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Explanatory gaps in evolutionary theory

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Abstract
Proponents of the extended evolutionary synthesis have argued that there are explanatory gaps in evolutionary biology that cannot be bridged by standard evolutionary theory. In this paper, we consider what sort of explanatory gaps they are referring to. We outline three possibilities: data-based gaps, implementation-based gaps, and framework-based gaps. We then examine the purported evolutionary gaps and attempt to classify them using this taxonomy. From there we reconsider the significance of the gaps and what they imply for the proposed need for an extended evolutionary synthesis.

Keywords Evolutionary theory · The extended synthesis · Selection explanation · Natural selection · The active role of the organism · Explanatory gap

Introduction

Discussions of the explanatory limits of evolutionary theory are rampant in contemporary evolutionary biology. One especially contested area concerns the need for an extended evolutionary synthesis (EES). Recently, some EES proponents have argued that there are *explanatory gaps* that need to be bridged for evolutionary theory to be able to explain the diversity of ways in which organisms and populations change

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over time (Laland et al. 2019; Sultan et al. 2022; Uller [forthcoming]). In particular, they argue that the gene-centric approach to evolutionary theory—sometimes referred to as 'neo-Darwinism' or 'standard evolutionary theory' (SET)—cannot properly incorporate development, behavior, and other intra- and intergenerational processes as both explanantia and explananda in evolutionary explanations. EES proponents hold that SET takes evolution to consist solely in changes to gene frequencies in a population over time, and since these gene frequencies (partly) determine the available phenotypic variation for selection to act on (cf., Futuyma and Kirkpatrick 2017; Scott-Phillips et al. 2014), SET renders non-genetic intra- or intragenerational (organismic) processes as products of evolution, not as potential evolutionary causes (Watson and Szathmáry 2016; Uller and Helanterä 2017). A large portion of the EES vs. SET debate concerns what has been called the *active role of the organism* in evolutionary theory, and most of the purported explanatory gaps obtain in virtue of SET's perceived inability to incorporate in evolutionary explanations the effects of organismic activities that are not attributable to underlying genetic variation (Laland et al. 2012; Uller and Laland 2017).

In this paper we examine the notion of an explanatory gap and how such gaps relate to the practices and scope of evolutionary theory. We begin by exploring where the purported explanatory gaps seem to emerge in evolutionary biology. We suggest an initial line of response open to proponents of SET before arguing that in order to assess what sort of action an explanatory gap warrants, one must specify what *kind* of explanatory gap one is dealing with. To better understand what an explanatory gap is or could be, we first consider the classic notion of explanatory gap from the philosophy of mind and suggest that EES proponents do not wish to argue that evolutionary theory is rife with explanatory gaps of this kind. This leads us to move beyond the classic explanatory gap and provide a taxonomy of kinds of explanatory gaps. We argue that three kinds of gaps can usefully be distinguished: data-based gaps, implementation-based gaps, and framework-based gaps. There are also elusive gaps, which are cases in which one is unable to determine what sort of explanatory gap one is dealing with. The classic gap in the philosophy of mind appears to be an elusive gap.

We then argue that the way in which one conceives of the explanatory gaps in evolutionary biology (as data-based, implementation-based, or framework-based gaps) has consequences for the acceptable bridging of these gaps. We conclude by arguing that being clear on what kind of explanatory gap one is referring to is crucial for the notion to have any precise significance in the debates about the explanatory scope and structure of evolutionary theory.

Explanatory gaps and evolutionary theory

Over the last couple of decades there has been a debate over whether the current theoretical framework of evolutionary theory is in need of extension or revision (e.g., Laland et al. 2014; Wray et al. 2014). Proponents of an extended evolutionary synthesis (EES) argue that standard evolutionary theory (SET)[1] fails to properly incorporate causal factors and processes such as multilevel selection, developmental plasticity, niche construction, and extragenetic inheritance (e.g., Pigliucci and Müller 2010). Recently, some EES proponents have highlighted the need to include the active role of organisms in evolutionary explanations (Laland et al. 2014, 2019; Sultan et al. 2022; Uller [forthcoming]), also referred to as *organismic agency* (Laland et al. 2019) or *biological agency* (Sultan et al. 2022).

In particular, Laland et al. (2019) introduced the notion of an explanatory gap in evolutionary biology to argue that SET's gene-centric view of development, alongside SET's general skepticism of the transgenerational effects of soft inheritance systems, lead to incomplete explanations of the interplay between the capacities and activities of organisms (manifested through development, behavior, and organism-mediated environmental changes) and the selective environment they experience.

To appreciate their argument, let's first examine the way EES advocates view standard explanations of evolutionary outcomes. SET clearly treats the phenotype—or the distribution of types of phenotypes in a population—as an explanandum. Adaptative changes to phenotypes over generations are a key domain of SET. At the heart of SET explanations lies the idea that natural selection acts on iterations of genotype-environment relationships in a population over generations—i.e., on heritable fitness differences among different phenotypes in a population. In other words, the organism (i.e., phenotype or phenotypic traits) is the *product* of the interaction between the genotype and the environment—both during ontogeny and over generations (phylogeny). The traits that engender fitness differences are subject to natural selection only insofar as they are transmitted via genetic inheritance.

