of classic papers. Ayala and Arp 2009 introduces central debates as pairs of opposing essays.

Ayala, Francisco, and Robert Arp. *Contemporary Debates in Philosophy of Biology*. Oxford: Wiley-Blackwell, 2009.

Offers pairs of essays staking out opposing views on topics in the philosophy of biology.

Hull, David J., and Michael Ruse, eds. *The Cambridge Companion to the Philosophy of Biology*. Cambridge, UK: Cambridge University Press, 2008.

Some chapters concern particular concepts (such as information or embryo), while others focus on fields within the philosophy of biology (such as ecology or neurobiology).

Rosenberg, Alexander, and Robert Arp, eds. *Philosophy of Biology: An Anthology*. Oxford: Wiley-Blackwell, 2010.

A collection of thirty of the most important articles published over the previous four decades in the philosophy of evolutionary biology.

Ruse, Michael, ed. *The Oxford Handbook of Philosophy of Biology*. Oxford: Oxford University Press, 2008.

Twenty-five essays on a wide range of topics in the philosophy of biology.

Sarkar, Sahotra, and Anya Plutynski, eds. *A Companion to the Philosophy of Biology*. Oxford: Blackwell, 2008.

A companion focusing on topics that often receive less attention, including molecular biology, genetics, developmental biology, medicine, and ecology.

Sober, Elliott, ed. *Conceptual Issues in Evolutionary Biology*. Cambridge, MA: MIT, 2006.

Covers the major areas of philosophical research within evolutionary biology.

Basic Evolutionary Concepts

One major area of research in the philosophy of biology concerns explicating and clarifying the concepts at the foundation of evolutionary theory. These basic concepts include fitness, drift, adaptation, and function.

Natural Selection

Natural selection is at the heart evolutionary theory, and its original target was to explain how organisms can be adapted to their environments without being divinely created. The concept of natural selection is a rich one and has spawned a number of debates in the philosophy of biology dedicated to various aspects of natural selection (see Fitness, Function, Levels of Selection, Adaptationism, Causal Nature of Natural Selection). As a consequence, there is no single debate dedicated to natural selection in all its aspects. Nonetheless, Sober 1984 and Brandon 1990 are central works that synthesize the various issues concerning natural selection into a comprehensive vision.

Brandon, Robert. *Adaptation and Environment*. Princeton, NJ: Princeton University Press, 1990.

Offers a conception of fitness and selection and focuses on articulating the concept of environment and its role in understanding adaptive evolution.

Sober, Elliot. *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. Chicago: Chicago University Press, 1984.

A canonical statement of the interpretation of natural selection as a causal force, in analogy to Newtonian forces. It introduces important concepts into the selection literature, such as that of selection-for versus selection-of.

Fitness

Evolution by natural selection operates through the fitter individuals prospering and passing on their traits at a disproportionate rate. But what precisely is fitness? If it is equivalent with reproductive success, then it appears one cannot explain evolutionary outcomes in terms of fitness, since such outcomes simply are fitness. Philosophers have answered this question mainly by arguing that fitness is a propensity: Brandon 1978 took this approach early on. Specifying what this propensity is and how to characterize it mathematically,

while answering the skeptical arguments of the statistical approach to fitness and natural selection (see Causal Nature of Natural Selection), has been the central current of the fitness debates. Characterizing the nature of this propensity is no trivial task, as Beatty and Finsen 1989 show. It may require new mathematical models and conceptual advances, as suggested by Pence and Ramsey 2013.

Beatty, John H., and Susan Finsen. "Rethinking the Propensity Interpretation of Fitness: A Peek Inside Pandora's Box." In *What the Philosophy of Biology Is: Essays for David Hull*. Edited by Michael Ruse, 18–30. Dordrecht, The Netherlands: Kluwer Academic, 1989.

This shows that the propensity interpretation of fitness is rife with difficult problems. In particular, quantifying fitness as the expected number of offspring is subject to counterexamples—cases in which organisms have different fitness values, yet the same expected number of offspring.

Brandon, Robert N. Adaptation and Evolutionary Theory." *Studies in History and Philosophy of Science Part A* 9 (1978): 181–206.

This is the first attempt at offering a propensity interpretation of fitness. It quantifies fitness in terms of expected number of offspring.

Pence, Charles H., and Grant Ramsey. A New Foundation for the Propensity Interpretation of Fitness." *British Journal for the Philosophy of Science* 64 (2013): 851–881.

This paper takes seriously the problems raised by the Beatty and Finsen article. It shows that they are right that the propensity interpretation of fitness is associated with a problematic mathematical foundation and is subject to counterexamples. This paper then offers a new mathematical foundation in an attempt to avoid these counterexamples.

Drift

Evolution sometimes occurs in ways that are not expected given the fitness values associated with members of the population. Fitter types do not always leave the most descendants, and evolution can even occur in absence of fitness differences. This failure of a match between fitness differences and reproductive outcomes is linked to the concept of drift. But specifying what drift precisely is and how it differs from selection (if at all) is a challenge. Can drift cause evolutionary outcomes? Or is it merely a way of characterizing these outcomes? Or is drift perhaps a kind of evolutionary process? Millstein 2002 argues that drift is a distinct kind of evolutionary process, Gildenhuys 2009 holds that it is instead a kind of cause, while Ramsey 2013 offers a new concept, driftability, which is intended to identify the cause of drift.

Gildenhuys, Peter. An Explication of the Causal Dimension of Drift." *British Journal for the Philosophy of Science* 60 (2009): 521–555.

Argues that drift is not a process but rather a class of causes—ones that are non-interactive, non-pervasive, and indiscriminate.

Millstein, Roberta L. Are Random Drift and Natural Selection Conceptually Distinct?" *Biology and Philosophy* 17 (2002): 33–53.

Argues that drift is a distinct kind of process, one in which the physical differences among individuals are not causally relevant to differences in reproductive success.

Ramsey, Grant. "Driftability." *Synthese* 190 (2013): 3909–3928.

Offers a new concept, driftability, which is argued to be the foundation for drift.

Function

With the advent of the theory of natural selection, teleology no longer seemed necessary to explain the apparent design of the traits of organisms. Nonetheless teleological notions such as function have survived. There has been a long-standing debate concerning the precise account of what functions mean and how they can be defined in a way that does justice to scientific practice and yet does not invoke any final causes. Wright 1973 argues how function can be defined in terms of selective past, whereas Cummins 1975 focuses more on defining function in terms of present capacities.

Cummins, Robert. "Functional Analysis." *Journal of Philosophy* 72 (1975): 741–765.

A classic articulation of the causal role account of function.

Millikan, Ruth G. "In Defense of Proper Functions." *Philosophy of Science* 56 (1989): 288–302.

An influential defense of the etiological account of function.

Wright, Larry. "Functions." *Philosophical Review* 82 (1973): 139–168.

A foundational paper on the etiological account of function.

Levels and Individuals

Ontological questions concerning biological individuals and levels of selection go to the heart of biological practice and yet are philosophically controversial. There are dedicated philosophical debates on these notions, but results from these debates have been applied to various other issues, including altruism, major transitions in evolution, and reductionism.

Biological Individuality

Being able to distinguish between and count biological individuals is crucial for both biological theory and biological practice. For example, evolution is often quantified in terms of rates of change in the frequency of individual genes or traits. To count individuals, we must first individuate them. Within the topic of biological individuality, three separate philosophical subdebates may be distinguished. The first centers on explicating the concept of biological individuality. The second concerns how individuality has changed over the course of evolutionary history and is closely related to the debate concerning major transitions in evolution. The third attempts to draw lessons for metaphysics from the first two, in particular with regard to the tenability of essentialism. Buss 1987 is a classic work in the field and a good place to begin for those wanting to examine these issues in depth. Michod 1999 considers the issue of individuality in relation to evolutionary transitions, while Pradeu 2012 considers it from the perspective of immunology.

Buss, Leo W. *The Evolution of Individuality*. Princeton, NJ: Princeton University Press, 1987.

Includes discussion of the evolution of development, life-cycle evolution, and the evolution of hierarchical organization.

Michod, Richard. *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton, NJ: Princeton University Press, 1999.

Analyzes how lower-level units (gene, chromosome, genome, cell, multicellular organism) combine into higher levels of organization through cooperation.

Pradeu, Thomas. *The Limits of the Self*. Oxford: Oxford University Press, 2012.

Addresses the problem of biological identity from the perspective of immunology.

Wilson, Jack. *Biological Individuality: The Identity and Persistence of Living Entities*. Cambridge, UK: Cambridge University Press, 1999.

Argues that evolutionary theory need not imply anti-essentialism and defends sortal essentialism.

The Levels of Selection

Evolution by natural selection, as described in Darwin's *On the Origin of Species*, is something that primarily occurs among competing organisms of the same species within a population. However, as the abstract conditions for natural selection became clearer, biologists realized that natural selection could act on other biological entities, such as on competing genes or groups of organisms. Philosophical debate arises here out of the fact that the conditions for natural selection are often imperfectly realized at these other levels. This has led to the question whether natural selection truly acts on these other levels and whether it has causal import, or whether natural selection at these other levels is to be understood as a mere metaphor. Lewontin 1970 is a classic and is worth reading for anyone interested in the nature of selection. Lloyd 2001 offers a useful perspective on what the levels of selection debate is all about. Okasha 2006 is valuable if one wants an in-depth treatment of the philosophical debates about levels of selection.

