



## Biological functions are causes, not effects: A critique of selected effects theories

Miguel García-Valdecasas<sup>a,b,\*</sup>, Terrence W. Deacon<sup>c</sup>

<sup>a</sup> University of Navarra, Institute for Culture and Society, Campus Universitario, 31009, Pamplona, Spain

<sup>b</sup> University of Navarra, Facultad de Filosofía y Letras, Campus Universitario, 31009, Pamplona, Spain

<sup>c</sup> Anthropology Department, University of California at Berkeley, Anthropology and Art Practice Building, Berkeley, CA, 94720-3710, USA

### ARTICLE INFO

#### Keywords:

Selected effects theory  
Natural selection  
Biological function  
Teleology

### ABSTRACT

The theory of Selected Effects (SE) is currently the most widely accepted etiological account of function in biology. It argues that the function of any trait is the effect that past traits of that type produced that contributed to its current existence. Its proper or etiological function is whatever effect was favoured by natural selection irrespective of the trait's current effects. By defining function with respect to the effects of natural selection, the theory claims to eschew the problem of backwards causality and to ground functional normativity on differential reproduction or differential persistence. Traditionally, many have criticised the theory for its inability to envisage any function talk outside selective reproduction, for failing to account for the introduction of new functions, and for treating function as epiphenomenal. This article unveils four additional critiques of the SE theory that highlight the source of its critical problems. These critiques follow from the fact that natural selection is not a form of work, but a passive filter that merely blocks or permits prior functioning traits to be reproduced. Natural selection necessarily assumes the causal efficacy of prior organism work to produce the excess functional traits and offspring from which only the best fitted will be preserved. This leads to four new incapacities of the SE theory, which will be here analysed: (i) it provides no criterion for determining what distinguishes a proper from an incidental function; (ii) it cannot distinguish between neutral, incidental, and malfunctioning traits, thus treating organism benefit as irrelevant; (iii) it fails to account for the physical work that makes persistence and reproduction possible, and (iv) in so doing, it falls into a vicious regress. We conclude by suggesting that, inspired by Mills and Beatty's propensity interpretation, the aporia of backward causation implicit in anticipatory accounts of function can also be avoided by a dispositional approach that defines function in terms of work that synchronously counters the ubiquitous tendency for organism entropy to increase in the context of far-from-equilibrium thermodynamics.

### 1. Introduction

Current debates concerning the concept of function in biology have primarily focused on how function statements or functional ascriptions can provide explanations that meet scientific standards or acquire “explanatory depth” (Garson, 2019, p. 11), as Garson puts it. Attributing function to processes like photosynthesis in the production of chemical energy is an intuitive way of understanding plant metabolism, but the causal interpretation of such function statements is problematic for a straightforward reason: if function is defined with respect to its contribution to a goal, i.e., an as-yet-unrealised state of affairs, it becomes unclear how this future outcome might plausibly contribute to the

existence of its antecedent cause. In the case of photosynthesis, the critical question is “How does energy production explain the existence and causal properties of chlorophyll?” Since the causal link between any two successive events is irreversible, and future possibilities cannot produce prior causes, defining a function as existing because of its possible consequence appears to violate a core axiom of natural science.

Explanations that appeal to unrealised states of things are teleological. These appeal to some *telos*, that is, an end for the sake of which the current state of a system exhibits the features it has. Because teleological ascriptions are presumed to invoke Aristotelian final causes, and these have often been misunderstood, they appear to imply backward causation. As a result, such ascriptions have often been marginalised, reduced,

\* Corresponding author. University of Navarra, Institute for Culture and Society, Campus Universitario, 31009, Pamplona, Spain.

E-mail addresses: [garciaval@unav.es](mailto:garciaval@unav.es) (M. García-Valdecasas), [deacon@berkeley.edu](mailto:deacon@berkeley.edu) (T.W. Deacon).

<https://doi.org/10.1016/j.shpsa.2023.11.002>

Received 25 December 2022; Received in revised form 11 June 2023; Accepted 8 November 2023

Available online 18 November 2023

0039-3681/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

or simply eliminated from biology. In the view of some (e.g. [Godfrey-Smith, 2009](#), p. 145), questions such as “to what end?” or “who benefits” are useless to biology and should be broken down into more prosaic questions about underlying mechanisms. And yet, despite the problematic links of function talk to teleology, recent philosophical work on the concept of function overwhelmingly supports function talk in biology (e.g. [Lewens, 2007](#), pp. 525–6) and the normative connotations of this vocabulary.