There is one further presupposition that SET makes (at least according to EES critics): the only changes to a trait that are of any importance in evolutionary explanations are changes due to the genetic basis of the trait. This is because it is only (genetically) inherited traits that can respond to natural selection.

Within the SET framework, novel phenotypic variation subject to natural selection can arise in three different ways: mutation, recombination, or novel expressions of extant genotypes. Thus, according to advocates of the EES, in an SET explanation, the explanandum phenomena—the phenotypes or phenotypic traits and their distribution in a population—are the product of iterations of genotype-environment interactions. As a result, anything a phenotype *does* to increase its fitness during its lifetime is either the result of chance or the prior action of selection (Laland et al.

[1] While EES proponents contrast their views with "standard evolutionary theory," it is not clear that there is a unified standard version of evolutionary theory shared by prominent figures in twentieth century evolutionary biology (e.g., Smocovitis 1996, 2023; Delisle 2009; 2011). We therefore acknowledge that our use of 'SET' is guilty of simplifying the complex dynamical nature of twentieth century evolutionary biology. However, for the sake of this paper, SET can be viewed as an anti-thesis to the EES thesis—that is, as the family of views that take evolutionary theory to not be in need of a major revision. A critical debate of the label 'SET' is beyond the scope of the paper, but it is also not necessary for the arguments being made. The same goes for a characterization of the EES. There are considerable differences among proponents of the EES. In this paper, we follow Buskell (2019) in speaking of the EES and SET broadly when discussing the debate around the extended evolutionary synthesis. We thank an anonymous reviewer for suggesting a bit more nuance regarding this point and acknowledging the complexity of characterizing a "standard" view of evolutionary theory.

2017). With this backdrop, we can locate the purported explanatory gaps in evolutionary theory: First, many organisms seem to have capacities whose function it is to combat the potential rigidity of genetically preconfigured traits. Learning and, more generally, phenotypic plasticity are capacities that allow organisms to shape their phenotypes based on experience, rendering the genetic basis of those capacities *less* salient and the encounters with their environment *more* salient.

Second, plastic responses to environmental conditions allow organisms to respond to selection pressures while their underlying genetic basis remains unchanged. This is especially evident in behavioral innovation in social species (Ramsey et al. 2007), in which an individual might innovate and their innovation could subsequently spread as culture through the population, even within the same generation (Ramsey 2013). A response to selection might even be realized not as a change to the organism itself, but a change to environmental conditions mediated by the organism, as occurs in niche construction.

Finally, many organisms can transmit these responses to subsequent generations without a genetic basis for the specific response. This might occur through epigenetic inheritance, social learning, ecological inheritance, or cultural inheritance. The transmission of these responses over generations—either in the short run over a few generations or in the long run over several generations—is what makes them potentially relevant in evolutionary explanations.

Now, an SET-style explanation of phenomena that exhibit these features might run into (at least) two difficulties. First, there can be cases of persistent phenotypic change while the genotype remains unchanged—or at least the changes to the genotype are causally insignificant at the level of the phenotype. Second, there can be cases in which the activities of organisms affect the selection pressures met by the population, and consequently alter gene frequencies over generations. Particularly interesting are cases of adaptive bias, in which the effects of the novel phenotypic expression (e.g., organismic activity) alter selection pressures such that variation associated with the novel phenotypic expression is selected for. Burrowing behavior, for example, might introduce positive selection for smaller and more elongated bodies, thus biasing the direction of selection in ways associated with the activities of the organisms.

As we have seen, the explanandum of SET explanations—the phenotype or phenotypic traits and their distribution—is the product of the interaction between the genotype and the environment. But in the phenomena outlined above, EES advocates claim that we cannot account for the changes to the phenotype in virtue of changes to the genotype—in relation to environmental factors—alone. Accordingly, the SET advocate must either argue that such cases are *not* instances of evolution or that there is an alternative explanandum phenomenon that should be addressed. The latter option amounts to admitting that there are explanatory gaps in evolutionary theory. Thus, for SET advocates to avoid admitting the existence of explanatory gaps, they must argue that cases such as those mentioned above are not "real" evolutionary phenomena in need of explanation.

The problem with this response, according to EES advocates, is that these cases arguably obtain through evolutionary processes and consequently are cases in which evolutionary explanations are appropriate. For example, natural selection is not privy to whether a phenotype is altered in virtue of changes to the genetic basis of the trait or something else. The only thing relevant to selection (at least selection at the population level or higher) is that there is fitness-relevant variation among the phenotypes. Whether the variation is due to genetic or, say, cultural differences does not matter. Consequently, a selection-based, evolutionary explanation can be appropriate even if the relevant features selected for are not due to underlying genetic variation (Aaby 2021).