Lewontin, Richard C. "The Units of Selection." *Annual Review of Ecology and Systematics* 1 (1970): 1–18.

A classic paper on the topic of levels of selection, formulating the abstract conditions for natural selection.

Lloyd, Lisa. Units and Levels of Selection: An Anatomy of the Units of Selection Debates." In *Thinking about Evolution: Historical, Philosophical, and Political Perspectives*. Vol. 2. Edited by Rama Shankar Singh, Costas B. Krimbas, Diane B. Paul, and John Beatty, 267–291. Cambridge, UK: Cambridge University Press, 2001.

Argues that the units and levels of selection debates center on four distinct questions.

Okasha, Samir. *Evolution and the Levels of Selection*. Oxford: Oxford University Press, 2006.

A comprehensive overview of the levels of selection debates.

Altruism

Evolution by natural selection is often characterized as selfish: organisms are selected to maximize their individual fitness. But the behavior of humans and other species often appears altruistic, where individuals help one another, at times at a considerable cost to themselves. Two questions arise: first, do such behaviors genuinely constitute altruism? Or are they merely a result of a sophisticated egotism? Second, if such behaviors are truly altruistic, how can they have evolved through natural selection? Trivers 1971 is an early attempt at identifying and accounting for reciprocal altruism. West, et al. 2007 offers a useful overview of a host of related concepts, such as altruism and cooperation. Wilson 2015 is an approachable argument for the existence of genuine altruism.

Birch, Jonathan. "Hamilton's Rule and its Discontents." ***British Journal for the Philosophy of Science*** **65 (2014): 381–411.**

A discussion of Hamilton's rule—one of the tools used to explain altruism—and recent controversies concerning its explanatory power.

Trivers, Robert L. "The Evolution of Reciprocal Altruism." ***Quarterly Review of Biology*** **46 (1971): 35–57.**

A classic paper showing how reciprocal altruism can evolve and can be individually advantageous.

West, Stuart A., Ashleigh S. Griffin, and Andy Gardner. "Social Semantics: Altruism, Cooperation, Mutualism, Strong Reciprocity and Group Selection." ***Journal of Evolutionary Biology*** **20 (2007): 415–432.**

An attempt to clarify and distinguish key concepts related to altruism, including kin selection, benefit, reciprocity, and direct fitness.

Wilson, David Sloan. ***Does Altruism Exist? Culture, Genes, and the Welfare of Others*****. New Haven. CT: Yale University Press, 2015.**

Covers altruism in nonhuman animals as well as humans. Focuses on human altruism, discussing psychological altruism, religion, economics, and everyday life.

Major Transitions

Major transitions refer to certain crucial events or stages in macroevolutionary history where in many cases the natures of individuality and heredity of the units of selection have been changed. Originally proposed by Maynard Smith and Szathmáry 1995, major transitions remain controversial, and the volume Calcott and Sterelny 2011 focuses on various problems facing the notion. Philosophical discussions of the major transitions are related to the level of selection debate but also to the literature on complexity and on large-scale trends in evolution.

Calcott, Brett, and Kim Sterelny, eds. ***The Major Transitions in Evolution Revisited*****. Cambridge, MA: MIT, 2011.**

A collection of essays that critically examine the concept of major transition, or explore philosophical consequences for issues surrounding biological individuality, levels of selection, and contingency in macroevolution.

Maynard Smith, John, and Eörs Szathmáry. ***The Major Transitions in Evolution*****. Oxford: Oxford University Press, 1995.**

The original text introducing the concept of major transition and identifies eight such transitions in the history of evolution, ranging from the origin of chromosomes to the origin of social groups and human society.

Reductionism

Reductionism in the philosophy of biology refers to a variety of issues. One of the most important includes the derivation of particular concepts or laws at one level of organization from what might be considered a more basic level of organization. Another important aspect of the debate about reductionism concerns how entire subfields of biology relate to each other, such as the relationship between classical genetics and molecular genetics. Kitcher 1984 argues against reducing classical genetics to molecular genetics, while Waters 1990 is skeptical of arguments for nonreduction. Rosenberg 2006 explores an explicitly reductionist picture.

Kitcher, Philip. "1953 and all that: A Tale of Two Sciences." ***Philosophical Review*** **93 (1984): 335–373.**

Considers reductionism in the case of classical and molecular genetics.

Rosenberg, Alexander. ***Darwinian Reductionism: Or, How to Stop Worrying and Love Molecular Biology*****. Chicago: University of Chicago Press, 2006.**

Argues for reductionism and suggests that one cannot be a physicalist without being a reductionist.

Waters, C. Kenneth. Why the Anti-reductionist Consensus won't Survive: The Case of Classical Mendelian Genetics. ***Proceedings of the Biennial Meeting of the Philosophy of Science Association*** **1 (1990): 125–139.**

Aims to undercut the arguments in favor of the non-reducibility of Mendelian genetics to molecular biology.

Macroevolution and Classification

Macroevolution is commonly understood to involve evolution of species and higher taxa (as opposed to evolution of populations) and raises its own set of distinctive philosophical problems. The first concerns how the history of evolutionary lineages—phylogeny—should be reconstructed given different sources of evidence, including morphological and DNA evidence. Phylogeny is used in biological practice to define species and, in general, classify biological organisms into various taxa. However, this practice raises a host of issues concerning the identity of species: Are they natural or historical kinds? Can they have essences? Are they to be thought of as individuals? Finally, a broad range of issues arise concerning the shape of macroevolutionary history. What role does contingency play, are there any trends, and is there such thing as progress over evolutionary history?

Phylogenetics

Phylogenetics is the reconstruction of evolutionary history through genealogical lineages, often represented by phylogenetic trees or networks. Philosophical issues arise concerning the values governing phylogeny choice (e.g., simplicity, empirical adequacy), how data are classified (e.g., what homology is), and the reliability of different methods for inferring a certain phylogeny given certain evidence. Sober 1988 is a sustained and multifaceted analysis of explanation in phylogenetics, and Velasco 2013 provides a recent overview of the key sub-debates in this area.

Sober, Elliott. ***Reconstructing the past: Parsimony, Evolution and Inference*****. Cambridge, MA: MIT, 1988.**

One of the first substantial works on the philosophical problems arising from phylogenetics.

Velasco, Joel D. "Philosophy and Phylogenetics." *Philosophy Compass* 10 (2013): 990–998.

An introduction describing the main contemporary areas of debate within the philosophy of phylogenetics.

Species

A topic with links to the debates about biological individuality and levels of selection (species selection in particular), the main question here concerns whether species are classes—where traits or combinations of traits define membership conditions for individual organisms—or individuals, where individual organisms are constituents of species, and species are four-dimensional entities. Ghiselin 1974 and Hull 1976 are the classic papers defending the account that species are individuals, whereas Mishler and Brandon 1987 are skeptical of this approach and propose a phylogenetic account instead. Wilkins 2009 is an historical overview of species concepts.

Ghiselin, Michael T. "A Radical Solution to the Species Problem." *Systematic Zoology* 23 (1974): 536–544.

Comparing species to firms, this article is first proposal that species are individuals, defining species as "the most extensive units in the natural economy such that reproductive competition occurs among their parts" (p. 538).

Hull, David. "Are Species Really Individuals?" *Systematic Zoology* 25 (1976): 174–191.

A classic elaboration of Ghiselin's proposal that species are individuals.

Mishler, Brent D., and Robert N. Brandon. "Individuality, Pluralism and the Phylogenetic Species Concept." *Biology and Philosophy* 2 (1987): 397–414.

Identifies four components to the notion of individual—having spatial boundaries, temporal boundaries, integration, and cohesion. Proceeds to criticize the individuality account and formulates an alternative phylogenetic concept, where species are understood as a monophyletic group.

Wilkins, John S. *Species: A History of the Idea*. Berkeley: University of California Press, 2009.

Outlines the history of our understanding of species as well as an overview of modern species debates.

Chance, Contingency, and Historicity

Macroevolution is characterized by many random events that yet seem to have a decisive impact on how evolution occurs. The question then arises how to understand the relative importance of contingent events in evolutionary history as opposed to global trends or evolutionary convergence. Beatty 2006 identifies two main contingency concepts, and Desjardins 2011 connects this with the notion of path-dependence. Ramsey and Pence 2016 explores different facets of the concept of evolutionary chance.

Beatty, John. "Replaying Life's Tape." *Journal of Philosophy* 103 (2006): 336–362.

A systematization of different senses in which evolutionary events may be considered contingent.

Desjardins, Eric. "Reflections on Path Dependence and Irreversibility: Lessons from Evolutionary Biology." *Biology and Philosophy* 26 (2011): 339–364.

Uses the notion of path-dependence to further formalize different senses of contingency and historicity.

Ramsey, Grant, and Charles Pence. *Chance in Evolution*. Chicago: University of Chicago Press, 2016.

Offers chapters from historians, philosophers, and biologists on the history of chance in evolution, on core concepts related to change (such as randomness, stochasticity, and historicity), and on what contemporary research in paleontology and experimental evolution shows about chance in life's history.