Etiological theories of function (e.g. [Wright, 1973, 1976](#)) have attempted to justify a teleological concept of biological function by reference to consequences that support their continued existence. The most widely accepted version of an etioloical account of function—the theory of “selected effects” (SE)—claims to provide a teleological conception of function that does not invoke backwards causality. To be sure, the SE theory is not a single theory, but a collection of theories that purport to explain teleological function naturalistically. Born out of the work of [Neander \(1983, 1991\)](#) and [Millikan \(1984, 1989a, 1989b, 1993\)](#), the SE theory has gradually evolved to argue that the logic of natural selection justifies function talk, and that fitness assessed in terms of reproductive success, differential reproduction or differential retention, grounds its normativity. By linking function with the workings of natural selection, the theory claims to avoid the problem of teleology by replacing final causes with concepts that are scientifically amenable. Allegedly, this is how the SE theory successfully avoids the aporia of backward causation while justifying the continued use of teleo-functional concepts in biology.

Even though many philosophers of science support the SE theory (see [Garson, 2011](#), p. 548), it relies on assumptions that deserve closer scrutiny. Problems with these assumptions have not gone unrecognised. Standard criticisms stress its inability to (i) articulate a plausible definition of functional causality, (ii) account for the emergence of new functions, (iii) provide a philosophical warrant for function talk in biology, and (iv) reflect the work that the function performs. The objections that we raise below, confirm and expand these ills, pointing to further and deeper problems that remain to be addressed despite the effort of its most recent variants.

This article is divided into five sections. The first section introduces the SE theory and its most recent developments, describes its advantages, and summarises some of its standard critiques. In so doing, it will leave out some other criticisms, as well as the answer given by the SE theory. This is inevitable given the multiplicity of forms in which the SE theory has been adapted to meet criticisms. The second section articulates four additional and partially new critiques of the theory, including the idea that using natural selection as a criterion for defining function is misplaced. In particular, it is argued that if natural selection does no physical work, any effort to locate the causal source of a given function leads to vicious regress. To try to locate this source, the third section briefly examines Mills and Beatty’s propensity interpretation. But because this theory is also unspecific about the causality underpinning selection processes, SE theories seem unable to explain the critical source of functional causality. The fourth section sketches a theory apt to resolve this problem and ground functional causality thermodynamically. Finally, the conclusion restates the challenge of accounting for organism work and the self-beneficial effects that this work produces with the merely retrospective view of selection etiology.

## 2. The theory of selected effects

The SE theory was inspired by the idea that Darwinian processes of natural selection can explain the normativity of functions. Its core tenets were initially developed by [Neander \(1983, 1991\)](#) and [Millikan \(1984, 1989a, 1989b, 1993\)](#), and later substantially articulated and ramified by [Brandon \(1990\)](#), [Griffiths \(1992, 1993\)](#), and [Godfrey-Smith \(1994\)](#) among others. Roughly, it holds that a function of a trait like the distribution of oxygen and nutrients to cells through the blood is the effect this trait was selected for in the evolutionary past. To avoid circularity,

the SE theory holds that what a trait currently produces is not its function, only that which a previous token of the trait produced in the evolutionary past is its proper function. This is because what a trait currently produces does not explain its prevalence. Rather than a consequence of what it currently does, its prevalence in current populations is a consequence of natural selection.

A successful theory of functions should be able to exhibit, at a minimum, the following six characteristics: it should (1) distinguish functionality from malfunction, (2) distinguish neutral from non-neutral traits, (3) avoid the undesirable consequences of backward causality, (4) explain the normativity of function attribution, (5) account for organism benefit, and (6) most critically, explain how functional work is done, that is, provide a causal theory of the work that individual organisms must do to stay alive and reproduce in the context of the second law of thermodynamics. We believe that while the family of SE theories can account for (3) and (4), only some versions of it succeed in explaining (1) and (2). By contrast, none of them addresses (5) and (6) because of the basic causal presuppositions that most—if not all—SE variants share, as we shall argue. And yet, accounting for (5) and (6) is the only way in which any theory of function can be successful at avoiding the problem of explaining how living organisations survive, reproduce and adapt to changing conditions despite constant extrinsic perturbation.