Thus, the purported explanatory gaps consist in SET's apparent inability to explain cases in which phenotypes are simultaneously explanantia and explananda in evolutionary explanations.[2] In other words, the explanatory gaps consist in cases where organisms play an active role in their evolution. As Sultan et al. argue:

> While these explanatory deficits [i.e., gaps] affect a range of different phenomena—phenotypic determination, inheritance, and the origins of novelties—they originate from a common source: a tendency for our explanations to overlook the contribution of a definite property of all living systems [...] Living systems have evolved to be robust, responsive, flexible, self-synthesizing and self-regulating. This dynamic flexibility is manifest across diverse levels of biological organization, from cells, to tissues, to entire organisms, to reproductive lineages, to social colonies, and throughout a variety of organismal activities. (Sultan et al. 2022, p. 4)
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> And as Uller argues:
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> [W]hat can an explanation that refers to organismal goals contribute to the scientific understanding of evolution? One possibility is that naturalistic teleological explanations fill an explanatory gap that mechanistic explanations simply cannot fill. [...] That is, a purely causal account of adaptive convergences seems to leave an explanatory gap: it refers to the adaptive biases on phenotypic evolution caused by development or differential fitness, but it struggles to make sense of why those biases (and not others) exist. (Uller 2023, p. 334)

The explanatory gaps are said to obtain in SET because it cannot incorporate these organismic factors into evolutionary explanations. In other words, the notion of explanatory gap is used to highlight the need to incorporate organismic agency (Laland et al. 2019), biological agency (Sultan et al. 2022) or organismic goals (Uller 2023) in evolutionary theory, which is similar to previous calls to incorporate the active role of the organism in evolutionary theory (e.g., Lewontin 1983; Levins and Lewontin 1985; Bateson 2004; West-Eberhard 2003 etc.).[3]

[2] Cases like this, in which the phenotype is both the product and the producer of an evolutionary outcome, are sometimes referred to as *reciprocal causation* (Laland et al. 2011).

[3] While Sultan et al. (2022) use the term 'biological agency' and Laland et al. (2019) use the term 'organismic agency', we take these to both refer to instances of the challenge from 'the active role of the organism' (e.g., Bateson 2004; Lewontin 1983). While Sultan et al. (2022) argue that dynamic flexibility can be predicated to living systems above and below the level of the individual organism, we nonetheless think that the arguments from the active role of the organism in evolutionary theory encompass sub-organismal (e.g., cells, tissues) as well as extra-organismal (reproductive lineages, social colonies) features. The active role of the organism in evolutionary theory amounts, first and foremost, to a focus on the role of non-genetic, organismic (including sub- and extra organismic) factors in evolutionary theory.

At this point, we need to introduce an important caveat. We do not wish to come across as arguing that anyone who adheres to a broadly speaking "standard" formulation of evolutionary theory is incapable of addressing—or otherwise denies the importance of—phenotypic plasticity, behavior, extragenetic inheritance, ("apparent") goal directedness, or any other phenomena that might be used in arguing for the active role of the organisms in evolutionary theory. A researcher might, for example, be interested in the cumulative evolutionary effects of extragenetic inheritance without considering this to be an instance of the organism playing an active role in evolution. Similarly, another researcher might study the evolution of plastic responses in the purview of environmental conditions, and allow for reciprocity to play a causal role in engendering evolutionary outcomes without counting it as an instance of organismic activity.[4] The salient point is that these phenomena can be disentangled from the EES vs. SET debate, and one does not have to be in one camp or the other to take them seriously as phenomena that are in the purview of evolutionary theory. When we discuss the active role of the organism, we are thinking about those that take these phenomena (or a combination of them) to constitute a challenge to the explanatory sufficiency of standard evolutionary theory.

Conflating the explananda with the explanantia?

Before moving on to considering what possible consequences the explanatory gaps may yield for evolutionary theory, we want to explore a possible response an SET advocate might offer to counter the challenge from the active role of the organism described above.

As we have seen, the active role of the organism in evolutionary theory points to cases in which non-genetic intra- and intergenerational (organismic) processes are involved in engendering evolutionary change in the form of changes to gene frequencies in a population. However, it is not clear that cases of organismic activity are appropriately conceived as both explananda and explanantia in evolutionary explanations. That is, the active roles of the organism might seem to engender explanatory gaps in virtue of being treated as explanandum phenomena, when in reality they are simply (parts of) the explanantia. To better see what we mean by this, take the example of learning. From the perspective of SET, it is the capacity for learning that is under selection, not what specifically is learned. Of course, in order for the capacity to learn—and skills associated with that capacity—to come under selection there needs to be something that is learned. To see why distinguishing between these two is important, let's borrow and extend a hypothetical example from Ramsey and Aaby (2022). Imagine that an individual Macaque learns how to crack clams using rocks. Further, imagine that the behavior provides a fitness advantage and is transmitted with high fidelity vertically through parent-offspring learning. This is enough to say that the behavior is under selection (Aaby 2021).