Trends and Complexity

A long-standing concern in paleontology is whether there are any long-term macroevolutionary trends, and if so, whether there is a mechanism driving these trends. For example, complexity seems to have increased over evolutionary history, but, as Gould 1996 argues, it remains unclear whether that is simply the result of evolution randomly exploring biological possibilities from a state of minimal complexity. Other trends, such as increases in size or autonomy, have also featured prominently, but it is difficult to establish such trends against skeptical responses. McShea and Brandon 2010 attempts to establish a carefully defined trend in complexity that is immune to at least the most important skeptical arguments. Turner 2011 is a broad overview of various issues directly and indirectly concerning evolutionary trends.

Gould, Stephen J. *Full House: The Spread of Excellence from Plato to Darwin*. New York: Three Rivers Press, 1996.

Contains an influential critique of inferring trends from data.

McShea, Dan W., and Robert Brandon. *Biology's First Law: The Tendency for Diversity and Complexity to Increase in Evolutionary Systems*. Chicago: University of Chicago Press, 2010.

An argument, based on probabilistic analysis, that part-type diversity will tend to increase in evolution. The authors argue that this tendency constitutes a zero-force law in evolution (and is thus a rival to the Hardy-Weinberg law).

Turner, Derek. *Paleontology: A Philosophical Introduction*. Cambridge, UK: Cambridge University Press, 2011.

Overview of the philosophical issues arising from paleontology, including trends and complexity, as well as progress and contingency.

Progress

Since Darwin, the question of whether evolution is progressive has had wide ramifications for understanding the place of humans in the tree of life. Progress implies some improvement in evolution, often with similarity to human beings as the measure of improvement. This has been criticized by many as inapplicable to evolution, even though perhaps many biologists today, as Ruse 1996 argues, still implicitly hold to some belief in progress. Today, most scientific debate follows the line of thought in Ayala 1974 and Gould 1988 and concerns the more operationalizable notion of directionality rather than progress.

Ayala, Francisco J. "The Concept of Biological Progress." In *Studies in the Philosophy of Biology*. Edited by Francisco J.

Ayala and Theodosius Dobzhansky, 339–355. Berkeley: University of California Press, 1974.

Introduces the distinction between progress and directionality.

Gould, Steven J. "On Replacing the Idea of Progress with an Operational Notion of Directionality." In *Evolutionary Progress*. Edited by Matthew H. Nitecki, 319–338. Chicago: University of Chicago Press, 1988.

Criticizes the notion of progress in favor of directionality.

Ruse, Michael. *Monad to man: The Concept of Progress in Evolutionary Biology*. Cambridge, MA: Harvard University Press, 1996.

Traces how, in various ways, the concept of progress has influenced evolutionary thought from Darwin until today.

Microbiology and Molecular Biology

Evolution is the single domain within biology that sparks most philosophical interest; however, what is sometimes also called "experimental biology" is receiving increased attention. In the case of molecular biology, the philosophical interest goes back to the 1970s and 1980s, but the interest in microbiology and oncology is much more recent.

Philosophy of Microbiology

Biological theory has traditionally tended to search for paradigmatic examples among multicellular plants and animals. However, concepts designed with such examples in mind are not always transportable to the microbiological world of single-celled organisms. Franklin-Hall 2007 shows how this is the case for species concepts. For example, defining species in terms of reproductive isolation (the biological species concept) is not applicable to asexual species, where reproductively connected populations do not arise. Following the increased attention to microbiology among biologists, philosophers have examined how some fundamental biological concepts should be rethought. O'Malley and Dupré 2007 and especially O'Malley 2014 are multifaceted analyses of various issues in microbiology.

Franklin-Hall, Laura. "Bacteria, Sex, and Systematics." *Philosophy of Science* 74 (2007): 69–95.

Argues that species concepts that work well in the multicellular realm do not work for bacteria.

O'Malley, Maureen A. *Philosophy of Microbiology*. Cambridge, UK: Cambridge University Press, 2014.

A philosophical overview of microbial classification, evolution, and ecology.

O'Malley, Maureen A., and John Dupré. "Size doesn't Matter: Towards a More Inclusive Philosophy of Biology." *Philosophy of Biology* 22 (2007): 155–191.

A defense of the philosophical importance of issues in microbiology.

Philosophy of Molecular Biology

Ever since the discovery of DNA, molecular biology—the study of how the macromolecules central to life are constituted and interact with each other—has had a central place in biology. From a philosophical perspective, molecular biology raises questions concerning reductionism (can biology be reduced to molecular biology?), information (how can macromolecules transmit information?) and mechanism (how can macromolecular interaction be understood in terms of mechanistic causality?). Kitcher 1999, Darden 2006, and Weber 2006 are, respectively, important papers dealing with each of these topics. Hence there is important overlap with the sections dedicated to these issues; nonetheless, the philosophy of molecular biology is seen as a stand-alone subdomain. Sarkar 1996 is a broad overview of the subdomain.

Darden, Lindley. "Flow of Information in Molecular Biological Mechanisms." ***Biological Theory*** **1 (2006): 280–287.**

A discussion of the information metaphor in context of the protein synthesis mechanism.

Kitcher, Philip. "The Hegemony of Molecular Biology." ***Biology and Philosophy*** **14 (1999): 195–210.**

Argues against the view rigorous and complete biological explanations trace biological properties to interactions between molecules.

Sarkar, Sahotra, ed. ***Philosophy and History of Molecular Biology: New Perspectives*****. Dordrecht, The Netherlands: Kluwer, 1996.**

A collection of essays concerning various issues in the philosophy of molecular biology and essays on historical topics.

Weber, Marcel. "The 'Central Dogma of Molecular Biology' as a Thesis of Causal Specificity." ***History and Philosophy of the Life Sciences*** **28 (2006): 565–610.**

Argues that Crick's Central Dogma can be interpreted as a claim about the difference-making cause in protein synthesis.

Philosophy of Oncology

A new development in oncology has been to understand the origin and progression of cancer in terms of evolution by natural selection. The resulting conceptual problems concerning adaptationism, the nature of selection, and biological individuality are analyzed by philosophers of biology. Germain 2012 and Lean and Plutynski 2016 debate to what extent the progression of cancer can be explained in terms of natural selection. Bertolaso 2016 is an overview of this new subdomain.

Bertolaso, Marta. ***Philosophy of Cancer: A Dynamic and Relational View*****. Dordrecht, The Netherlands: Springer, 2016.**

Gives an overview of cancer biology and discusses epistemological and ontological questions related to cancer development.

Germain, Pierre-Luc. "Cancer Cells and Adaptive Explanations." ***Biology and Philosophy*** **27 (2012): 785–810.**

Argues that although natural selection acts on cancer cells, it does not play an important role in explaining the development of a cancer.

Lean, Christopher, and Anya Plutynski. "The Evolution of Failure: Explaining Cancer as an Evolutionary Process." *Biology and Philosophy* 31 (2016): 39–57.

Replies to Germain's argument, and highlights how selection is acting at different levels in the progression of a cancer.

Ecology and Conservation Biology

Ecology is the study of how organisms interact with each other and with their environment. Of specific interest is how population sizes grow and decline through such interactions. In this respect, ecology and conservation biology overlap significantly, as conservation biology seeks to make decisions about what possible human interventions are appropriate or desirable. And ideally such decisions would be grounded in a deep understanding of the ecological impact of those interventions on natural populations. Important philosophical questions in this area include: What does biodiversity mean? What are ecological communities and how can they be modeled? What norms should govern conservation decisions?

Philosophy of Ecology

Ecological systems are complex, with numerous interactions between many organisms within a population and between organisms and an ever-changing environment. A first problem that arises in light of this complexity is how ecological communities should be modeled, as any model inevitably needs to make a selection of variables. Colyvan, et al. 2009 contains a useful discussion of this issue. A second problem, explored in Odenbaugh 2007, concerns the identity of ecological communities: are such communities anything more than an aggregation of the individuals that constitute them? De Laplante, et al. 2011 is a collection of papers on the topic.

Colyvan, Mark, Stefan Linquist, William Grey, Paul E. Griffiths, Jay Odenbaugh, and Hugh P. Possingham. "Philosophical Issues in Ecology: Recent Trends and Future Directions." *Ecology and Society* 14 (2009): 22.

Considers the importance of philosophy of ecology to the philosophy of science, to ecology, and to conservation and policy.

de Laplante, Kevin, Bryson Brown, and Kent Peacock. *Philosophy of Ecology*. Amsterdam: Elsevier, 2011.

A collection of essays covering major areas in the philosophy of ecology.

Odenbaugh, Jay. "Seeing the Forest and the Trees." *Philosophy of Science* 74 (2007): 628–641.

Argues for realism concerning ecological communities.

Conservation Biology and Environmental Philosophy

Issues concerning the conservation of species and ecological habitats have become pressing as human economic development continues to lead to extinction of species and the destruction of habitats. However, extinction has been a fact of evolution since its inception, so to what extent should we even worry about conservation? A further problem concerns what biodiversity is, and whether it should be measured at the species level or a higher or lower taxonomic level. Sarkar 2005 offers an introduction to biodiversity and environmental philosophy, whereas Maclaurin and Sterelny 2008 is a rich and critical discussion of biodiversity. Warren 1990 articulates a feminist perspective on environmental philosophy.

Maclaurin, James, and Kim Sterelny. *What is Biodiversity?* Chicago: University of Chicago Press, 2008.

Investigates the different components of biodiversity and makes the case that the unity of biodiversity is species richness. Includes a discussion of whether biodiversity is intrinsically valuable.

