Philosophy and Evolutionary Biology

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Abstract

The relationship between evolutionary biology and philosophy has been fruitful for both fields. Philosophy has often brought conceptual rigor to bear on foundational issues in evolutionary biology, and has, at times, played an important role in helping to clarify the complex role that evidentiary standards played in the acceptance (or rejection) of particular hypotheses. Evolutionary biology has opened new avenues of exploration in a number of traditional philosophical domains, and, in providing answers to some questions traditionally thought of as philosophical, has solved (or perhaps dissolved) some philosophical problems.

Key Points

- To demonstrate that there is a dynamic interaction between philosophy and evolutionary biology that has mutually benefited both fields. Philosophy has been beneficial for evolutionary biology insofar as it allows for the sort of conceptual engineering and analysis required in evolutionary theory and evolutionary biology has expanded philosophical thinking in a number of important ways.
- To expand briefly on a number of topics in the philosophy of evolutionary biology, including natural selection, the species concept, mechanisms, the nature of populations, et cetera.
- To discuss the ways in which interactions between philosophy and evolutionary biology can contribute to social change by pursuing anti-essentialist and anti-reductionist projects.

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Introduction: Philosophy and Evolutionary Biology

The interaction between philosophy and evolutionary biology has been particularly a fruitful one. Evolutionary biology has generated a considerable number of conceptual puzzles that have attracted interest from both biologists and philosophers. And evolutionary biology has generated a considerable number of controversies, both internally (arguments among practicing biologists) and in public discourse surrounding the discipline; in both cases, philosophers have participated in these debates. Finally, evolutionary biology has sometimes been thought to have implications for some traditional philosophical problems, making some long-standing positions in philosophy either more or less plausible.

In this article, some of the key issues and positions in each of these broad areas will be briefly sketched. First, the role that philosophy has played in conceptual analysis within evolutionary biology will be explored. In many fields, questions arise that are not strictly speaking about the subject area, as they involve primarily conceptual issues rather than empirical questions. In evolutionary biology, questions regularly arise that cannot be answered merely by gathering more data. They are, for example, questions about the meanings of terms, or the best perspectives from which to view certain phenomena. Empirical evidence is often relevant to answering these questions—indeed, since some of the questions turn on the fruitfulness of particular perspectives, whether in fact a perspective is to be preferred will depend in part on whether it will really lead to more fruitful future research than alternative perspectives. But no particular empirical findings or experimental results are dispositive in these cases. Next, the role of philosophy in controversies surrounding particular aspects of evolutionary biology and the relationship between evolutionary biology and social and political issues, including those relevant to public discourse, will be addressed. Philosophy has often weighed in on particular debates within evolutionary biology, suggesting that in particular areas reasonable evidentiary standards are not being upheld, or suggesting that standards of evidence differ unreasonably between different areas. And philosophy has played a role in the analysis arguments surrounding, for example, the teaching of evolutionary biology in public schools. Finally, some of the ways in which it has been suggested that evolutionary biology might bear on traditional philosophical problems will be noted. The fact that humans are the product of biological evolution, it has been suggested, at least makes some more or less traditional philosophical positions less plausible, and makes others more plausible, and may play a part in settling some philosophical disputes.

Before getting into these arenas, it is worth noting that the philosophy of biology has been, with only a relatively few exceptions, the philosophy of "evolutionary" biology; the central questions and challenges that philosophers have taken up have emerged primarily (though not entirely) from evolutionary biology, broadly construed. This sometimes results in the philosophy of biology giving a skewed impression of the state of biological research, suggesting that most biological research is deeply wrapped up in evolutionary analyses. While **Dobzhansky's (1973)** dictum that "nothing in biology makes sense except in the light of evolution" may well be true, it is worth remembering that in practice, many research agendas in biology do not make continual or robust use of evolutionary biology in their day-to-day work. Philosophy of biology's focus on evolution to the exclusion of other domains, and its habit of seeing other domains through the lens of the questions most relevant to evolutionary biology, may in some cases be misleading.

Philosophy and Conceptual Analysis

There are questions in evolutionary biology that are not merely biological in nature, but rather centrally involve conceptual issues. The distinction is not always clear in practice, but in principle, it is the distinction between questions that can be answered by further research into the biological phenomena in question and questions that are better viewed as being about how to interpret the results of research, or how to think about an area of research. So for the most part, questions regarding when, say, some particular trait arose in a particular lineage are biological questions—if we want to know when, for example, swords arose in a particular lineage of sword-tailed *Xiphophorus* fish, the question may be difficult to answer definitively, but it is generally agreed what kinds of evidence are relevant to answering it (see, e.g., **Marcus and McCune, 1999**; **Basolo, 1990**).

Contrast this with the ongoing debates surrounding the nature of species (the "species problem"). **Hey (2001)** lists some two dozen species concepts, and notes that these are, with a few exceptions, generally viewed as "competitors for the single best meaning" (p. 326). But it should be obvious, by now, that the inability of biologists to settle on a single best species concept is not because of a lack of biologically relevant data; indeed, one cannot easily imagine what new biological discoveries even in principle could determine, once and for all, that one of these competing concepts was the correct or the best one. Rather, any solution proposed must try to make sense of the different work that species concepts do in biology, and perhaps recognize that no single concept can do everything that one might have wished a species concept could do (see, e.g., **Hey, 2001**, **2006**; **Dupré, 2001**). Similarly, arguments surrounding the ontological status of species—whether species are best thought of as individuals (**Ghiselin, 1974**; **Hull, 1978**; **Haber, 2016**), or as sets (see **Kitcher, 1984**), or kinds of some sort (see **Boyd, 1999**)—is not a question that more biological data on the behavior of individual organisms or of populations would permit us to settle.