But is a population-level change in the clam cracking behavior an *evolutionary* outcome? Well, yes and no. In terms of it being manifested by Macaques who have acquired the necessary traits to be able to accommodate the relevant steps in learn-

[4] Polyphenism in insects, for instance (Simpson et al. 2011).

ing how to crack clams through evolution, then sure, it counts as an evolutionary outcome. However, in the sense that evolution is responsible for all the idiosyncratic steps of the clam cracking behavior, then no it is not an evolutionary outcome, but rather an intergenerational behavioral outcome. (Some may wish to call this an instance of animal traditions, e.g., Avital and Jablonka 2000.) If we also imagine that this behavior reaches fixation in just a few generations, there would not be enough time to engender any meaningful evolutionary difference in the population, at least when evolution is understood as changes to gene frequencies in a population over generations (e.g., Futuyma and Kirkpatrick 2017). That is to say, if the behavior were lost in the subsequent generation, no evolutionary trace of it would persist.

This is not to say that clam cracking behavior is impotent when it comes to engendering evolutionary change. It can act as an adaptability driver (Bateson 2017a). In such a case, the clam cracking behavior creates a stable selective environment for other traits that are associated with underlying genetic variation, such that they can undergo adaptive evolution. The clam cracking behavior could, for example, create selection pressures in which manual dexterity, observational learning, and hand-eye coordination are favored by natural selection and subsequently evolve. In fact, as Baldwin (Bateson 1986) Waddington (1953); West-Eberhard (2003); Bateson (2017a, b) have pointed out, if a behavior—which initially is not linked with a genetic basis—manifests repeatedly over generations, it can over time come to have a genetic basis (thus transitioning from learned behavior to instinctual or fixed behavior). These are instances of genetic accommodation or assimilation. The phenotypic expression (or organismic activity) biases what gets favored by selection. However, on the SET perspective, evolution occurs only when selection acts on a phenotypic expression with a genetic basis.

A SET advocate could thus argue the following: If a novel phenotype obtains in a population through non-genetic processes (e.g., learning or plasticity), selection may act on it. However, *evolution* does not occur in the absence of a genetic change in population. That the novel selective environment is engendered by organismic activity is in principle no different from any other selection pressure or selective environment caused by another environmental factor, be it abiotic or biotic. The only difference is that the novel selective environments have been generated by organismic activity and not through purely environmental conditions, and perhaps that it is the organisms' activities themselves that generate and maintain the selective environments and, consequently, the adaptive bias. Invasive species create novel selective environments for native species and volcanic eruptions create novel selective environments. There is nothing standing in the way of SET to allow behavioral traditions (or idiosyncrasies) to do the same. The same is true for any other cases in which non-genetic organismic processes are linked to evolutionary change, such as phenotypic plasticity or ecological inheritance.

Thus, an SET advocate might question whether the active role of the organism really does create explanatory gaps in evolutionary theory. If they concede that some explanations are incomplete, then in that sense there are explanatory gaps. But they could qualify such gaps as being nothing more than the result of a lack of adequate data, or that they simply include too many variables for our models to be empirically tractable (e.g., Dawkins' 2004 argument against niche construction theory). But SET advocates could still argue that such explanatory gaps are due to a conflation of the explanantia with the explanandum, and that if we provide more detailed accounts of our explanantia, the explanandum phenomena would become, at least in principle, fully explainable on the SET framework. Thus, unless one specifies what kind of gap one is dealing with, it is difficult to evaluate what sort of action these explanatory gaps warrant.

As has now hopefully become clear, describing the explanatory limitations engendered by the active role of the organism in evolutionary theory as explanatory gaps per se does not provide a very informative challenge to evolutionary theory. The notion of an explanatory gap carries with it important connotations concerning what sort of problem we are facing and what possible solutions are available to us. In the following section, we characterize three different explanatory gaps and argue that each requires a distinct (though sometimes overlapping) bridging response.

Three kinds of explanatory gaps

The notion of an explanatory gap was introduced by Levine (1983) in his discussion of what is now known as the "hard" problem of consciousness (Chalmers 1995). He used it to refer to the epistemological chasm that divides mechanistic accounts of the neurophysiological dynamics of experience from the qualitative, subjectively felt features of experience. In particular, the notion of an explanatory gap in this context is meant to point out that a scientific account of subjective experience would be bound to failure because the qualitative aspect of experience is epistemologically inaccessible to a physicalist (or neurophysiological) theory of consciousness (Levine 1983). Hence, this explanatory gap does not indicate a lack in our understanding of the physical or mechanistic underpinnings of the phenomenon of subjective experience, but rather a limit in our overall capacity to provide an account of a key feature of subjective experience—namely its qualitative character. There are (at least) three ways one can go about dealing with the explanatory gap in philosophy of mind: deny that it exists (e.g., Dennett 1991), learn to live with it (e.g., McGinn 1991), or reinterpret the conceptual framework through which we understand the natural world (e.g., Godfrey-Smith 2019; Strawson 2006; Chalmers 2015).

An important question, then, is whether in evolutionary biology we are dealing with the same kind of gap that exists in the philosophy of mind. We think we are not. While the explanatory gap in the philosophy of mind appears to some to be unbridgeable—at least without reevaluating our metaphysical worldview—there are other kinds of explanatory gaps that may be better models for understanding the gaps referenced by biologists and philosophers of biology. Let's take a brief detour into physics to explore other kinds of explanatory gaps.