Sarkar, Sahotra. *Biodiversity and Environmental Philosophy: An Introduction to the Issues*. New York: Cambridge University Press, 2005.

An overview of theoretical and ethical issues concerning biodiversity.

Warren, Karen J. "The Power and the Promise of Ecological Feminism." *Environmental Ethics* 12 (1990): 125–146.

Introduces a feminist perspective on environmental ethics, drawing a parallel between the patriarchal domination of women and the domination of nature.

Causation and Explanation

How precisely biology explains phenomena has long been a fascination for philosophers, partially because biological explanation seems to be so different from explanation in physics. This has spawned a large and multifaceted debate on laws, the structure of explanation, and the role of contingency and causality in biological explanation. Somewhat independently of this application of general philosophy of science to biology, there have been a number debates concerning the specific explanatory structure of natural selection, including the debates on adaptationism, adaptive landscapes, and the causal nature of natural selection.

Laws

Unlike generalizations in physics, generalizations in biology seem to admit of exceptions. The questions then arise whether such generalizations may be considered laws regardless, and if not, whether laws are even possible in biology. One important strategy, discussed in Lange 1995, for arguing that such generalizations are laws is the *ceteris paribus* strategy of adding conditions of applicability to the law. The main arguments against the possibility of laws draw variously on the contingency of biological phenomena (Beatty 1995) or their supervenience on lower-level entities and processes. A separate ongoing question, discussed for example in Sober 1997, concerns the causal interpretation of mathematical models in biology and whether generalizations arising from such models may be considered biological laws.

Beatty, John. "The Evolutionary Contingency Thesis." In *Concepts, Theories, and Rationality in the Biological Sciences*. Edited by Gereon Wolters and James G. Lennox, 45–81. Pittsburgh, PA: University of Pittsburgh Press, 1995.

An argument that biological generalizations either are mathematical, physical, or chemical, or are only contingently true.

Lange, Marc. "Are There Natural Laws Concerning Particular Biological Species?" *Journal of Philosophy* 92 (1995): 430–451.

A discussion of the ceteris-paribus strategy concerning laws in biology.

Sober, Elliott. "Two Outbreaks of Lawlessness in Recent Philosophy of Biology." *Philosophy of Science* 64 (1997): S458–S467.

An argument that mathematical generalizations in biology may be considered laws.

Biological Explanation

Regardless of whether laws or exceptionless generalizations are obtainable in biology, philosophers of biology have also considered the more general question of what forms biological explanations may take. One set of issues concerns what the role is of history in biological explanation, what the role is of chance, and how biological explanations may attain a certain degree of robustness. Another specific question is to what extent biological explanation can be analyzed within a single account of explanation (e.g., the causal approach), or whether there is an unavoidable pluralism of forms of biological explanation. Woodward 2010 and Mitchell 2003 take contrasting approaches to this question. In general, discussions of biological explanation often overlap with philosophical discussions about laws in biology, and with general discussions about the nature of scientific explanation. Braillard and Malaterre 2015 is dedicated to mapping the various forms of biological explanation.

Braillard, Pierre-Alain, and Christophe Malaterre, eds. *Explanation in Biology: An Enquiry into the diverSity of Explanatory Patterns in the Life Sciences*. Dordrecht, The Netherlands: Springer, 2015.

A collected volume of papers surveying different forms of explanation in biology, including mechanistic, mathematical, and heuristic explanation.

Huneman, Philippe. "Topological Explanations and Robustness in Biological Sciences." *Synthese* 177 (2010): 177–213.

Explores the structure of noncausal and nonmechanistic explanation in biology and argues that topological properties of systems (robustness, fragility, etc.) may be considered explanatory.

Mitchell, Sandra. *Biological Complexity and Integrative Pluralism*. Cambridge, UK: Cambridge University Press, 2003.

A defense of explanatory pluralism, arguing that the varieties of complexity exhibited by biological systems call for different types of explanation.

Woodward, James. "Causation in Biology: Stability, Specificity, and the Choice of Levels of Explanation." *Biology and Philosophy* 25 (2010): 287–318.

The interventionist account of causal explanation in biology.

Adaptationism

Natural selection has long been seen as a central evolutionary cause, accounting for how organisms can be adapted to their environment. However, controversy arises as to just how important natural selection is in the evolution of traits relative to constraints and other evolutionary causes. Gould and Lewontin is a seminal work in bringing this to the attention of the scientific and philosophical communities. Ensuing philosophical debates have tried to analyze what it precisely means for a trait to be an adaptation—an issue discussed in Lloyd 2009—and to disentangle the ways in which natural selection could be said to dominate evolution as different senses of "adaptationism"—as done in Godfrey-Smith 2001.

Godfrey-Smith, Peter. "Three Kinds of Adaptationism." In *Adaptationism and Optimality*. Edited by Steven H. Orzack and Elliott Sober, 335–357. Cambridge, UK: Cambridge University Press, 2001.

Introduces the influential distinction between empirical, explanatory, and methodological adaptationism.

Gould, Stephen J., and Richard Lewontin. "The Spandrels of San Marco and the Panglossian paradigm: A Critique of the Adaptationist Programme." *Proceedings of the Royal Society B* 205 (1979): 581–599.

This classic paper argues that explaining a trait as an adaptation is only one among many possible evolutionary explanations. Also argues that natural selection does not always lead to adaptation and that adaptations can arise without natural selection.

Lloyd, Elisabeth Anne. *The Case of the Female Orgasm: Bias in the Science of Evolution*. Cambridge, MA: Harvard University Press, 2009.

Focusing on the female orgasm, this study considers what criteria are used in determining whether a trait is an adaptation and how biases in how we understand traits can play a role in whether we consider it an adaptation (and what we consider it to be an adaptation for).

The Causal Nature of Natural Selection

Natural selection is often referred to as a causal force driving evolution. However, how literally can this metaphor be taken? While natural selection is clearly not a fundamental physical force, does natural selection constitute a genuine cause of evolution, or is it merely a way of representing statistical patterns that occur in natural populations? Matthen and Ariew 2002 presents the skeptical argument toward the "causalist" position and offer a statisticalist interpretation of natural selection. Millstein 2006 is an important subsequent attempt to shore up the causal interpretation of natural selection. Otsuka 2016 provides a useful overview of the debate.

Matthen, Mohan, and André Ariew. "Two Ways of Thinking about Fitness and Natural Selection." *Journal of Philosophy* 99 (2002): 55–83.

An influential critique of the causalist view, and one of the first formulations of the statistical interpretation.

Millstein, Roberta. "Natural Selection as a Population-level Causal Process." *British Journal for the Philosophy of Science* 57 (2006): 627–653.

A defense of the causalist view, applying various difference-making accounts of causality to natural selection.

Otsuka, Jun. "A Critical Review of the Statisticalist Debate." *Biology and Philosophy* 31 (2016): 459–482.

Critically examines arguments for and against the statistical account of evolution by natural selection.

Adaptive Landscapes

Natural selection is sometimes understood as an optimizing process, driving populations to states of maximal fitness. This insight was visualized by Sewall Wright as natural selection pushing a population to peaks on a landscape, akin to how gravitation pulls objects to

valleys of minimal potential energy. However, there has long been skepticism toward the use of the metaphor, and toward the general idea that natural selection is an optimizing process. Gavrilets 2010 discusses how the metaphor becomes increasingly meaningless as the number of variables (traits, loci) determining fitness increases. Plutynski 2008 is a historical overview of adaptative landscapes, and Kaplan 2008 presents a skeptical account of adaptive landscape metaphors.

Gavrilets, Sergey. "High-dimensional Fitness Landscapes and Speciation." In *Evolution: The extended synthesis*. Edited by Massimo Pigliucci and Gerd B. Müller, 45–81. Cambridge, MA: MIT, 2010.

A survey of the problems associated with the landscape metaphor from a leading scientist for a philosophical audience.

Kaplan, Jonathan. "The End of the Adaptive Landscape Metaphor?" *Biology and Philosophy* 5 (2008): 625–638.

Argues that the adaptive landscape metaphor is incoherent; instead, we should rely solely on formal modeling without pictorial representation.

Plutynski, Anya. "The Rise and Fall of the Adaptive Landscape?" *Biology and Philosophy* 23 (2008): 605–623.

An overview of the current and past positions on the issue of adaptive landscapes.

Extended Synthesis

The modern synthesis was forged in the 1920s and 1930s by integrating Mendelian genetics into the Darwinian theory of evolution by natural selection, and presents a view of evolution as changes in gene frequencies through various mechanisms, including natural selection and mutation. While this paradigm has not been overthrown, since the 1970s and 1980s many have called for it to be extended. For example, while other forms of inheritance have been discovered rather than simply the transmission of genes, there is increased attention to how developmental mechanisms significantly constrain evolution and to the way in which natural selection shapes adaptive responses is understood to be more complicated than previously realized (through niche construction and plasticity). These phenomena are believed to be insufficiently accounted for in the Modern Synthesis and form the basis for what is loosely described as the Extended Synthesis. This frontier of evolutionary biology is continually changing; it is also a domain where interaction between biologists and philosophers is especially fruitful.

General Issues

It remains an open question what the extended synthesis actually involves and to what extent an extension of the modern synthesis is even necessary. Laland, et al. 2014 is an informative example of this debate. Further general issues concern key conceptual innovations involved in the extended synthesis, such as a rethink of causation discussed in Laland, et al. 2011. Pigliucci and Müller 2010 is a comprehensive overview of many different lines of research contained within the extended synthesis.