It is of course not always clear whether a question is primarily a more or less straightforward biological question, or whether it involves important arguments over conceptual issues. Consider, for example, the current debates surrounding the necessity and/or the advisability of an "extended evolutionary synthesis" (e.g., **Pigliucci, 2007**; **Pigliucci and Müller, 2010**; **Baedke et al. 2020**), and the related arguments surrounding "Developmental Systems Theory" (DST) (e.g., **Oyama, 2000**; **Oyama et al. 2001**) and "Devo-Evo" (e.g., **Hall, 2000, 2012**). There are, obviously, a number of more or less straightforward biological questions that are relevant to arguments surrounding the advisability (and/or necessity) of these projects, though that doesn't, of course, mean that the questions are easy to answer. For example, how often is selection on heritable but non-genetic variation in fact relevant to a population's evolution? Are changes in heritable but non-genetic developmental resources in fact implicated in any major evolutionary transitions (see, e.g., **West-Eberhard, 2003**; **Jablonka and Lamb, 2005**; for a more skeptical view, see, e.g., **Hoekstra and Coyne, 2007**).

But there are also some clearly deep conceptual issues. For example, philosophers of biology have been crucial in picking out some problematic and underdetermined concepts of "information"—understood as both a developmental and heritable resource (see, e.g., **Smith, 2000**; **Griffiths, 2001**; **Shea, 2013**)—and in understanding how the uses of this concept became part of the standard stories surrounding accounts of evolution. In the modern synthesis understanding of the relationship between evolution and development, more rigorous analyses of the meanings and uses of "information" in biology can be relevant to understanding some of the concerns to which proponents of "extended synthesis" and related views see themselves as responding (see, e.g., **Moss, 2003**). Or more generally, while arguments surrounding whether it makes sense to think in terms of some privileged class of "replicators" that can be meaningfully distinguished from "interactors" in evolution make use of empirical facts about development and evolution, they involve, critically, disagreements about conceptual issues, as well (see, e.g., **Sterelny and Griffiths, 2010** and citations therein). The broad areas of research noted above—the species concept, the ontology of species, and extensions or modifications to the so-called modern synthesis—represent a few of the areas where the philosophy of biology has engaged with issues that emerge from the conceptual foundations of evolutionary biology. Below, several additional places where this kind of conceptual analysis seems important, and where philosophers and biologists have engaged in this kind of conceptual analysis, are sketched. This is not meant to be a complete list, but rather representative of the sort of work constitutive of philosophy of biology.

Levels of Selection/Multilevel Selection Theory

When discussing evolution by natural selection, debate sometimes focuses on which sorts of entities and which levels natural selection acts upon whether it be genes, species or groups. **Williams (1966, 2019)** provided a strong critique of sloppy group-selectionist thinking, and is often credited with introducing gene-selectionism into evolutionary biology (**Dawkins, 1976/2016** popularized this approach). Gene-selectionism, narrowly understood, never attracted the full support of more than a minority of practicing evolutionary biologists, but the position was nevertheless quite influential. More generally, the questions raised by this work—What is it that gets selected? At what levels can selection operate to produce adaptations? What is it that is adapted? Is there an important distinction between replicators and interactors, and if so, what work does that distinction do?—remain active areas of both empirical research and contention regarding the proper interpretation of both the questions and the results of the research.

Consider the question of what should count as "group selection." Most would agree that group selection is the proper account of a situation in which the groups themselves (1) survive and reproduce as wholes and (2) where the features of the group that lead to fitness differences between groups are not the same features as the features that make the individuals making up the groups more or less fit. But what of the case where the fitness of individual organisms depends upon the group (the context) to which they belong—Is that also an example, or is it merely a perfectly ordinary case of individual fitness depending upon the environment in which the organism finds itself (see, e.g., **Okasha, 2013**; **Okasha and Paternotte, 2012**)?

Some of the questions in this area are fairly technical, but no less conceptually loaded for all that. **Okasha's (2013)** work on the different formal approaches to multilevel selection (the Price equation, Contextual Analysis, etc.) reveals both the deep mathematical compatibilities of what are sometimes interpreted to be competitors for the best approach (see also **Kerr and Godfrey-Smith, 2002**), as well as the places where, while each approach makes the correct predictions, only one approach seems to provide a causally satisfying explanatory story. What is the proper role of multilevel selection theory within evolutionary biology—(merely) proper accounting of evolutionary change, or providing accounts that not only get the right answer, but seem causally compelling? If there is often only one account that is correct, what kinds of biological facts determine which account is the correct one?

The Organism and Individuality

Organisms are usually thought to be of central importance to evolutionary biology, and in any event would seem to be a central ontological category for biology more generally. But individuating organisms—determining where particular individual organisms begin and end—has long been recognized as a challenge (for the review of several philosophical distinctions when it comes to individuality see **Love and Brigandt (2017)**). Complex vertebrates would seem to be paradigmatic cases of individual organisms ("pace," perhaps, the near ubiquity of commensal bacteria in vertebrates). On the other hand, the eukaryotic cells that make up vertebrate bodies clearly seem not to be individual organisms, but rather parts of a more complex whole. But what to make of, for example, eubacteria that engage in obligate mutualism within particular environments (see, e.g., **Dupré and O'Malley, 2009**)? And are the colonies of eusocial organisms best thought of as collections of individual organisms (only some of which reproduced) or as some kind of organism-like entity in their own right (e.g., **Hamilton et al. 2009**)?