Consider the following scenario: You take two synchronized atomic clocks, load one on an airplane, and fly it around the world. When you return, the clocks are no longer synchronized. How do you explain this? If you look to classical physics for an explanation, there will be a gap. There is nothing in Newton's laws that would lead you to predict the asynchrony of the clocks. The asynchrony is simply not explainable within the framework of classical physics. If we change our framework to relativistic physics, however, the gap disappears. Within the latter framework, the asynchrony is accounted for by the equations of special relativity.

The explanatory gap due to the clock asynchrony is thus not an artifact of a lack of data. It isn't bridged by taking new measurements or refining our observational tools. Instead, we have all the data we need. This explanatory gap is bridged by moving from one framework to another. This sort of gap is thus framework based since it can be bridged by changing frameworks. We label such gaps 'framework-based gaps'. This is in contrast to gaps that are merely due to a lack of data, which we will label 'data-based gaps'.

There is a third category of gap that can occur even with sufficient data and an apt framework. Such gaps are based on the inability to use the data and framework to form the desired explanation. This can be due to such things as a failure of modeling or correctly tracing the implications of theory or data, or perhaps limitations on computational abilities. Our inability to explain why a particular protein folds in the way that it does, for instance, may have nothing to do with the framework we are using or the data at hand. It may merely be that the computations required are beyond current computing power. We will label explanatory gaps of this kind 'implementation-based gaps' since they concern how the data and the framework are implemented.

Data-based and implementation-based gaps are everywhere. Most research projects that propose to fill explanatory lacuna propose to gather new data or create new analyses to bridge such gaps. The "easy" problems of consciousness can be considered instances of data- or implementation-based gaps.

If the gap is mysterious, if it is unknown whether a new framework or dataset or analysis is required, then it is an 'elusive gap'. An elusive gap is not a fourth kind of gap but is the absence of knowledge about the nature of the gap. The hard problem gap in philosophy of mind seems to be an elusive gap. We are unsure how (or even if) it can be filled. But the philosophy of mind is not the sole domain of elusive gaps. To take physics again, there is the missing mass problem. It seems that the universe is more massive than it appears. But the source of this missing mass is not known. Some physicists back the idea that something labeled 'dark matter'—matter that doesn't interact with electromagnetic fields and emits no radiation—could explain the apparent missing mass. To solve this mystery, do we need to change our theory of gravity? Or can that theory stand, but we need new observational approaches or models to shed light on dark matter? In the absence of clarity on such questions, we should consider the missing mass problem to be an elusive gap.

How to respond to the explanatory gaps

As we laid out in the preceding section, there are three basic explanatory gaps in the sciences. Each of these kinds of gaps brings with it different challenges—and bridging them requires distinct, but sometimes overlapping, responses. In this section we outline these challenges as well as the possible bridging responses associated with each type of gap.

Let's begin with data-based gaps. These obtain in virtue of a lack of empirical data. Such gaps may arise due to insufficient research on a specific issue, to a dataset we thought was robust turning out not to be, or to the difficulty in obtaining the data (as, for example, occurs in paleontology). The challenge posed by data-based gaps is thus to keep on with the research and gather more data. This does not mean that facing this challenge will be easy, but simply that our modeling, methods, or theories do not need to be altered in order to bridge such a gap. Thus, for data-based gaps, there is a dearth of data and the bridging response is to collect data. In an epistemological sense, such gaps are straightforward. What Kuhn (1962) describes as "normal" science largely concerns filling such explanatory gaps.

In the case of implementation-based gaps, it is a lack of methods, models, or computational power required to appropriately combine theory and data. As such, the challenge runs deeper than with data-based gaps. In this case, merely collecting more data will not be a suitable way to bridge the explanatory gap. Instead, methodological and potentially technological improvements are needed to bridge an implementation-based explanatory gap. These gaps, however, do not threaten the general theoretical or conceptual framework. Indeed, refining a model of a given phenomenon or interpreting the available data with improved computational power are both bridging responses, which can be executed within the general theory or framework for the field to which the gap belongs. So, in the case of implementation-based gaps, there is a lack of methodological or technological resources and the bridging response is methodological and/or technological refinements or improvements.

Implementation-based gaps can be quite difficult to bridge, since it is often difficult to know what kinds of solutions are necessary. In many cases, one might even have to enlist help from other disciplines, especially when dealing with large datasets, many variables, and so on. For instance, the protein folding problem has effectively been solved by training artificial neural networks to predict folded forms from primary structures (Callaway 2020).[5] Thus, the prospects of bridging implementation-based gaps may in many cases be dependent on methodological improvements from other fields—perhaps especially from mathematics and computer science.[6]

With a framework-based gap, we are not simply facing a lack of appropriate data or an inability to successfully combine theory and data. Instead, the problem rests on the theoretical framework at play. Framework-based gaps can obtain in at least two

Table 1 An overview of the different kinds of gaps, the challenge they present, and what is needed in order to bridge the gaps

	Data-based gap	Implementation-based gap	Framework-based gap
Nature of the gap	Lack of data	Lack of methodological and/or technological resources	Insufficient or inconsistent theoretical and/or conceptual framework
Bridging response	Data collection	Methodological and technological improvement	Theory change

[5] There is, however, the question in this case of whether *predicting* protein structures via AI counts as *explaining* them. Such a discussion is beyond the scope of this paper.