Laland, Kevin, Kim Sterelny, John Odling-Smee, William Hoppitt, and Tobias Uller. "Cause and Effect in Biology Revisited: Is Mayr's Proximate–Ultimate Dichotomy Still Useful?" *Science* 334 (2011): 1512–1516.

An argument that Mayr's distinction between proximate and ultimate causation is no longer adequate according to this article. And in light of phenomena such as niche construction, the causal nature of evolutionary processes needs to be recast in terms of "reciprocal causation."

Laland, Kevin, Tobias Uller, and Marc Feldman, et al. "Does Evolutionary Biology Need a Rethink?" *Nature* 514 (2014): 161–164.

A recent discussion in *Nature* between two camps of biologists and philosophers on whether or not the modern synthesis needs a revision and extension.

Pigliucci, Massimo, and Gerd B. Müller. *Evolution: The Extended Synthesis*. Cambridge, MA: MIT, 2010.

A collection of articles highlighting various aspects of the extended synthesis. Includes contributions about major transitions and about adaptive landscapes.

Evo-devo

Evolutionary developmental biology is a family of different research programs focusing on how development has changed over evolutionary history, and on how development may facilitate (through evolvability) or constrain evolution. This active role of development in evolution is of special interest for the extended synthesis. Arthur 2011 is a defense of the developmental approach. Amundson 2005 is a historical overview of the role of development, whereas Love 2015 focuses on some key philosophical problems.

Amundson, Ron. *The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo*. Cambridge, UK: Cambridge University Press, 2005.

Traces the changing importance of development for understanding evolution after Darwin, to its irrelevance for the modern synthesis, and how attention increased in the second half of the 20th century for the developmental perspective.

Arthur, Wallace. *Evolution: A Developmental Approach*. Oxford: Wiley-Blackwell, 2011.

An overview and defense of the developmental approach to evolution.

Love, Alan. "Evolutionary Developmental Biology: Philosophical Issues." In *Handbook of Evolutionary Thinking in the Sciences*. Edited by Thomas Heams, Philippe Huneman, Guillaume Lecointre, and Marc Silberstein, 265–283. Dordrecht, The Netherlands: Springer, 2015.

An overview of the philosophical issues that arise when taking a developmental perspective on evolution.

Homology and Convergence

Explaining similar (homoplastic) structures has always presented a special challenge for evolutionary biologists: is the similarity due to descent from a common ancestor (homology) or due to natural selection exerting pressure to find a similar solution to a similar problem (parallelism or convergence)? Inferring the cause of similarity is methodologically challenging, not least because it is not clear how parallelism, convergence, or homology should be defined. Hall 2003 provides an overview of homology and related concepts. Powell 2007 uses homology to formulate an argument skeptical of the idea that homoplasy is a form of convergence and links this to the question of macroevolutionary contingency. Ramsey and Peterson 2012 suggests that prior work on homology has not been sufficiently clear about how we should define homology and what evidence supports claims of homology. They offer a general framework that attempts to clarify homology and related concepts.

Hall, Brian K. "Descent with Modification: The Unity Underlying Homology and Homoplasy as Seen through an Analysis of Development and Evolution." ***Biological Reviews*** **78 (2003): 409–433.**

Through the lens of development and evolution, offers a conception of homology and clarifies a host of related concepts, including reversals, rudiments, vestiges, atavisms, and parallelism.

Powell, Russell. "Is Convergence More than an Analogy? Homoplasy and its Implications for Macroevolutionary Predictability." ***Biology and Philosophy*** **22 (2007): 565–578.**

A critical evaluation of convergence, argues for homology over convergence and connects it to issues concerning macroevolutionary contingency.

Ramsey, Grant, and Anne Siebel Peterson. "Sameness in Biology." ***Philosophy of Science*** **79 (2012): 255–275.**

Argues that the common way of describing homology in terms of similarity instead of sameness is problematic. It offers a novel conception of sameness and ties it to related concepts.

Plasticity and Accommodation

Plasticity, in the broadest sense of the term, is the phenomenon of environmentally induced phenotypic variation: developmental, physiological, or behavioral processes respond to the state of the environment to produce a phenotype. The importance of plasticity for understanding evolution lies in the fact that plasticity represents a source of variation other than genetic mutation. For instance, through phenotypic accommodation and genetic assimilation (which involves a change in genotype so that an adaptive phenotype is automatically produced), evolutionary change may be mediated by in first instance by plasticity and only second by genetic change. Pigliucci 2001 is a broad overview of plasticity research. West-Eberhard 2003 considers how plasticity may play a crucial role in macroevolution. DeWitt and Scheiner 2004 considers how we should understand the nature of plasticity.

DeWitt, Thomas J., and Samuel M. Scheiner, eds. ***Phenotypic Plasticity: Functional and Conceptual Approaches*****. New York: Oxford University Press, 2004.**

A collection of essays on conceptual issues relating to plasticity from leading researchers.

Pigliucci, Massimo. ***Phenotypic Plasticity: Beyond Nature and Nurture*****. Baltimore: Johns Hopkins University Press, 2001.**

A synthesis of research on plasticity. Argues that plasticity is a central concept in evolutionary biology, and considers plasticity from molecular, developmental, and ecological perspectives.

West-Eberhard, Mary Jane. ***Developmental Plasticity and Evolution*****. Oxford: Oxford University Press, 2003.**

A rich and wide-ranging book, the central thesis is that plasticity, together with the process of genetic accommodation, has played a major role in evolution. Genes are followers, not leaders in evolutionary change.

Evolvability and Modularity

Evolvability is roughly understood as a measure for a lineage's capacity to evolve. Some lineages are relatively constrained in their evolutionary possibilities and have low evolvability; other lineages are much more capable of change. Evolvability itself is thought to have evolved over time, and important changes in evolvability are sometimes linked to the major transitions, where new spaces of biological possibility were opened up. Various kinds of modularity, such as segmentation, are also often linked with evolvability, as modularity allows individual parts of organisms to vary more freely (without other parts having to coevolve). A specific philosophical debate has sprouted up concerning whether the multitude of uses of the term "evolvability" refers to a single underlying concept (as defended in Sterelny 2007 and Brown 2014), or whether there is no such underlying concept (Pigliucci 2008).

Brown, Rachael L. "What Evolvability Really is." ***British Journal for the Philosophy of Science*** **65 (2014): 549–572.**

An article that synthesizes much of the philosophical literature on this topic and offers a unified account of evolvability as an abstract and robust dispositional property. Distinguishes between a broad use of the concept of evolvability, describing how internal features of populations affect possible evolutionary trajectories, and a narrower use within evo-devo, where evolvability itself is an explanandum.

Calcott, Brett. "Engineering and Evolvability." ***Biology and Philosophy*** **29 (2014): 293–313.**

Draws an analogy between evolvability and engineering, highlighting the importance of modularity.

Pigliucci, Massimo. "Is Evolvability Evolvable?" ***Nature Reviews Genetics*** **9 (2008): 75–82.**

Offers a cluster-concept account of evolvability.

Sterelny, Kim. "What is Evolvability?" In ***Philosophy of Biology*****. Edited by Mohan Matthen and Christopher Stephens, 177–192. Amsterdam: Elsevier, 2007.**

Offers an account of evolvability in terms of the evolutionary potential of lineages.

Extended Inheritance and Epigenetics

The modern synthesis only recognizes inheritance though a single channel: the transmission of genes. An early philosophical debate emerged in reaction to Dawkins's concept of the extended phenotype and concerned whether the gene-centered view of evolution is justified. Griffiths and Gray 1994 and Sterelny, et al. 1996 are important contributions to this debate. Oyama 2000 is a fundamental critique of the gene-centric approach from perspective of developmental systems theory. Since then, advances in molecular biology and ecology have led to a further recognition of epigenetic inheritance and other channels of inheritance. Jablonka and Lamb 2005 is an important synthesis of this research.

Griffiths, Paul E., and Russell D. Gray. "Developmental Systems and Evolutionary Explanation." ***Journal of Philosophy*** **91 (1994): 277–304.**

Criticizes the gene-centered view of organisms and argues for a developmental systems approach.

Jablonka, Eva, and Marion J. Lamb. ***Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*****. Cambridge, MA: MIT, 2005.**

A synthesis of decades of research into extended inheritance by two prominent scientists in the field. Presents a vision of evolution where there are three other channels of inheritance besides genetic inheritance: epigenetic, behavioral, and symbolic inheritance.

Oyama, Susan. *The Ontogeny of Information: Developmental Systems and Evolution*. Durham, NC: Duke University Press, 2000.

An early treatment of developmental systems theory, criticizing key metaphors such as genetic programs and genes carrying information.

Sterelny, Kim, Kelly C. Smith, and Michael Dickison. "The Extended Replicator." *Biology and Philosophy* 11 (1996): 377–403.

Argues for an extension of Dawkins's replicator/interactor framework to include non-genetic replicators.