Note that some have suggested that this problem is closely related to issues involving multilevel selection—the move to having to think in terms of "collectives" in order to make sense of the evolution of a population is at least part of what it means for those "collectives" to count as biological individuals (**Korb and Heinze, 2004**; **Okasha, 2013**). Others (**Okasha, forthcoming**) point out the possibility that several of these categories have been collapsed into the overarching category of biological individual. Answers to one set of conceptual questions will sometimes influence the way other related questions are viewed. Furthermore, while some have emphasized an approach based on practices, both epistemic and otherwise (see, e.g., **Kovaka (2015)** and **Love (2018)**) others have emphasized a close relationship between theory and practice (i.e., **Fagan, 2015**).

Niche Construction

Lewontin (1983, 1985) noted that a standard view of adaptation was that of populations of organisms adapting to the external environment, where changes in the external environment were conceived primarily as exogenous—"the environment proposes, natural selection disposes" (**Stephen Jay Gould, 2002**, 31). But this view, he argued, was fundamentally mistaken: here was not an external environment independent of the organisms that made it up, at least not in any meaningful sense. This critique had at least three distinguishable threads. First, the niche of an organism, Lewontin argued, could only be determined by observing the actions of the organism itself. There were no "preexisting" niches to be filled, there was no privileged way of divvying up the world. Second, and closely related, what counted as a feature of the environment was determined not by the external world per se, but rather by how the organisms in fact lived in it. For example, what kind of environment "water" is depends critically on the size of the organism trying to live in it; ways of moving through water that are very effective for large ocean predators (e.g., sharks and dolphins) would be hopeless for microorganisms (for whom water behaves less like the low-viscosity liquid most people are familiar with, and more like a very high-viscosity material such as warm tar—see, e.g., **Yates, 1986**). Finally, Lewontin suggested that the fact that organisms actively modified the environments in which they lived, through their actions in the world, had important implications for correctly understanding the ways that fitness differences emerged from the reciprocal relationship between organisms and their environments.

One research path articulating some of the implications of these observations is known as "niche construction" (**Odling-Smee et al. 2003**; **Odling-Smee et al., 2013**). It is uncontroversial that for some organisms, proper development requires environments deliberately formed by their parents or other conspecifics—nests, for example, are an important part of the developmental environment of many organisms. And the environment in which most beavers, say, are born is very different from what it would be like without previous generations of beavers creating and maintaining those environments (see, e.g., **Naiman et al. 1988**). But what to make of these facts is controversial—does niche construction fundamentally change how evolution should be understood, or is niche construction rather a small wrinkle that does not require any profound changes to the usual understanding of evolution and the environment?

In a somewhat different context, Dawkins argued that the effects of genes should sometimes be seen as extending beyond the organisms that housed them, such that features of the environment could be thought of as part of the gene's "extended phenotype" (see **Dawkins, 1982**, **2008**); Dawkins did not, however, wish to endorse the whole niche-construction package, which he viewed as too detached from genetic differences that can influence fitness more or less directly (**Dawkins, 2004**). For Dawkins, part of the value of gene-selectionism was that it permitted one to track the effects that genes have on the external environment (nest-building behaviors, parasites subverting their hosts' behaviors, etc.) in the same way as genes that have their effects in the "usual" way—on the phenotypes of the organisms that house them (see, e.g., **Hughes (2013)** for a review of the extended phenotype in parasitism). For Dawkins, while it was ultimately the genes that are the beneficiaries of selection, selection can act on genes through the external environments associated with those genes in just the same way it can act on genes through organismal phenotypes so-associated. In this way, questions about the role of the organism (or the genes of organisms) in producing environments gets tied to questions about the levels at which selection operates, and the nature of selection more generally.

The Nature of Selection, Fitness, and Drift

There have been a number of positions defended on the nature of selection, fitness, and drift. It is sometimes claimed, usually by people ignorant of the basics of evolutionary theory, that evolution by natural selection rests on a tautology, because fitness is defined in terms of actual reproductive success; if the fit are simply those that survive, differential fitness cannot explain evolutionary change (see, e.g., **Bethell, 1976**). But this mistake is revealing—expressing precisely what fitness is, and what natural selection and drift are, is more difficult than it is sometimes imagined.

Probably the dominant view today is some variant of a propensity view—fitter organisms are those that, all else being equal, have a propensity to leave more offspring (or grand-offspring) than their less-fit counterparts in the range of environments in which organisms of that type are found (see, e.g., **Mills and Beatty, 1979**). Natural selection is responsible for those propensities, and drift is the main reason that actual outcomes fail to match those propensities (see, e.g., **Richardson and Burian, 1992**). One can understand evolution, on a closely related view, by thinking of selection and drift as separable forces, each of which has a distinct kind of impact on population dynamics (see, e.g., **Sober, 1993**). But more recently, some have argued that the natures of selection and fitness have been fundamentally misunderstood. According to defenders of the "statisticalist" position, neither selection, nor drift, are properly thought of as processes nor as causes of evolution per se; rather, they are best thought of as ways of characterizing particular kinds of outcomes (e.g., **Matthen and Ariew, 2002**). Others have argued that defenders of these views move too quickly from statistical interpretations to rejecting casual efficacy, and suggest that a causal interpretation of fitness and drift can still be defended (e.g., **Millstein, 2006**, **2010**).