Perhaps the most attractive feature of SE theory is its success at avoiding (3) the pitfalls of backward causality. By assuming that past selection is the ultimate criterion for establishing the presence of a successful trait in the population—i.e. the reason why the trait exists—causality only operates from past to present. The relevant cause for a current organ or trait should be traced back to the selective pressures that enabled the system to be reproduced. In this way, only prior causal processes are invoked to account for the normativity of a trait’s current causal dependencies. As a result, “whether a thing has a proper function depends on whether it has the right sort of [evolutionary] history” ([Millikan, 1989b](#), p. 292). By implication, then, “function claims are already historical explanations in disguise” ([Lewens, 2007](#), p. 535), and historical persistence becomes the sole criterion for defining biological function and grounding its normativity.

While an organ may have multiple functions, in Millikan’s view its “proper function” is the one (or few) that explains its presence. She argues, e.g., that hearts derive their proper function from their evolutionary history, rather than from their current contributions to the health and reproductive effort of the individual. Thus, hearts function to distribute oxygen and nutrients because this is “how hearts in the past contributed to their maintenance in the population” ([Wouters, 2005](#), p. 125). So, in Millikan’s view, the proper function of the heart is the distribution of oxygen and nutrients only because doing this in previous generations contributed to hearts being produced in current generations. This leads to a counterintuitive implication:

“[the theory] does not require that a trait currently performs its function, neither that it regularly performs its function. It is sufficient that in the past the trait produced a certain effect and that past performance explains its current presence. This makes it possible that items have a function, without actually performing it” ([Wouters, 2005](#), p. 125).

An advantage of separating proper function from current causal effects is the ability to explain (1) malfunction. The SE theory is able to fence-off possible objections concerning the normative value of traits that may only have an effect periodically or rarely, but are retained in the population because of their periodic past utility. So, for example the ability to digest the milk sugar lactose may not be utilised by an individual organism for many generations but is retained because it once contributed to survival and reproduction. And yet, this leads to other more convoluted implications. It also could be invoked to attribute function to vestigial traits like the wings of ostriches or the eyes of certain cavefish, which no longer contribute to their continued prevalence. As we will see below, this prospect exemplifies an over-inclusive

ascription of function to traits that would be normally described as having lost function.

In this way, the SE theory grounds the normative value of present effects, whether currently beneficial or deleterious, in past contributions to reproduction. This conflict with the common sense understanding of functional norms is usually accepted as an unavoidable consequence to overcome backwards causality. Neander elaborates on this reconception of function by arguing that the role of etiological functions is “purely descriptive” (2017, p. 1152). To the extent that selected effects are causally disconnected from the workings of current mechanisms, they are not meant to explain why a specific organ is currently performing a specific activity.

The SE theory has been revised several times to address various critiques. For example, it is often pointed out that biologists do not usually use the term “function” to speak about the history of a trait, but rather to indicate its current or “proximate” contribution to survival and reproduction (Tinbergen, 1963). To accommodate this view, Godfrey-Smith argues that functions are “dispositions or effects of a trait that explain the recent maintenance of the trait under natural selection” (Godfrey-Smith, 1994, p. 199). On a dispositional conception, a function is a property of a trait that may or may not be expressed presently even if passed on, and so could also have a current effect. In other words, to say that the functionality of a trait explains its persistence, as SE theorists claim, is not to say that the trait’s persistence implies its functionality. And the qualification of recency additionally leaves room for a graded sense of proper function. Griffiths further added to the logic of proximate functions the idea that any trait must have contributed to its prevalence in a population during the last “evolutionary significant time period”, which can be defined as the period in which some regression could have been expected if the trait did not make any contribution to fitness<sup>1</sup> (Griffiths, 1992, p. 128).

In many camps it is believed that some version of the family of SE theories provides the only possible naturalist explanation of norms (Christensen & Bickhard, 2002, p. 12). Nevertheless, its different and ramified versions are beset by difficulties that reduce its real explanatory value. Its manifold problems have been extensively discussed (e.g. Boorse, 1976; Cummins, 2002; Davies, 1994, 2000; Wouters, 2005). Here we will summarily review four of these.