Niche Construction

Niche construction refers to how organisms modify their natural environment affecting the selection pressures acting on them. One significant consequence of niche construction is that an arrow of causality is introduced from population to selective environment, instead of there being only the arrow from selective environment to population that is recognized in the modern synthesis. Odling-Smee, et al. 2003 was one of the first authoritative statements on the importance of niche construction, and Laland, et al. 2005 provides an interesting discussion of philosophical issues raised in reviews by Paul Griffiths, Samir Okasha, and Kim Sterelny. Laland and Sterelny 2006 responds to skepticism toward the notion of niche construction.

Laland, Kevin N., John F. Odling-Smee, and Marcus W. Feldman. "On the Breadth and Significance of Niche Construction: A Reply to Griffiths, Okasha and Sterelny." *Biology and Philosophy* (2005): 37–55.

An informative discussion of some key conceptual problems facing niche construction. For the original reviews, see the journal *Biology and Philosophy*.

Laland, Kevin N., and Kim Sterelny. "Perspective: Seven Reasons (not) to Neglect Niche Construction." *Evolution* 60 (2006): 1751–1762.

A succinct defense of the important role of niche construction.

Odling-Smee, John F., Kevin N. Laland, and Marcus W. Feldman. *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton University Press, 2003.

An authoritative statement of what niche construction is and why it has played a significant role in evolution.

Biological Information

Given that genes guide development and can be transmitted from one generation to the next, they are sometimes interpreted in information-theoretic terms. This implies a view of evolution as a flow of information: the flow of genes and other units of inheritance is a

flow of information via distinct channels. Philosophical discussion has aimed at clarifying this metaphor and delineating its boundaries of applicability, with supportive (Maynard Smith 2000) and skeptical positions (Griffiths 2001). Godfrey-Smith 2007 is an overview of the usage of the information metaphor in biology.

Godfrey-Smith, Peter. "Information in Biology." In *The Cambridge Companion to the Philosophy of Biology*. Edited by David Hull and Michael Ruse, 103–119. Cambridge, UK: Cambridge University Press, 2007.

An overview of the research on applying information-theoretic concepts to biology.

Griffiths, Paul E. "Genetic Information: A Metaphor in Search of a Theory." *Philosophy of Science* 68 (2001): 394–412.

A critical response to Maynard Smith's article, arguing that the teleosemantic treatment of genes is unconvincing.

Maynard Smith, John. "The Concept of Information in Biology." *Philosophy of Science* 67 (2000): 177–194.

A defense of the information analogy.

Mind and Culture

The evolutionary perspective puts considerable pressure on one traditional view of the human mind as a disembodied intelligence separate from nature. For instance, evolutionary psychology has attempted to show how the human mind can be understood as a collection of special-purpose modules, each evolved to solve a specific problem in the human evolutionary past. However, it remains controversial to what extent biological evolution can explain the human mind, human behavior, and human culture. An important development, represented by research programs such as cultural evolution and evolutionary epistemology, has been to extend the evolutionary explanatory scheme to human culture and human beliefs by introducing new forms of inheritance and selection such as cultural selection.

Evolutionary Psychology

Evolutionary psychology is a research program that applies adaptationist thinking to the origin of mental faculties. Some core tenets are: (1) the human mind is largely adapted to the environment in which *Homo sapiens* spent most of its evolutionary history, (2) the human mind has a modular architecture, consisting of many different information-processing units, each specialized for solving some problem in the ancestral environment, and (3) pathological behaviors and thought processes can often be explained as being adaptive in the ancestral environment, but maladaptative in the current environment. Barkow, et al. 1992 contains the original authoritative statement of evolutionary psychology as a research program. Carruthers 2006 is an in-depth defense of the architectural hypothesis underlying evolutionary psychology: massive modularity. Frankenhuis and Ploeger 2007 is an overview of some sub-debates concerning the massive modularity hypothesis.

Barkow, Jerome H., Leda Cosmides, and John Tooby. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. Oxford: Oxford University Press, 1992.

The original authoritative statement of the evolutionary psychology research program. Contains a monograph-length first chapter about methodological and conceptual issues, and various contributions about specific topics, such as the psychology of parental care, sex, perception, and cooperation.

Carruthers, Peter. *The Architecture of the Mind: Massive Modularity and the Flexibility of Thought*. Oxford: Oxford University Press, 2006.

A defense of one of the key hypotheses of evolutionary psychology, namely that the human mind has a modular architecture.

Frankenhuis, Willem E., and Annemie Ploeger. "Evolutionary Psychology versus Fodor: Arguments for and Against the Massive Modularity Hypothesis." *Philosophical Psychology* 20 (2007): 687–710.

An overview of the conceptual issues surrounding evolutionary psychology.

Human Evolution

The philosophy of human evolution is a highly interdisciplinary domain, where philosophers have directly contributed to scientific investigation, and where scientific advances often have direct implications for philosophical topics, such as human nature or human morality. Recent research in this area tends to explore alternatives to the standard picture offered by evolutionary psychology, which combined a selective hypothesis (humans evolved in response to selective pressures of an ancestral environment) with an architectural hypothesis about the structure of the mind (modularity). After Tomasello 1999, culture is considered a crucial factor in human evolution. Sterelny 2012 proposes a causal feedback process between individuals, culture, and physical environment, whereas Henrich 2015 is a further elaboration of the gene-culture coevolution hypothesis.

Henrich, Joseph. *The Secret of our Success: How Culture is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter*. Princeton, NJ: Princeton University Press, 2015.

Claims that the human species is an exceptionally successful species and argues that culture-based cooperation and gene-culture coevolution can explain this success.

Sterelny, Kim. *The Evolved Apprentice*. Cambridge, MA: MIT, 2012.

Proposes a causal feedback process between environmental change, social organization, and individual cognitive, partially mediated by the mechanism of apprentice learning. A challenge to a nativist conception of human cognitive capacities is offered.

Tomasello, Michael. *The Cultural Origins of Human Cognition*. Cambridge, MA: Harvard University Press, 1999.

One of the first accounts of the central role culture has played in the evolution of human cognitive capacities.

Anthropomorphism

We attribute human emotions, motivations, and other characteristics to nonhuman animals, especially when confronted with similarities between nonhuman and human behavior. Doing so often appears to aid in understanding these organisms, but it is not always clear to what extent such attributions are justified. Recently there have been voices calling for a reevaluation of anthropomorphism, with some criticizing the avoidance of anthropomorphism as an unjustified bias. De Waal 1999 made an influential step toward rehabilitating anthropomorphism, terming the categorical rejection of anthropomorphism as "anthropodenial." Sober 2005 further supports De Waal's skepticism toward anthropodenial with the technical apparatus of cladistics. Andrews and Huss 2014 aims to undercut Sober's arguments. Datson and Mitman 2005 is an overview of issues pertaining to anthropomorphism.

Andrews, Kristin, and Brian Huss. "Anthropomorphism, Anthropectomy, and the Null Hypothesis." *Biology and Philosophy* 29 (2014): 711–729.

Argues against Sober that skeptics of anthropomorphism are not committing methodological errors.

Datson, Lorraine, and Gregg Mitman. *Thinking with Animals: New Perspectives on Anthropomorphism*. New York: Columbia University Press, 2005.

Offers a collection of essays on anthropomorphism in the past and present, both within and outside of a scientific context.

de Waal, Frans B. M. "Anthropomorphism and Anthropodenial: Consistency in our Thinking about Humans and Other Animals." *Philosophical Topics* 27 (1999): 225–280.

Proposes that skepticism toward ascribing human emotions to nonhuman animals has gone too far—terming it "anthropodenial"—and defends a version of anthropomorphism.

Sober, Elliott. "Comparative Psychology Meets Evolutionary Biology: Morgan's Canon and Cladistic Parsimony." In *Thinking with Animals: New Perspectives on Anthropomorphism*. Edited by Gregg Mitman and Lorraine Datson, 85–99. New York: Columbia University Press, 2005.

Analyzes anthropodenial as setting dissimilarity between human and animal emotion as the null-hypothesis, and subsequently committing the methodological error of biasing type-II errors (mistakenly accepting the null hypothesis) over type-I errors (mistakenly rejecting it).

Behavioral Ecology

Behavioral ecology applies adaptationist methodology to animal behaviors. However, in contrast to evolutionary psychology, behavioral ecology explains current behaviors as adaptations to the *current* environment (instead of an ancestral environment). Philosophical issues arise from a number of issues, including the phenotypic gambit: the assumption that an animal adopts a behavior that maximizes fitness (and thus overcomes any possible constraints). The phenotypic gambit is formulated in Grafen 1984, and critically discussed in Rubin 2016.

Grafen, Alan. "Natural Selection, Kin Selection and Group Selection." In *Behavioral Ecology*. Edited by John R. Krebs and Nick B. Davies, 62–84. Oxford: Blackwell, 1984.

The first statement of the phenotypic gambit.

Rubin, Hannah. "The Phenotypic Gambit: Selective Pressures and ESS Methodology in Evolutionary Game Theory." *Biology and Philosophy* 31 (2016): 551–569.

A critical discussion of the limits of the phenotypic gambit.

Cultural Evolution

It is widely recognized that evolution by natural selection cannot explain all aspects of human behavior and culture, not least because there is no one-to-one relation between behavior and genotype. Nonetheless, researchers from a diverse set of disciplinary backgrounds (psychology, philosophy, anthropology, biology) have begun to consider the extent to which the concepts and models developed for biological evolution can be applied to the cultural realm to help shed light on culture in humans and other animals. Richerson and Boyd 2004 is an accessible account of their dual inheritance theory of cultural evolution. Mesoudi 2011 offers an overview of what he takes to be the explanatory strength of cultural evolution, whereas Lewens 2015 offers a more skeptical discussion.