This debate may seem quite distant from the concerns of practicing biologists. But one might reasonably ask what is being measured when biologists attempt to detect selection and measure fitness differences in the wild, and whether what is being measured in those cases fits in reasonably well with the notions of fitness that emerge from formal work in, for example, population genetics (see, e.g., **Pigliucci and Kaplan, 2006**). The debates over the proper interpretations of fitness highlight some of these conceptual difficulties.

A different kind of issue related to the nature of selection emerges from consideration of the in-principle minimum requirements for evolution by natural selection to occur. Under what conditions, in other words, can we legitimately expect cumulative selection to result in adaptations? Evolutionary biology is concerned primarily with the actual state of the world, and the features that living things in fact have that permit evolutionary change. But explorations of the more general question of what abstract features of systems make evolution by natural selection possible can shed light on important features of the actual world (see, e.g., **Godfrey-Smith, 2009**).

Adaptations and Functions

What is it for a trait to be an adaptation, and how does being an adaptation differ from being adaptive? Below, arguments surrounding adaptationism are considered, from the standpoint of the project of critique, especially because philosophy has played a role in arguments surrounding the appropriate evidentiary standards for adaptive hypotheses (for more on testing adaptive hypotheses, see, e.g., **Lloyd,**

1994; **Sober, 2009**; **Forber, 2009**). But before one can argue about the evidence required to support the claim that some particular trait is an adaptation for performing some particular function (or set of functions), one needs to know what it means to claim that a trait is an adaptation. Philosopher of biology **Godfrey-Smith (2001)** provides a good summary of the ways in which the debates surrounding adaptationism has often been ambiguous between empirical, explanatory, and methodological projects. iologists themselves have also provided what many regard as the definitive solutions, with **Williams' (1966**, **2019)** notes regarding the "onerous" nature of adaptive explanations (p. 41), and **Lorenz's (1966)** claim that "[u]nless selection is at work, the question "What for?" cannot receive an answer with any real meaning." (p. 11) pointing toward what the clearly dominant view is.

For a trait to be an adaptation for performing some function, the explanation for its current form and prevalence in the population in question must be due to past selection on traits with variation in their ability to perform that function. It is worth noting, though, that this position is not universal; in his textbook *Evolution*, **Futuyama (2009)** notes that some biologists still defend an ahistorical definition of adaptations (p. 284), though this is clearly a minority position. **Gould and Vrba (1982)** introduced a complication with their term "exaptation" for traits that are now used by an organism in a way that increases fitness, but which did not arise in the population because of their association with that use; however, neither the terminology nor the concept ever caught on. Indeed, **Godfrey-Smith's (1994)** "Modern History" view of functions entails that for a trait to be functional, and hence to be an adaptation, it must have been subject to selection for that function in its relatively recent evolutionary history, whatever else it was or was not selected to do in the more distant evolutionary past.

Process Philosophy and Evolutionary Biology

One way to think about issues discussed so far in this article—natural selection, adaptation, and the like—is to view it from the point of view of process philosophy. Process-oriented philosophy advocates a picture of the world that is not made up of discrete entities but rather as ever-changing processes. Viewing evolution from the point of view as a process, for example, might invoke an intuitive metaphysical premise that life, and nature at large, are the result of a dynamic state of being that is continually being updated and revised. In philosophical treatments of science, the use of process concepts is primarily borne out of the idea that there is an important conceptual relationship between science and philosophy and in order for philosophy to accurately capture scientific practice, it must account for those practices using conceptual tools.

Dupré et al. (2018) propose that "the living world is a hierarchy of processes, stabilized and actively maintained at different timescales," a concept which has several important consequences. Their argument rivals a substance view of the world which partitions life into various entities, or things, and they argue that their point of view captures the actual findings of biology far better than the substance view. Some of these "things"—the liver, for example—are more appropriately viewed as processes rather than entities. **Dupré et al. (2018)** mention that the liver needs both the organism in which it resides as well as the hepocytes within itself in order to thrive; in other words, these entities require each of their respective activity as processes in order for them to thrive.

This attention to process challenges a more mechanistic view of the world, discussed at a later section of this entry. Processes, however, are important to biology more broadly. When specifically applied to evolutionary biology, **Bapteste and Anderson (2018)** contend that the interlocking processes that contribute to our understanding of the history of life are left out of some of the tools used by those who study evolutionary history, such as phylogenetic trees. They put forth a case for evolutionary biologists to take network concepts more seriously, arguing that a better understanding of networking patterns might also lend itself well to a better picture of larger concepts such as the evolutionary picture of life. This lines up with earlier work by **Griffiths and Gray (1994)** which conceives of evolutionary lineages as a series of developmental processes, an enterprise which is continued in P. **Griffiths and Stotz (2018)** (for more on this topic, see also **Oyama et al., 2001**).