[6] The collection of data and methodological choices might, of course, be influenced by one's theoretical framework. So, it is important to note that appropriate bridging responses to data- and implementation-based gaps will to some extent be determined by the theoretical framework one is working with. However, the salient point is that data- and implementation-based gaps do not challenge the theoretical framework. If they do, then there is an accompanying framework-based gap. We thank an anonymous reviewer for urging us to point this out.

different ways. First, a theory may fail to correctly address phenomena that the scientific community agrees is, or should be, within its purview (like in the time dilation in space travel example above). Second, the theory or its conceptual underpinnings may bias how we approach certain phenomena such that things are left unexplained. When an explanatory gap is rooted in these aspects, the bridging response may require one to reformulate an entire theory or reconceptualize key aspects, such as its theoretical terms—or both as in the case of the change from Newtonian to relativistic physics. For framework-based gaps, there are theoretical or conceptual inconsistencies or limitations, and the bridging response is theory change. See Table 1 for a summary of the various gaps and the responses necessary to bridge them.

Because the original notion of an explanatory gap from philosophy of mind evokes deep, mysterious, or even unsolvable problems, one needs to be clear about what kind of gap one is referencing when pointing out explanatory gaps. Let us now return to the explanatory gaps referred to by Laland et al. (2019) and Sultan et al. (2022). Are these elusive gaps like that of the hard problem in the philosophy of mind, or are they data-, implementation-, or framework-based gaps?

Classifying the explanatory gaps in evolutionary theory

As has now hopefully become clear, describing the explanatory limitations engendered by the active role of the organism in evolutionary theory as "explanatory gaps" does not provide a very informative challenge to evolutionary theory. In the preceding two sections, we characterized three different explanatory gaps and argued that a sufficient bridging response to each would be different (though sometimes overlapping). Thus, unless one specifies what kind of gap one is dealing with it is difficult to evaluate what sort of action the explanatory gaps in evolutionary theory warrant. In this section, we wish to show how explanatory gaps caused by the active role of the organism can be construed as a data-based, implementation-based, or framework-based gap. We will also reference authors that seem to tacitly offer solutions to different challenges from the active role of the organism, which corresponds to the bridging responses outlined in the previous section.

Let's say an SET proponent is confronted with the argument that the active roles of the organism engenders explanatory gaps.[7] They would likely respond by saying that if there are such gaps, they are data-based or implementation-based gaps or, more likely, a combination of both. Consider, for example, the classic case of dam building in beavers. On the assumption that adaptive evolution generally occurs gradually, the transition from non-dam-building to dam-building beavers occurred gradually, and the activities of the proto-dam-building beavers biased the selective environment towards dam building. That adaptive bias was then maintained in the selective environment due to the activities of the beavers. Through random mutation, novel

[7] As we argued above, a proponent of SET could also hold that there are no explanatory gaps in evolutionary theory, perhaps by maintaining that the challenges offered by the active role of the organism merely show us that evolutionary explanations could always be *more* complete.

gene expression, and recombination, genetic variation beneficial to dam-building will occur and be selected for.

Thus, the "whole" story of the evolution of dam-building behaviors in beavers will include these intermediate steps (and a lot of other information). However, not including this part of the explanation—leaving it tacitly assumed—can be vindicated by the gradualist assumption. If we provide a reason why proto-dam building was (and dam building is) adaptive, and assume that the traits related to dam-building can evolve, then we can also assume that dam building has gradually evolved from proto-dam building. If need be, the SET proponent could gather more data to explicitly spell out the details of the evolutionary transition from non-dam-building through proto-dam building to dam-building beavers. In some cases, this is exactly what the project of a SET researcher consists in—especially in explaining major transitions and other macro-evolutionary trends. Thus, some proponents of SET might argue that the explanatory gaps caused by the active role of the organism are only data-based gaps. These gaps can then be bridged by gathering and incorporating more data and detail in our evolutionary explanations if need be. Some of the current proponents of SET (e.g., Futuyma 2017; Gupta et al. 2017) seem to argue along similar lines.

Another response SET proponents could take is to acknowledge that the active role of the organism does point out limitations of evolutionary theory that cannot be solved by simply gathering more data.[8] They could hold that instead of data-based gaps, there are implementation-based gaps. Returning to the example of the beavers, an SET proponent could acknowledge that providing a complete explanation of the evolutionary outcome (i.e., how and why dam building evolved in beavers) that includes an account of how the activities of individual beavers shaped and maintained the selective environment introduces too much causal complexity for our models, and in this sense constitutes an implementation-based gap.