First, if a proper function is the result of selective reproduction of a past token of it, how can the function of a given trait be identified without awareness of selective reproduction? Consider William Harvey’s case. On the view of selection etiology, Harvey’s discovery of the chief function of the heart may have been ungrounded. Since he lived two centuries before Darwin and was unaware of the role of natural selection in determining the current presence of the heart within the body, he could not have identified the “proper function” of the heart. In other words, implicit in SE logic is the idea that Harvey was mistaking its current causal effects for the reason that hearts are prevalent, and was just lucky that this also corresponds with their selective effect. Second, we should be unable to ascribe new functions to an organ that lacks any selection history, such as one that appears *de novo* due to mutation. Would it only be considered functional in a succeeding generation? Contrary to intuition, the SE theory lacks the conceptual resources to ascribe “proper function” to such a trait, irrespective of whether it contributes to current survival and reproduction. Third, the SE theory fails to capture the standard use of function attribution in biology. Wouters points out that “the kinds of explanations that biologists call “functional” employ counterfactually defined relations rather than historical ones. The etiological theory offers no insight into that kind of explanation” (Wouters, 2003, 2005). A counterfactual definition of function is expressed with respect to what something “would” produce

<sup>1</sup> These qualifications help to soften the sharp dissonance between etiological function and the commonsense notion, but they still retain the dissociation of current effect from selected effect.

in a certain context and what “would not” be likely to be produced in its absence. But this again invokes an unwelcome teleological implication. Fourth, as a consequence of denying that the current contribution of a trait to an organism’s well-being is its proper function, the theory has been accused of being epiphenomenal. If, according to the SE theory, “functional ascriptions bear no relation to the current contribution of the trait to the system” (Christensen & Bickhard, 2002; Moreno & Mossio, 2015) then the work that organisms presently do to resist external perturbation or promote self-beneficial ends is inevitably treated as non-functional. In summary, although the SE theory is allegedly successful at eluding backwards causality, it achieves this at the expense of remaining hostage to a number of ills whose solution does not seem straightforward.

Aware of the limits of taking reproductive success as an indispensable criterion for functionality, some variants of the SE theory contemplate that non-reproductive selection processes may also create functions. For instance, Papineau (1987, 1993) argued for the existence of selection processes in the differential transmission of beliefs. Likewise, Godfrey-Smith (1994) suggested that learned behaviours that are reinforced by trial and error could also be considered functional because they are selectively retained, while non-reinforced behaviors are extinguished.

This conception of learning on the model of natural selection has a long and checkered history. In his introduction of the early tenets of behaviorist psychology, Edward Thorndike (1905) characterised the process of reinforcement learning as exemplifying his “Law of Effect.” He predicted that initially unorganised behaviors could be shaped by selective reinforcement so that undesired behaviors would be extinguished and desired behaviors reproduced. The structure of the reinforcement schedule, whether structured by an experimenter or by environmental consequences, would thus be responsible for the relative fit of behavior to its context.

In a similar vein, Garson has recently expanded the SE logic to include processes like learning, antibody production, and the competitive elimination of superfluous neural synapses during brain development. Like Thorndike’s “Law of Effect”, these each involve selection processes taking place within an individual’s lifespan (Garson, 2016, p. 57).

The development of acquired antigen immunity results from the initial random generation of a vast and highly diverse pool of antibody molecules. These are subsequently culled by removal of antibodies that bind to self, and preserving those that do not. As a result, the remaining highly diverse pool of immunoglobulin molecules selectively responds to the unpredictable diversity of potential disease agents by reproductive amplification of that subset that by chance binds to the invader.

Similarly, in the early development of the brain, neurons, axons and synaptic connections between neurons are initially generated in excess of those that will survive to maturity. Initially, these connections are also more promiscuous and nonspecific. During development most of these connections are selectively eliminated by a kind of competitive exclusion. This substantive loss of neurons and culling of their connections is believed to be driven by the degree of signal synchrony between competing synapses, selectively preserving those that tend to fire together and eliminating those that do not. Garson describes this process as “a mechanism that creates new synapses and decides<sup>2</sup> which ones to keep” (Garson, 2019, p. 79), a process that is commonly called “neural Darwinism”—after the title of the 1987 book by Gerald Edelman, 1987.<sup>3</sup> to highlight the superficial parallels to natural selection logic.