The Nature of Populations

The concept of a population plays important roles in evolutionary biology, but, again, stating precisely what constitutes a population is more challenging than is often recognized. There is no consensus on necessary conditions for some collection of organisms to form a biologically meaningful population. Some authors have tried to identify how, in practice, working biologists in different fields in fact pick out populations (see, e.g., **Winther and Kaplan, 2013**) while others have defended stronger claims regarding what biologists ought to be picking out when they identify populations (e.g., **Millstein, 2010**). Some of the interest in this work comes from investigations of population structure using genomic data; especially when applied to human population structure, how to interpret the results of such research remains controversial (see, e.g., **Weiss and Fullerton, 2005**). But more generally, whether a collection of organisms is itself a population, rather than merely being part of a larger population, can have important implications for conservation efforts (including the application of the Endangered Species Act, in the United States) and for thinking about the evolution of the (putative) population (see, e.g., **Allendorf et al., 2013**).

The Gene Concept

Stotz and Griffiths (2004) identify a number of different gene concepts in regular use in different domains in biology. Genes are sometimes conceived of as difference-makers (see **Waters, 2007**; **Tabery, 2009**) and sometimes as relatively abstract entities associated with phenotypic differences (this gene concept is very roughly what Moss dubs the “Gene-P” concept; see **Moss, 2003**). It is this concept of the gene that is most like Mendelian genes, and also most like the genes referred to in much of population genetics. But genes are also regularly thought of as particular physical strands of DNA—physical molecular entities. These physical stretches of nucleic material are used in various ways during development, and Moss dubs the gene thought of in this way the “Gene-D” concept (**Moss, 2003**). This sets up a fairly recognizable dichotomy between the Mendelian and the molecular concept of the gene (for more on this and for its implications for the meaning of “causation” in genetics, see **Lynch, 2021**).

Even the most cursory investigations reveal the difficulty with reconciling genes as difference makers related to phenotypic traits (roughly, Mendelian genes) with molecular genes (stretches of DNA that involved in protein synthesis and its regulation) (see, e.g., Section 6 of Sterelny and Griffiths, 2010, entitled “Mendel and Molecules”). There is no one-to-one relationship between stretches of DNA and gene-products. A given stretch of DNA can produce multiple different proteins (e.g., alternative splicing) and a particular protein may be produced by the interactions of multiple different stretches of DNA that are transcribed separately (**Stotz and Griffiths, 2004**). Researchers working in different traditions identify different kinds of things as genes, and hence even those who work primarily on molecular genes can count them differently—some, for example, focus on the total number of discrete gene-products (proteins), and others on the number of distinct functional elements, etc. (**Griffiths and Stotz, 2006**).

Indeed, the arguments surrounding the claims emerging from ENCODE regarding the functionality of so-called junk DNA emerge in part from arguments surrounding what will count as a gene, as well of course from arguments surrounding the nature of biological functions (see **Graur et al., 2013**). Is having a sequence similar to sequences that are actively used in development enough to call something a gene, or need there be evidence that the sequence is actually used—that, for example, when transcribed the transcription products are in fact put to biological use? Does a sequence have to be used in some way during development, such that the details of the sequence itself matters, or does the fact that some sequence (rather than none) is needed (to serve as a “spacer” perhaps) suffice to identify something as a gene (**Graur et al., 2013** call the latter sequences “indifferent DNA,” pp. 586–587)? These questions, and others similar, have generated the addition of a new gene concept—that of the “post-genomic gene”—said to be more flexible and pluralistic than its previous counterparts (**Griffiths and Stotz 2006**).

Mechanisms in Biology and the New Mechanist Movement

As philosophy of science entered the 21st century, the field left behind a largely logical empiricist framework focused on the epistemic side of science and moved more towards an approach focused more on scientific practice. An aspect of this newly found approach, which developed beginning in the 1960s, asserted the facts that a large part of scientific practice was centered upon a search for the underlying mechanisms of the workings of life. A popular definition used for mechanisms is that they are “entities and activities organized such that they are productive of regular changes from start or set-up to finish or termination conditions” (**Machamer et al. 2000**). Two other frequently cited definitions include **Bechtel and Abrahamsen (2005)** and **Glennan (2002)**.

Mechanisms are often associated with explanations, and a dominating construal of the term is in the search for causal mechanisms. Although various accounts have been put forth, a leading one that both stands the test of time and allows for an account of explanation in science has been the counterfactual accounts of causation. Woodward's (2003) manipulationist account of causation prevails within these views as a non-reductionist account of causation. Stated simply, manipulationist accounts of causation take the form of “X causes Y if and only if changing X also means a change in Y.” Attention to causal mechanisms in evolutionary biology has sparked conversation regarding such mechanisms across levels of organization (**Woodward, 2010**) without risking reductionism (**Dupré, 2013**).

Some have also considered whether or not natural selection might be a mechanism of the sort analyzed by e.g., **Glennan (2009)** and **Machamer et al. (2000)**. **Skipper and Millstein (2005)** and **Havstad (2011)** argue in the negative, whereas **Barros (2008)** offers an argument in the affirmative. These conversations successfully pull apart the issues of mechanism and causal process, since while **Skipper and Millstein (2005)** do not consider natural selection a mechanism, they very clearly maintain its status as a causal process. The crux of the issue, however, turns upon whether or not natural selection operates mechanistically in the above-senses at the individual- or population-levels, what entities are important to this debate, and ultimately have bearing upon the success of the mechanistic movement in philosophy of science as a whole. As mentioned earlier in this entry, the mechanist view is often contrasted with the process view of life. Whereas the mechanist view purports to put forth a view of life that is bound up in substances, the process view recasts mechanisms as idealized heuristics with which to view the world that help us better understand what is, in practice, a process at its core (**Dupré et al., 2018**).