However, given that all organisms are in some sense "active," how are we to decide when we have included all the necessary causal information to have reached a "complete" explanation? We need to make assumptions about the salient factors in causing an evolutionary outcome in order to formulate hypotheses and explanations. Some causes should be treated as background conditions. This is simply a function of tractability. We do not possess the methodological or technological resources to include all the potential variables in our explanations. Adaptive bias, reciprocal causation (or feedback), and other impacts engendered by the active role of the organism are not denied, but rather assumed or treated as background conditions if their impact (as statistical measure) is not significant enough to alter the explanation. Nevertheless, a SET proponent could still argue that we can use the framework and methods of SET to decide what counts as significant and what can be treated as background conditions. Dawkins (2004) and Svensson (2018) argue along such lines, concluding that there is nothing in SET that precludes organisms being active participants in their evolution, but that the causal detail of such activity is best left tacitly assumed or relegated to a background condition. Thus, an SET proponent might agree that certain evolutionary explanations are idealized and leave out detail that could, in principle,

[8] Again, the proponents of SET might hold that some explanatory gaps can be bridged by gathering and incorporating more data, but others require something further.

be included in a complete explanation of a particular evolutionary outcome—i.e., acknowledge that the active role of the organism can create explanatory gaps in evolutionary theory (see also Dickins and Rahman 2012; Dickins and Barton 2013). However, they would argue that this is due to either a lack of data or to methodological or technological limitations, or most likely both. Another similar response can be found in Dickins and Dickins (2018), who acknowledge that while the modern synthesis (cf. SET) is a general framework that can provide explanations and predictions, it might not provide complete and detailed accounts of organismal form in their ecological context. In their words:

> The Modern Synthesis in evolutionary biology is a theory in the sense that it provides a framework for understanding diverse phenomena […] While it does not offer an exhaustive state description, it does explain some of the most interesting features of organismal design in terms of their ecological context. (Dickins and Dickins 2018, p. 173).

This view is similar to Dawkins (2004) and Svensson (2018) in that it takes the epistemic scope of evolutionary theory to be limited. It is a theoretical framework that fulfils certain epistemic tasks—i.e., prediction and explanation—but it is not suited to fulfill others. Many of the phenomena that the EES takes to be within the purview of evolutionary theory can thus be seen by such SET proponents to fall outside the epistemic scope of evolutionary theory.

Above we showed how proponents of EES maintain that the active role of the organism creates explanatory gaps that warrant significant changes to be made to evolutionary theory. They maintain that SET precludes organisms from being active participants in their own evolutionary trajectories, and thus that the active role of the organism cannot be incorporated into evolutionary theory without an accompanying alteration of the theoretical and conceptual framework of evolutionary theory. We will not rehearse the argument here, but one thing we should note is that there are differences among proponents of the EES. Some argue that all that is needed to incorporate the active role of the organism into evolutionary theory is to allow more causal processes to be considered evolutionary (e.g., Müller 2017; Pigliucci 2009; Pigliucci and Finkelman 2014.). Others, however, maintain that we need to reevaluate the theoretical and conceptual framework of evolutionary theory as a whole (e.g., Laland et al. 2014, 2019; Sultan et al. 2022). In other words, these take the active role of the organism to engender framework-based gaps.

What should we do about the explanatory gaps in evolutionary theory?

Let's say that most agree that, at least in some sense, there are explanatory gaps in evolutionary theory. What then should we do about it? It is not at all clear what sort of action or change these explanatory gaps prompt. This is mostly due to the fact that the notion of explanatory gap, left unqualified, does not offer a particular means to bridge the gap. As we argued above, the bridging response is relative to the kind of explanatory gap in question.

Our arguments imply that the burden of proof for identifying the kind of explanatory gap in question rests on those who argue that there are explanatory gaps in evolutionary theory. For explanatory gaps to play a meaningful role in fostering theory change, one must convincingly establish that the gaps are of the kind with which the proposed bridging response (viz. theory change) is associated. One difficulty is that the proponents of the EES and SET will have different ideas about the nature (and possibly the existence) of the explanatory gap, and thus any prospect of bridging it will be relative to how the gap is conceived. Proponents of the EES have outlined how they believe that the gap can be bridged—incorporating into evolutionary theory the active role of the organism in evolution—while it seems that proponents of the SET are left with three choices: (1) They can acknowledge that there are in fact gaps that need to be bridged, but that more data and/ or more powerful computational tools and methodological resources will eventually bridge these gaps. This effectively amounts to arguing that the framework of SET is adequate and can *in principle* explain everything there is to explain concerning evolutionary changes in biological form. (2) They can simply argue that any empirical and inductive science will *always* have explanatory gaps, and thus not be particularly concerned with their existence. (3) They can refrain from acknowledging that there are gaps. For example, a SET advocate could argue that the active role of the organism points out cases in which there are general capacities that have evolved (e.g., plasticity, learning, niche construction) and that these capacities allow for organisms to exhibit phenotypic difference or environmental manipulation that are simply due to changes to the underlying genetic variation of these capacities. Or they could argue that there are no gaps because the aforementioned cases are not instances of evolution—or are not suitable phenomena to be approached with the epistemic tools provided by evolutionary theory—and thereby fall outside of the scope of evolutionary explanation.