The processes of selection of autogen immunity and brain development are non-reproductive. They are initiated by an initial

<sup>2</sup> Note that the expression “decides” carries misleading anthropomorphic connotations.

<sup>3</sup> Not coincidentally, Edelman received the Nobel prize for his work on the adaptive immune response.

overabundance of variant forms that are subsequently selectively culled to yield a resultant that is fine-tuned for interaction with the given context. So, by the logic of SE, not being culled is evidence of greater functional value compared with those that are culled. In this way, the generalized theory of selected effects (GSE) can now account for non-reproductive notions of function.

### 3. Four additional problems with the SE theory

While the criticisms sketched in section 1 have been partly contested, and their success is still a matter for dispute, we will not pursue them here. Instead, we will describe four additional and partially novel objections to the SE theory that question some fundamental assumptions that underwrite its different versions, from Neander and Millikan's theory to Garson's generalized theory. Given the multiplicity of SE variants, the next sections specify which specific brand of the theory is affected in each case. By drawing attention to these problems we hope to show that the SE theory is being held hostage to its idea that function is an effect of natural selection rather than the cause that explains functional work. These additional objections belong to two distinct categories: classification-related problems, and location-related problems with the notion of function. We will develop each set of criticisms independently.

Classification-related problems follow from the fact that (i) some variants of the SE theory cannot adequately distinguish between proper and incidental functions. As a result, the theory provides no basis for determining which of the many properties of a given trait confers its proper or proximal function. Likewise those versions (ii) cannot distinguish between functioning, neutral, and malfunctioning traits. The two location-related problems of the SE theory are that (iii) natural selection does no physical work, and as a consequence, (iv) any effort to locate the causal source of a given function leads to vicious regress, from which the theory cannot easily extricate itself.

Let us address these criticisms in order.

- (i) The SE theory cannot adequately distinguish between proper and incidental functions

The first criticism concerns versions of the SE theory that do not emphasise the role of selection “for” as a criterion of functionality. The theories that emphasise selection “for” have been called “strong” (Buller, 1998, p. 507). So, SE accounts that place emphasis on selection “for” will be treated separately. The argument of this section just concerns versions of the theory “with an emphasis only on the requirement that the functional trait be a reproduction of items that had the same effect(s)” (Buller, 1998, p. 507), and has also been called the “bare selected effects theory”<sup>4</sup>.

Of the six characteristics of an ideal theory of biological functions spelt out in section 1, this criticism affects (1). It will be as follows. If functionality is attributed to any trait that is passed on to progeny, bare selected effects variants of the SE theory are unable to distinguish “proper” functions, namely, those that have been “tested” by natural selection and are hence “etioloical”—from having being derived from the right causes, from merely “incidental” functions; i.e. beneficial effects that appear *de novo* in the course of evolution. For clarity's sake, a similar distinction describes the “proper” function of a screwdriver versus an incidental use, such as using it to pry open paint cans. Screwdrivers were designed for screws, not for prying; they can be used for this function because their physical properties just happen to enable

<sup>4</sup> Buller suggests that “bare selected effects” accounts of the SE theory, despite having “undesirable consequences” may have been originally intended as an elliptical formulation of the strong theory, but whether they are or not is an open question. The arguments in the first and the second sections exploit this crucial ambiguity.

it.

The distinction between “proper” and “incidental” function is particularly relevant to the concept of *exaptation* in evolutionary theory (Gould & Vrba, 1982). Consider a current exaptation theory about the evolution of feathers. Fossil evidence suggests that feathers initially evolved for temperature insulation in dinosaurs, so that their usefulness for flying was an incidental function that became selectively favoured much later in evolution. As they became recruited to aid flight, the structure of feathers changed, being thereby reshaped in ways that favoured flight over temperature regulation, since these functions prioritise slightly different structural properties.