Philosophy and Evidentiary Questions

Above, it was noted that one issue raised by the debates surrounding adaptationism was just what, precisely, was required in order for a trait to be an adaptation. But even after one has settled upon the definition of adaptation, there may still be arguments regarding the minimum evidence required in order to appropriately claim that a particular trait is in fact an adaptation for performing such and such a function. **Gould and Lewontin's (1979)** famous “Spandrels” paper criticized the so-called adaptationist program in part by claiming that too many biologists were willing to argue that a trait was an adaptation on the basis of far too weak evidence; indeed, they claimed that often the mere qualitative agreement between a plausible-sounding selective story and contemporary behavior was regarded as sufficient for accepting the selective story (587ff).

Contrast this, for example, with the work done to defend the claim that the sword-tails of male sword-tailed *Xiphophorus* were an adaptation to a preference that female *Xiphophorus* had for males with sword-tails. Here, observational work established that females really were more likely to mate with males that had longer sword-tails. Phenotypic manipulations were used to determine if it really was the tails that were doing the work, and phylogenetic analyses supported the claim that the female preference for males with sword-tails predated the appearance of males with sword-tails. The hypothesis that the swords arose in response to female preference, and that what explains the presence of the sword-tails is past selection based on female preference, seems, in this case, rather well supported, albeit not without some complications (see **Basolo 1990**; **Marcus and McCune, 1999**). On one reading, one of Gould and Lewontin's complaints in “Spandrels” was that this level of careful investigation and testing was too rarely exercised (for a summary of some methods available for testing adaptive hypotheses, see, e.g., (**Rose and Lauder, 1996**; **Pigliucci and Kaplan, 2000**).

Claims about human psychological adaptations were seen by Gould and Lewontin as particularly sloppy and ill-supported, and most philosophers who waded into the debates surrounding human sociobiology tended to agree. Philip **Kitcher's (1987)** *Vaulting Ambition* was a book-length critique of what Kitcher argued were the poor evidentiary standards being deployed by so-called sociobiologists. More recently, one can see David Buller's extended critique of “evolutionary psychology” (see **Box 1**), in Adapting Minds (2006), as fitting into the same framework—Buller argues that evolutionary psychologists have been too quick to draw (often quite sweeping) conclusions based on too little (and often fragmentary) data. **Lloyd's (2005)** work on the human female orgasm takes a similar critical tack—that in the human case, particular hypotheses involving traits as adaptations are too often made on the basis of poor evidence. Part of the problem is that it is very difficult to rigorously test hypotheses regarding adaptations in humans (especially for psychological or behavioral traits) (see **Table 1**; see, e.g., **Kaplan, 2002**).

While most philosophical discussions of issues surrounding arguments for and against the need for an extended synthesis, or DST as a plausible research program, etc., have focused on the conceptual issues engendered by these arguments, some philosophers have taken on the interpretations of the empirical data, arguing, for example, that a careful review of the evidence makes certain positions untenable (see, e.g., **Oyama et al. 2001**; **Moss, 2003**). Here, the results of biological research are deployed in order to support particular research programs, and to make particular analyses seem more plausible.

In a somewhat similar vein, arguments surrounding adaptive and fitness landscapes rely on the results of empirical research to support particular positions regarding the advisability (or coherence) of particular models (and metaphors). Here, some philosophers have argued that relatively recent advances in modeling make certain uses of fitness landscapes problematic (see, e.g., **Gavrilets, 2004**; **Pigliucci and Kaplan, 2006**; **Kaplan, 2008**; **Pigliucci, 2012**); others have argued that these objections are at least overstated, and at most apply to only some potential uses of fitness landscapes (see **Svensson and Calsbeek, 2012**; **Skipper and Dietrich, 2012**).

Finally, philosophy has played some role in the debates surrounding the teaching of evolution in public schools in the US context; Michael Ruse, for example, was called as an expert witness in the famous “McLean v. Arkansas Board of Education” (1981) case regarding the teaching of creation science and several philosophers testified at the “Kitzmiller v. Dover Area School District” (2005) trial regarding so-called Intelligent Design. And more recently, **Kampourakis (2014)** has written on how educators might work to overcome what he regards as conceptual barriers to students' properly understanding evolutionary biology.

Feminist Evolutionary Biology

Feminist thought is one area of philosophical thought that has been particularly important in supporting anti-reductionist and anti-essentialist programmes in evolutionary biology. First and foremost, work in this area reveals that socio-cultural values enter into scientific practice a lot more frequently than was previously understood (see **Longino 1990**, among others). Recognizing these values might reveal places where values have influenced science in negative ways. **Lloyd (2003)**, for example, reveals adaptationist assumptions that have resulted in failures of methodology resulting in untrue claims regarding importance of sexual assault to natural selection. **Lloyd (2005)** similarly reveals adaptationist assumptions regarding the role of the female orgasm to human history. Others have revealed androcentrism in research resulting in assumptions regarding the perpetuation of the myth of the “coy” female (**Hrdy, 1986**) and the role of male aggression in hierarchies and mate selection (**Haraway, 2006**).

In recognizing these values and confronting them, philosophy of biology and evolutionary biology pursue mutual goals and values, including scientific rigor, truth, simplicity and anti-oppression.

Box 1

Evolutionary Psychology.