Lewens, Tim. *Cultural Evolution: Conceptual Challenges*. Cambridge, UK: Cambridge University Press, 2015.

Considers the explanatory goals of a cultural evolutionary theory and what conceptual problems arise with an attempt to build such a theory.

Mesoudi, Alex. *Cultural Evolution: How Darwinian Theory can Explain Human Culture and Synthesize the Social Sciences*. Chicago: University of Chicago Press, 2011.

Considers culture in humans and nonhuman animals and applies an evolutionary framework to attempt to explain features of this culture.

Richerson, Peter J., and Robert Boyd. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press, 2004.

An accessible overview of cultural evolutionary theory. It argues for the importance of a cultural evolutionary framework and offers a way of linking biological evolutionary theory with culture.

Innateness

Animal behavioral traits are often divided into those that are innate or instinctive and those that are learned or acquired. Despite the fact that this distinction is widespread, attempts to spell it out precisely have run into difficulties, with many philosophers arguing for the need to eschew references to innateness and instead use a more precise vocabulary. Lehrman 1953 is a powerful critique of the use of the concept of innateness in ethology. Mameli and Bateson 2006 and Griffiths, et al. 2009 provide critical overviews of the various senses of innateness.

Griffiths, Paul, Edouard Machery, and Stefan Linquist. "The Vernacular Concept of Innateness." *Mind and Language* 24 (2009): 605–630.

Combines critical analysis of the concepts of innateness with an empirical study of how the concepts are understood.

Lehrman, Daniel S. "A Critique of Konrad Lorenz's Theory of Instinctive Behavior." *Quarterly Review of Biology* 28 (1953): 337–363.

A classic paper challenging the distinction between innate/instinctive behavior and learned/acquired behavior.

Mameli, Matteo, and Patrick Bateson. "Innateness and the Sciences." *Biology and Philosophy* 21 (2006): 155–188.

Offers various interpretations of the concept of innateness and argues that none of them is satisfactory.

Evolutionary Epistemology

Evolutionary epistemology refers to two separate research programs. The first concerns problems that arise from the fact that belief-forming mechanisms (sensory apparatuses, cognition, etc.) have an evolutionary origin. This fact has been used for reliabilist arguments (e.g., epistemological mechanisms are reliable because selected for) and skeptical arguments (adaptive beliefs are not necessarily true). The second program concerns the growth of knowledge, and analyzes changes in belief state by drawing a parallel with biological evolution. A special application of this approach is to changes in scientific theories. The first is more the domain of epistemology than of philosophy of biology and will not be represented in the works below. Popper 1972 is a first exploration of the growth of knowledge from an evolutionary perspective, and Hull 1988 further develops this perspective. Wilkins 1998 is a critical discussion of some metaphors often used in this approach, including "lineages of theories" and the phenotype/genotype distinction in science.

Hull, David L. *Science as a Process: An Evolutionary Account of the Social and Conceptual Development of Science*. Chicago: University of Chicago Press, 1988.

A detailed evolutionary account of scientific change, with special attention for the social aspects of science.

Popper, Karl R. *Objective Knowledge: An Evolutionary Approach*. Oxford: Clarendon, 1972.

One of the first sustained accounts of epistemology from an evolutionary perspective.

Wilkins, John S. "The Evolutionary Structure of Scientific Theories." *Biology and Philosophy* 13 (1998): 479–504.

Seeks to identify criteria for individuating lineages of theories and to identify what plays the role of phenotype and genotype in the evolution of scientific theories.

Social and Ethical Dimensions

The evolutionary origin of human beings and human society suggests that human nature, human morality, and social mores are natural phenomena. This has led to the theory of evolution being used to argue for skeptical views concerning human nature, race, and morality. However, to what extent these arguments are legitimate, and more generally, to what extent topics such as human nature or ethics can be explained in purely biological terms, remains subject to much controversy.

Human Nature

It is common to invoke human nature in explaining human behaviors. We might, for instance, attempt to explain human violence by arguing that we are violent by nature. To see if explanations like this are possible, we need some account of what human nature is and how it is related to particular behaviors. Some philosophers have taken a skeptical stance, arguing that there is no such thing as human nature, especially given the anti-essentialism implied by evolutionary theory. Others recognize the problems inherent in constructing a

concept of human nature but nevertheless attempt to offer accounts that avoid these problems. Whereas Hull 1986 is critical of the concept of human nature, both Machery 2008 and Ramsey 2013 take human nature to be both a useful concept and one that can be rescued from Hull's critiques.

Hull, D. L. "On Human Nature." ***Proceedings of the Biennial Meeting of the Philosophy of Science Association*** **2 (1986): 3–13.**

Takes a skeptical stance toward human nature, arguing that if "human" refers to the biological species *Homo sapiens* and a nature is a necessary and sufficient trait, then there is no such thing as human nature.

Machery, E. "A Plea for Human Nature." ***Philosophical Psychology*** **21 (2008): 321–329.**

Answers Hull's skepticism by arguing that a scientifically tractable notion of human nature is possible, and that a trait is a part of human nature just in case it exists in most humans and is due to evolution.

Ramsey, G. "Human Nature in a Post-essentialist World." ***Philosophy of Science*** **80 (2013): 983–993.**

Agrees with Machery that we should seek a notion of human nature consistent with science, but disagrees with Machery about his solution. Instead, Ramsey argues that human nature lies in the patterns with which human traits are expressed over their lives.

Race

Racial discrimination has long been at the center of many social conflicts. However, even in absence of overt conflict, race plays an important role in categorization (governments and other institutions frequently collect data on race), and in attempts at reparation (giving advantages to those of particular races). Nonetheless, from a biological perspective it is unclear how races can be individuated, or whether they even have a biological basis at all. An important division running through the literature is that between social constructivists and those who attempt to ground race in biological structures. Mallon 2004 critiques the social constructivist stance, and Kaplan and Winther 2014 discusses how the philosophy of race is informed by biological research. Zack 2002 is an instance of the eliminativist approach to race.

Kaplan, Jonathan Michael, and Rasmus Grønfeldt Winther. "Realism, Antirealism, and Conventionalism about Race." ***Philosophy of Science*** **81 (2014): 1039–1052.**

Discusses the specific biological research informing different philosophical positions concerning race.

Mallon, Ron. "Passing, Traveling, and Reality: Social Constructionism and the Metaphysics of Race." ***Noûs*** **38 (2004): 644–673.**

A critique of the social constructivist account of race, it shows the overlap between the constructivist and skeptical (eliminativist) position. Provides a good overview of the debate on the metaphysics of race.

Zack, Naomi. ***Philosophy of Science and Race*****. New York: Routledge, 2002.**

Argues that race should be eliminated as a concept and category.

Evolutionary Ethics

Evolutionary biology has shed light on how certain moral dispositions evolved, such as love of kin. Evolutionary ethics investigates to what extent current moral beliefs and attitudes can be given an evolutionary explanation. Of particular philosophical interest are the implications of the evolutionary perspective for metaethical questions: does the evolutionary origin of moral beliefs, by explaining them as fitness-enhancing traits, undermine their justification and their likelihood of being true? Joyce 2006 is an influential exploration of how this question should be answered affirmatively. FitzPatrick contains a number of crucial counterarguments to Joyce's view. Maienschein and Ruse 1999 is a more general overview of issues in evolutionary ethics.

FitzPatrick, William J. "Debunking Evolutionary Debunking of Ethical Realism." ***Philosophical Studies*** **172 (2014): 883–904.**

Challenges debunking arguments such as the ones constructed by Joyce.

Joyce, Richard. ***The Evolution of Morality*****. Cambridge, MA: MIT, 2006.**

Argues how evolutionary biology can be used to debunk moral realism.

Maienschein, Jane, and Michael Ruse. ***Biology and the Foundations of Ethics*****. Cambridge, UK: Cambridge University Press, 1999.**

A collection of essays, each highlighting the relation between biology or nature and ethics at different stages in history.

Eugenics and Human Enhancement

Eugenics, the term coined by Francis Galton to refer to "the science of improving human stock," had many adherents early in the 20th century but was largely shunned after the Second World War. Nonetheless, today there is a lively debate concerning whether certain forms of eugenics and human enhancement more generally may be justified. Arguments in favor focus on the benefits of eugenics, and the apparent lack of an essential difference with other interventions on human development and abilities. Arguments against draw on disability rights, and on the nature of the parent-child relationship. Buchanan is an overview of the philosophical problems concerning human enhancement. Agar 2004 and Sandel 2007 take opposing positions toward human enhancement, with Agar arguing for human enhancement as a legitimate expression of individual choice whereas Sandel argues against the ethical legitimacy of human enhancement, seeing it as a manifestation of a perverse "drive to mastery."

Agar, Nicholas. ***Liberal Eugenics: In Defence of Human Enhancement*****. Oxford: Blackwell, 2004.**

Argues for the legitimacy of "liberal" eugenics, where embryonic enhancement is an individual choice, as opposed to the "authoritative" eugenics of the past, where enhancement was imposed by the state.

Buchanan, Allen. ***Better than Human: The Promise and Perils of Enhancing Ourselves*****. New York: Oxford University Press, 2011.**

An accessible analysis of the basic problems concerning human enhancement.