According to the SE theory, the proper function of feathers is the one that explains its presence in the system. If the inherited trait becomes no longer functional, the SE theory still attributes it functionality (Wouters, 2005, p. 125) on account of its long distant or recent evolutionary past. The exaptation of feathers, however, shows that being an inherited trait does not guarantee being a product of natural selection. By “being a product of natural selection” we mean “having been selected” rather than having just been “passed”. We should thus distinguish traits with “proper” functions from merely inherited traits. A trait that becomes a target of natural selection will tend to show marks of being fine-tuned for this function, whereas incidental functions will not be modified because, in many cases, there is no selection to cull the less well fitted variants.

The previous distinction is critical to account for exapted traits. Consider ostrich wings. These were inherited because of natural selection for their flight function in the distant ancestors of ostriches. As this function waned, ostrich wings have instead been exapted for body stability and display purposes. As a result, this trait includes the elaboration of features that enhance its role in display and the degeneration of features once consistent with flight. So while still inherited, their wing-like features have progressively degenerated and become incidental. If this is correct, the modifying terms “proper” or “incidental” distinguish *kinds* of function, not functional versus nonfunctional relations. Incidental functions *do* serve a function, only that it is orthogonal to its past function. So, to call ostrich wings “functional” on account of the function they once had in the past befuddles the function that they currently serve, even if this is incidental. Hence, distinguishing the contribution of the modifier from the contribution of the concept of function is critical for the way the SE theory deals with inherited traits that no longer perform the functions they were previously selected for, or became maladaptive, or are neutral, as we will soon see.

This suggests that a similar clarification can be made with respect to inherited traits that are vestiges of past functional traits which today may even be somewhat malfunctioning. Consider impacted wisdom teeth in humans. The presence of third molars is a highly conserved trait present in nearly all primates including great apes and more immediate fossil in human ancestors. So this trait almost certainly was under strong selection for tens of millions of years. But in about 25% of the population of modern humans third molars can emerge misaligned or impacted in the jaw. Darwin (1859) and many evolutionary biologists (see e.g. Kurten, 1983) have speculated that the reduced face and jaw of modern humans (Oeschger et al., 2020) along with other influences such as diet and reduction of jaw muscles has been a factor crowding the eruption of wisdom teeth. In these cases, wisdom teeth pose a potential health risk. There are also potential traits common to wisdom teeth, such as underdevelopment or complete failure to develop. These traits would also be considered functional in the view of the SE theory. Indeed, because this degeneration somewhat mitigates the risk to health it is conceivable to consider such degenerate features as selectively advantageous. This suggests a dilemma. Do we need to consider normal, impacted, and degenerate wisdom teeth as all providing “proper” functions and none disfunctional?

If only reproductive inheritance determines whether a trait is functional or not, we lack criteria for distinguishing between proper, incidental, and vestigial functions. As a result, in the view of the so-called



“bare selected effects theory” both the vestigial flight-related features of ostrich wings and the potential health risks of impacted wisdom teeth are “proper” functions.

- (ii) The SE theory cannot distinguish between functioning, neutral, and malfunctioning traits

The focus of this section also concerns the bare selected effects variants of the SE theory. Of the six characteristics of an ideal theory of biological functions spelt out in section 1, this criticism affects (2) and (5). The argument will be that the theory lets pass as functional, traits that were reproduced accidentally or fortuitously, despite not providing—or having provided—any specific beneficial effect either to the organism or to its own selective retention via reproduction. It thus fails to distinguish between functional, neutral, incidentally selected, or even deleterious traits. Consider the particular red colour of heart muscle that is passed on to succeeding generations along with the heart’s capacity to pump blood. Since both the heart’s capacity and its red colour are reliably inherited, the SE theory should treat both as functional, even though heart colour is functionally incidental because hearts were never selected because they are red. No function can be attributed to the heart muscle’s colour. So the colour of the heart is both reliably inherited and completely incidental to the properties that get hearts passed on.