As suggested in the main text, philosophers of biology have been interested in evolutionary psychology for a number of reasons. But what is the object of that interest? **Buller (2006)** distinguishes between Evolutionary Psychology (capitalized) and evolutionary psychology (while useful, this distinction is not universally used). The former is a particular research tradition associated with a particular set of claims and methodological practices, and the latter is any attempt to use evolutionary biology in the service of understanding human behaviors (and it is worth remembering that researchers engaged in evolutionary psychology will sometimes endorse some but not all of the basic claims and methodological practices of Evolutionary Psychology, so the lines are not as crisp as this might make them seem; see e.g., Confer et al., 2010). The latter, evolutionary psychology, is at least in principle uncontroversial—since the human brain is the product of biological evolution, and since its larger size and greater complexity are metabolically expensive and of relatively recent origin, the idea that the brain is an adaptation for some kinds of psychological abilities or other is fairly straightforwardly correct. Even here, though, Lewontin (1998) for example charts a very pessimistic course regarding what, precisely, we might learn about the evolution of human cognition, given the limitations of evidence available (see **Table 1** for some of these). But the former, Evolutionary Psychology, is associated with much more controversial claims. In its more or less canonical form, these include:

1) "Massive Modularity"—The human mind is made up of a very large number of "modules," each of which evolved to "solve" some particular adaptive problem.
2) "Human Universals"—The adaptions that make up the human mind are *universal* in the human species.
3) "Stone Age Minds"—The particular problems the human mind evolved modules to solve are those that were most important to our ancestors in the so-called "environment of evolutionary adaptedness" (EEA); for many traits, especially those that are supposed to be uniquely human, this is assumed by many EP practitioners to be the Pleistocene (2.6 million to 11,700 years ago).
4) "Adaptive Thinking"—Reflecting on the problems faced by our ancestors, and considering what solutions would have been both biologically possible and adaptive, is a useful technique for generating hypotheses regarding the existence of mental modules. One can then test for these hypothesized adaptations by thinking through the cognitive consequences of their existence, and making predictions about how people will behave on that basis (see e.g., Cosmides and Tooby, 1997; Downes, 2024; Tooby and Cosmides, 1990).

Different sorts of objections have been raised to these basic claims, such as: the empirical evidence for modularity of the sort proposed in (1) is weak, and the arguments that the mind must be modular in that way problematic; there is no reason to think that the mental problems faced by different human populations were universal as in (2) (consider: the evolution of lactase persistence in some but not all human populations); it is at least plausible that the problems faced during human evolution were not stable (3), but rather the result of living in cultures that changed with the changes in the people making them up, so there never was an environment of evolutionary adaptedness, even in aggregate; the suggested methodology (4) is not the primary methodology deployed in the study of non-human adaptations, including behavioral adaptations in non-human animals (see e.g., **Buller, 2006**; Downes, 2024; Lewontin, 1998; Sterleny and Griffiths, 1999). In addition, as the main text makes clear, there are objections to the many of the specific hypotheses put forward by practitioners of EP.

The Implications of Evolutionary Biology on Philosophical Problems

This article has so far mainly focused on the ways that philosophers of biology, and biologists working on conceptual issues in a philosophical way, have approached issues arising in evolutionary biology. But some have argued that evolutionary biology might have implications for traditional philosophical problems. On one view, this might be part of the expected progression of what were thought to be philosophical problems succumbing to scientific investigation—the claim that as more and more fields become empirically firmly grounded, less is left for philosophy. Some questions about basic ontology are now, for example, generally thought to be best addressed by physics, and not by philosophical investigation. And insofar as one thinks that design arguments of the sort defended by **Paley (1802)** (someone not generally considered a philosopher) and criticized by **Hume (1779)** (a canonical philosopher) were part of a philosophical tradition, evolutionary biology of course completely undermines them as reasonable philosophical questions (contemporary defenders of "intelligent design" theses notwithstanding). But whether evolutionary biology will result in similar usurpations of what are now thought of as traditional philosophical questions remains a live issue.

For example, one question that has received a fair bit of attention is the extent to which evolutionary biology might provide insights relevant to moral philosophy ("evolutionary ethics"). Certainly, insofar as our abilities to engage in moral reasoning require sophisticated cognitive systems, the fact that our ability to so-engage is the result of our recent evolutionary history must be at least relevant to understanding how moral reasoning is possible. But how it is relevant remains opaque. If our ability to engage in moral reasoning was the result merely of our ability to engage in particular general sorts of abstract reasoning (a view that would seem in line with, for example, Kant's interpretation of morality and its relationship to our moral abilities), then evolution would explain nothing in particular about our moral lives, but merely how we became the sorts of being capable in engaging in that kind of reasoning (compare: it is only because of the sorts of being we evolved to become that, for example, modern set-theory is possible, but the details of our evolutionary history are generally believed to be broadly mute on the issues considered interesting by set-theorists). On the other hand, if our moral lives emerged from ear-

Table 1 Human Adaptations: Why testing hypotheses regarding adaptations is so difficult for traits in humans