It is, we think, unlikely that an argument that there are explanatory gaps in evolutionary theory will trouble the proponent of SET any more than simply pointing out that there are cases of apparent (adaptive) evolution that SET has difficulties explaining. Thus, while the proponents of the EES have a framework that can bridge the gap, the effectiveness of the argument that this counts in favor of an extended evolutionary synthesis is conditional on the proponents of the SET acknowledging that there are gaps *and* that they conceive of the gaps as framework-based gaps, as do the EES proponents. We don't think this is the case, as it seems that one must implicitly accept many of the assumptions regarding the need for an extended synthesis to acknowledge that there are explanatory gaps in the first place, and certainly that these are framework-based gaps. Thus, in our view, the invocation of the notion of explanatory gaps in evolutionary biology amounts to little more than a catch-all term for what the proponents of EES have already argued is left unexplained by the modern synthesis and SET.

Conclusions

What, in the end, should be made of claims of explanatory gaps in evolutionary theory? From the preceding section, it seems that we are left with the view that pointing out explanatory gaps within a scientific theory or debate is merely a matter of rhetoric. In a certain sense, we think this is true. The notion of an explanatory gap is primarily used in philosophy of mind to point out the profound difficulty of explaining consciousness in a mechanistic universe. The explanatory gap is meant to be something that one does not readily bridge since it is difficult to know how to even go about bridging it. An entirely new metaphysical worldview may be in order. Such measures, we think, are not what EES proponents have in mind, as they offer an alternative framework to bridge the explanatory gaps in question. So why use the notion of explanatory gap to point out the limits of evolutionary theory? More importantly, why use an unqualified version of it? Clearly, the notion of explanatory gap has a certain rhetorical strength to it. If evolutionary theory does in fact have explanatory gaps, and our intuitive understanding of explanatory gaps is based on that of philosophy of mind, then there must be something significantly wrong with evolutionary theory. But if the notion of explanatory gaps includes data-based, implementation-based, and framework-based gaps, then it is no longer clear if the challenges evolutionary theory faces are so dire. Thus, for the notion of explanatory gap to play any significant role in fostering theory change or otherwise generating a productive reaction, a specification of what kind of gap we are dealing with is needed.

In this sense, we think that the notion of explanatory gap can play a valuable role in focusing the debate. If, for example, the EES proponents provide arguments for why we should consider the explanatory gaps to be framework-based gaps and not implementation- or data-based gaps, then an SET advocate needs to address such arguments. In our view, this is more or less what is happening in the debate already, only that it occurs implicitly and tacitly, rendering the debate more obscure than it has to be. If we wish to hold onto the notion of explanatory gaps in philosophy of science, conceptual clarity is key. Some of that clarity can be obtained by specifying which sense of explanatory gap one is using, thus offering an idea of what responses are warranted, and a target for opponents to address.

As a final point, we wish to emphasize that our analysis of explanatory gaps allows for a kind of pluralism. Explanatory gaps, even framework-based ones, do not necessarily imply problems with old frameworks that require their replacement with new ones. Returning to the example of framework-based gaps in physics, recall that classical physics cannot explain the asynchrony of the two clocks, but relativistic physics can. Such an observation implies that relativistic physics is required in this instance, not that it should be a wholesale replacement for classical physics. Indeed, for many questions in the natural sciences—in engineering, oceanography, geophysics, biophysics, and so on—classical physics is still used as the explanatory and predictive framework. For such uses, there are no significant gaps in classical physics. In fact, classical physics is arguably better in many cases, as the calculations are far simpler. This is not to deny the necessity of relativistic physics in some contexts. Someone engineering global positioning system satellites, for example, will need to use the equations of relativistic physics. There is thus room for both, and which theory is better depends on the problems at hand.

In a similar vein, we can find areas in evolutionary biology in which the framework offered by the EES is better suited, while in other cases the framework of the SET will suffice. For example, an evolutionary ecologist monitoring the health of a population of birds might find the explanatory framework of SET sufficient to explain and predict the dynamics of the population relative to some fluctuating environmental conditions and thus need not pay close attention to non-genetic organismic factors. However, someone who wants to, for example, study behavioral changes in a social species might find the phenomena hard to explain within SET and may fare better with an EES framework.

There is thus no need for us to choose a single framework that we must always stick to. Rather, we can examine an explanandum-phenomenon and ask ourselves whether we would do better with one or the other of the frameworks. One reason to be positive towards pluralism about theoretical frameworks is that different frameworks can fulfill different epistemic tasks. As De Regt (2018) argues, scientists often have different criteria for what counts as scientific understanding. In the case of evolutionary theory, we might find a similar phenomenon, where EES proponents might value a framework that allows us to understand the complex dynamics and effects of inter- and intragenerational non-genetic processes on evolutionary outcomes without that necessarily fitting the bill of what proponents of SET would call an *evolutionary* explanation.[9] We do not think, however, that such a pluralistic sentiment is alien to proponents of the SET or EES frameworks. After all, different problems may require different tools.

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