Sandel, Michael. *The Case against Perfection*. Cambridge, MA: Harvard University Press, 2007.

Argues that human enhancement is motivated by a "drive to mastery," which adversely affects human relationships.

Feminist Philosophy of Biology

One area of feminist philosophy of biology concerns issues in biology broadly relevant to the feminist program, ranging from the biological nature of female sexuality to the role of females in sexual selection. A recent work in this area is Roughgarden 2013. Another related area applies feminist methods to traditional philosophical positions relevant for the philosophy of biology, such as determinism, essentialism, or reductionism, arguing that such positions are motivated by male-centrist bias and that they are used to construct political narratives. Longino 1990 is an important representative of this approach. Fehr 2008 is a general overview of questions specific to feminist philosophy of biology.

Fehr, Carla. "Feminist Perspectives on Philosophy of Biology." In *Oxford Handbook on the Philosophy of Biology*. Edited by Michael Ruse, 570–594. Oxford: Oxford University Press, 2008.

An overview of the current issues in feminist philosophy of biology.

Longino, Helen. *Science as Social Knowledge: Values and Objectivity in Scientific Inquiry*. Princeton, NJ: Princeton University Press, 1990.

A wide-ranging work that argues how the background assumptions underlying scientific investigation include gendered social values.

Roughgarden, Joan. *Evolution's Rainbow: Diversity, Gender, and Sexuality in Nature and People*. Berkeley: University of California Press, 2013.

Examines issues of sexuality and gender in animals prompted by feminist, as well as LGTBQ critiques of behavioral sciences.

Origins of Life

While Darwin sidestepped questions concerning the origin of life, such questions have become more central in light of new work on how the biological realm can be grounded in organic chemistry. Two related questions concern what properties distinguish living from nonliving entities, and how the transition from nonliving to living can be conceived.

Definitions of Life

As biologists have learned more about basic forms of life, the boundary between living and nonliving systems has become blurred. How, precisely, life should be defined remains an open question, and answers to this question are closely linked to how the actual origin of life is understood. Of particular philosophical interest is what kind of system living systems are. Schrödinger 1944 is an early examination of this question, analyzing the living organism as a special type of thermodynamic system. Weber 2010 is a more recent approach in terms of complex system dynamics. Cleland 2012 is skeptical of the enterprise of searching for a definition of life.

Cleland, Carol E. "Life without Definitions." *Synthese* 185 (2012): 125.

Argues that the search for a definition of life is a flawed enterprise, partially because life on earth may not be representative for life generally.

Schrödinger, Erwin. *What is Life? The Physical Aspect of the Living Cell*. Cambridge, UK: Cambridge University Press, 1944.

A classic work analyzing life as a thermodynamic system. Proposes that ordered living systems can emerge, seemingly against the direction implied the second law of thermodynamics, by the local production of "negentropy."

Weber, Bruce H. "What is Life? Defining Life in the Context of Emergent Complexity." *Origins of Life and Evolution of Biospheres* 40 (2010): 221–229.

Takes a complex systems dynamics approach to the definition of life.

Origin Scenarios

Two crucial properties any living organism has is the ability to replicate and the ability to maintain itself in an environment (through metabolism). "Replication-first" views hold that the former arose first, while "metabolism-first" views hold the same for the latter. Both have problems and more recently the middle ground has been explored, with the RNA-world hypothesis being a prominent alternative. Penny 2005 is an overview of the most important views. Wilkins, et al. 2012 argues that the replicator-interactor distinction is inapplicable to early evolution, and introduces the weaker concept of a "reproducer."

Penny, David. "An Interpretive Review of the Origin of Life Research." *Biology and Philosophy* 20 (2005): 633–671.

A review of some of the most important hypotheses concerning the origin of life.

Wilkins, John S., Clem Stanyon, and Ian Musgrave. "Selection without Replicators: The Origin of Genes and the Replicator/Interactor Distinction in Etiobiology." *Biology and Philosophy* 27 (2012): 215–239.

Argues that replicators and interactors are sufficient but not necessary for Darwinian evolution to take place. Proposes an alternative origin of genes.

Modeling

Biological systems tend to be complex, with many interacting parts. Many biological models, by contrast, abstract away from this complexity and offer mathematically tractable representations of systems. In this way, general philosophical problems concerning modeling arise in the philosophy of biology, such as problems concerning model choice or concerning the realism of models.

Model Building

The challenges of building models are especially pertinent in biology. Due to the complexity of biological systems, fundamental issues arise concerning parameter selection, robustness analysis, and predictability. Levins 1966 and Wimsatt 1981 are important papers on these issues. Other philosophical issues concern the role of idealization in models: how is it that trading in veridicality can increase

explanatory power? Weisberg 2007 distinguishes between various types of idealization in explanations.

Levins, Richard. "The Strategy of Model Building in Population Biology." ***American Scientist*** **54 (1966): 421–431.**

An influential discussion of some of the methodological issues concerning model building.

Weisberg, Michael. "Three Kinds of Idealization." ***Journal of Philosophy*** **58 (2007): 207–233.**

An overview of three different explanatory roles idealization may play in the construction of models.

Wimsatt, William C. "Robustness, Reliability, Overdetermination." In ***Scientific Inquiry and the Social Sciences*****. Edited by Marilynn B. Brewer and Barry E. Collins, 124–163. San Francisco: Jossey-Bass, 1981.**

An analysis of robustness and an exploration of how it plays a role in models used in different fields.

Game Theory and Signaling Systems

Game theory models the interactions between individuals in terms of decisions made by utility-maximizing actors. The application of game theory to biology and evolution involves analyzing organisms as fitness-maximizing actors. Philosophical research can be located along two axes. The first is a reflection on the methods and concepts of evolutionary game theory (as formulated by Maynard Smith 1982). Huttegger and Zollman 2012 discusses some problems concerning the concept of evolutionary stable strategy. The second is an extension of Lewis's model of "conventional" signaling to the context of animal signaling. Skyrms 2010 is a recent work along this line of research, and draws on Maynard Smith and Harper 2003, which shows how game theory may be applied to animal signaling.

Huttegger, Simon, and Keven J. S. Zollman. "Evolution, Dynamics, and Rationality: The limits of ESS methodology." In ***Evolution and Rationality: Decisions, Co-operation, and Strategic Behaviour*****. Edited by Ken Binmore and Samir Okasha, 67–83. Cambridge, UK: Cambridge University Press, 2012.**

A critical discussion of the notion of evolutionary stable strategy.

Maynard Smith, John. ***Evolution and the Theory of Games*****. Cambridge, UK: Cambridge University Press, 1982.**

A synthesis of how game theory can be applied to evolution. Discusses the concept of evolutionary stable strategy.

Maynard Smith, John, and David Harper. ***Animal Signals*****. Oxford: Oxford University Press, 2003.**

An application of game theory to signaling between animals.

Skyrms, Brian. ***Signals: Evolution, Learning & Information*****. New York: Oxford University Press, 2010.**

An extension of David Lewis's work on convention to the context of evolutionary signaling. Draws on Maynard-Smith's and Harper's work.

Systems Biology

Systems biology treats biological entities at a high level of abstraction, and applies methods adopted from engineering and computer science for the analysis of biological systems. Kitano 2001 is a general overview of the foundations of systems biology, and Kauffman 1993 is an influential work on the self-organizing character of living systems and evolutionary processes. O'Malley and Dupré 2005 is a discussion of some conceptual issues in systems biology.

Kauffman, Stuart A. *The Origins of Order: Self-organization and Selection in Evolution*. New York: Oxford University Press, 1993.

Analyzes living organisms as self-organizing complex systems.

Kitano, Hiroaki. *Foundations of Systems Biology*. Cambridge, MA: MIT, 2001.

A collection of papers on the foundations of systems biology.

O'Malley, Maureen, and John Dupré. "Fundamental Issues in Systems Biology." *BioEssays* 27 (2005): 1270–1276.

A discussion of the difficulties of identifying biological systems and of how causality operates at different levels of organization in biological systems.

Mechanisms

Mechanisms are causal processes that, like the mechanism of a clock, integrate processes at different levels of organization in order to produce an effect. The mechanistic approach can be readily applied to some areas of biology, such as molecular biology or neurobiology; however, to what extent it can be applied to other domains such as evolution by natural selection is more controversial. Glennan 1996 was one of the first papers in late-20th-century literature to introduce the mechanistic approach to causality, and Machamer, et al. 2000 showed how it could be applied to various areas in biology. Craver and Darden 2013 is an authoritative and comprehensive defense of the mechanistic approach in life sciences.

Craver, Carl F., and Lindley Darden. *In Search of Mechanisms: Discoveries Across the Life Sciences*. Chicago: University of Chicago Press, 2013.

A systematic investigation into the role that mechanisms play in biological research.

Glennan, Stuart. "Mechanisms and the Nature of Causation." *Erkenntnis* 44 (1996): 49–71.

Introduces the mechanistic account of causality, which Glennan claims covers all causal relations in science except the fundamental laws of physics.

Machamer, Peter, Lindley Darden, and Carl F. Craver. "Thinking about Mechanisms." *Philosophy of Science* 67 (2000): 1–25.

Elaborates further on the mechanistic approach, giving examples from molecular biology and neurobiology, and discussing implications for traditional questions in the philosophy of science.

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