Technique	*Evidence generated*	*The trouble with humans*
Phenotypic manipulation (laboratory or field)	Fitness consequences of the traits in question, causal mechanisms associated with traits and fitness consequences	Ethical constraints + no controls in natural cases
Transplant studies	Fitness consequences, hypotheses re: selective pressures, hypotheses re: local adaptations	Ethical constraints + few ways to control for confounding variables in natural cases
Laboratory evolution	Robustness of pathways, strength of constrains	Ethical constraints + very poor model organism
Optimization analyses	Quantitative plausibility of qualitative assessments, sensitivity, path-dependence	Little knowledge of relevant selective history or specific functions for many of the traits of interest
Phylogenetic analyses	History of trait, homology (shared derived trait) versus homoplasy (independent derivation of trait)	Sparse clade; very few reasonably close extant relatives
Comparative method/ Regression analyses	Relationship between trait and environmental variables, strength of relationship, relationship between trait and fitness	Very little known about environment/trait relationships, little known about trait/fitness relationships, little known systematic variation between populations within species

For more on testing hypotheses involving putative adaptations, see e.g., **Rose and Lauder, 1996**; **Pigliucci and Kaplan, 2000**. For some of the specific difficulties in the case of testing adaptive hypotheses involving human traits (especially human psychological or behavioral traits), see e.g., **Kaplan (2002)**.

lier pro-social behaviors, and if selection acted on our abilities to engage successfully in those kinds of behavioral repertoires, then the details of our evolutionary history might explain, for example, some common intuitions or the reasons that certain ways of organizing our moral lives are more common than others. There is, with such work, often the concern that the "naturalistic fallacy" is lurking nearby—in this case, for example, one might worry that even a complete explanation of how particular tendencies related to our moral abilities evolved would not reveal anything about how we ought to behave (but merely about how we in fact tend to actually behave) (see, e.g., **FitzPatrick, 2021**; **Ruse, 1986**).

Other research areas that might be thought to impact on some traditional areas of philosophical enquiry include at least the following. Work on the evolution of language and communication more generally might have some implications for some issues in the philosophy of language (e.g., **Ruse, 1986**; **Skyrms, 1996**). Evolutionary epistemology—the study of evolution's role in the formation of beliefs about the world—may impact some approaches to epistemology in philosophy; it has in any event inspired some new approaches (see, e.g., **Millikan, 1984**; **Godfrey-Smith, 1996**). Some people have made claims about the implications of evolutionary biology for our understanding of the genesis and maintenance of religious beliefs and practices (**Norenzayan and Shariff, 2008**); while not precisely a philosophical issue, it seems related. Some philosophers have turned to evolutionary thinking in their work on aesthetics (e.g., Voland and Grammer, 2003). And, of course, some of the kinds of claims sometimes associated with some (particularly problematic) articulations of sociobiology (and later, evolutionary psychology) were thought to have implications, for example, the range of plausible political positions, the possibility of eliminating particular kinds of sexism or racism, etc.; though these positions never got much traction either in philosophy or biology properly speaking, they still attract some support.

Even where evolutionary (or biological) reasoning and empirical work are not the last word, it is worth noting that philosophical positions that are wildly at odds with broadly accepted biological theories are liable to be criticized harshly, especially if they fail to confront the empirical research that would seem to undermine them. For example, in her devastating review of McGinn's The Meaning of Disgust, **Strohminger (2014)** notes that McGinn fails to even mention "the most widely accepted theory of disgust today," namely that it is an adaptive behavioral extension of the immune system for pathogen avoidance (p. 214). While biology might only rarely settle a philosophical question, it can at least make certain avenues far less promising. At the very least, philosophers interested in explaining the etiology of particular human behaviors need to be aware of the contemporary biological work in the fields that they address.

Conclusion

There is, and has been for many years, a rich and ongoing exchange between philosophy and evolutionary biology; indeed evolutionary biology has been involved with philosophical questions from its very founding. Biologists interested in the conceptual foundations of their research areas have been forced to engage in conceptual analysis—forced, in other words, to tackle philosophical questions. Indeed, the line between the philosophy of biology and biology proper has often been blurred by both biologists and philosophers. Is Gould and Lewontin's famous "Spandrels" paper a biology paper, or a paper in the philosophy of biology that just happens to have been written by two practicing biologists? Is **Okasha's (2013)** *Evolution and the Levels of Selection* a philosophical work that just happens to be valuable to practicing biologists and hence regularly cited in primary research articles in straightforwardly biological journals, or is it (also) a contribution to biology itself? And the philosophy of biology has involved, and continues to involve, many fruitful collaborations between practicing research biologists and philosophers Eliot Sober, one of the founders of the philosophy of biology as a separate discipline, has published with R.C. Lewontin, with D.S. Wilson, and with S. Orzack; Elizabeth Lloyd, has published with Lewontin, with M. Feldman, with C.G. Anderson, and with Gould; Peter Godfrey-Smith has published with Kerr, as well as with Bergstrom; etc. Partly, as a result, efforts such as those demonstrated in **Pradeu et al. (2024)** differentiate between philosophy *of* science and philosophy *in* science, the latter of which has the aspiration of infiltrating science to some degree.

The relationship between evolutionary biology and philosophy has been valuable for both fields. Philosophy has brought a kind of conceptual rigor to bear on some foundational issues in evolutionary biology, and has, at times, played an important role in helping to clarify the complex role that evidentiary standards played in the acceptance (or rejection) of particular hypotheses. Evolutionary biology has opened new avenues of exploration in a number of traditional philosophical domains, and, in providing answers to some questions traditionally thought of as philosophical, has solved (or perhaps dissolved) some philosophical problems. This article merely sketches the broad outlines of some of these areas.

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