Consider the panadaptationism view. Inspired by the modern synthesis, panadaptationism advanced the now unpopular stance that every heritable trait that gets passed on must be some kind of adaptation. In their scathing critique of panadaptationism, [Gould and Lewontin \(1979\)](#) contend that natural selection does not work as an agent that promotes the most optimal outcomes. Together with highly adapted phenotypes, evolution produces genetic drift, allometrically correlated effects, as well as the transmission of suboptimal and even slightly deleterious biological traits—as wisdom teeth illustrate. Over the years, biologists identified many selectively inherited traits that do not produce any specific organismic or reproductive benefit. For instance, the so-called “synonymous” genetic mutations involve single nucleotide replacements that, due to the degeneracy of the genetic code, do not result in any difference in the amino acid sequence of a protein. These replacements are reliably passed on to progeny without any physiological or reproductive consequence. These “silent” genetic changes are effectively “hitchhiking” because the useful gene in which they are included gets passed on. In other words, it is assumed that many genetic changes get passed on to offspring because they lack negative consequences. Insofar as these traits produce no phenotypic difference that influences whether or not they are reproduced, they are called “neutral”.

The incidental preservation of neutral genetic changes is not an isolated occurrence. Neutrality repeats itself time and again at the phenotypic level. Consider the variability in the morphology of human ears. Human ears exhibit an astounding degree of morphological variation of uniquely characteristic ear shapes. In practice, most of these variations lack any distinguishable effect on auditory function or reproduction. Despite this, they tend to be inherited from parents. Neutrality is of course a ubiquitous consequence of the fact that many incidental features are inevitably associated with a certain beneficial trait. So, incidental trait inheritance—that is, inheritance of traits that lack any physiological or reproductive consequence—has been responsible for the evolution of a great many inherited traits that cannot be assigned any specific function.

So, if neutral traits are reliably inherited generation to generation—that is, they get successfully passed through the winnowing process of natural selection—do the examined variants of the SE theory consider such traits to have a proper function? This begs the question: what distinguishes (a) traits that were passed on despite having no positive or negative influence on organism reproduction, from (b) traits that were passed on because they aided organism reproduction?

If being a selected effect is only determined by the fact of being successfully passed on versus alternative traits that were not passed on,

then (a) and (b) must be judged to be functionally indistinguishable. This is in harmony with Millikan’s and Neander’s view that proper functions need not be causally active. However, this strategy empties the definition of function as “traits that were evolutionary selected for” of its meaning, since there is no “for” in differential reproduction. By ignoring the contribution of causality or benefit, the concept of function is replaced with inheritance and the distinction between (a) and (b) is explained away.

While the above argument concerns bare selected effects variants of the SE theory, could it be applied to other variants like the GSE theory? By focusing on proximal functions, the GSE seems better poised to circumvent this difficulty. Roughly speaking, proximal functions are the first effect of a trait, irrespective of whether this trait is beneficial to the larger system or not. So although the GSE opens up the possibility that a trait that has no causal relation with a past trait may produce a useful effect where there was none, it portrays itself as “an abashedly historical account, since it claims that nothing in biology can have a function until it’s gone through a few rounds of selection” ([Garson, 2019](#), p. 3). Contrary to [Bouchard \(2013](#), p. 94), who thinks that functions can be ahistorical, Garson stresses that functions must always be historical, and that they only emerge after several rounds of differential selection have taken place (2019, p. 95).

The use of proximate functions helps the GSE to better handle the distinction between (a) and (b). But the theory makes no account for organism benefit. Is it possible to ignore it? It may be assumed that without this benefit, the proximal function would not have been selectively retained. It seems then that this benefit is playing a role in the selection process. Thus, rather than saying that selection *per se* is what determines function, it seems more judicious to argue that immediate physiological benefit determines function, and that if this benefit is regularly achieved, other things being equal, selection processes will preserve or ratify the trait that achieved it.

There are three possible ways to deflate the benefit criticism. One is to argue that non-reproductive functions were selected for because of the survival value accrued by previous tokens of the same functions, and that these determined why these tokens were passed on. While this is the core of the SE theory, the argument seems flawed. Non-reproduction functions may take place in seconds, minutes or hours, rather than years. For many organs, waiting for the next generation, or for a few more rounds of selection processes for a trait to be functional would be late. Short-term or long-term beneficial consequences are hence explanatorily prior to prior causal dispositions. This priority provides the basis for recognising the fractionation of adaptive effects between those that are beneficial to the individual organism, its genes, and to the lineage or colony to which it belongs. This involves that the biological concept of function has a locus and temporal span that extends both below and above the level of an individual’s inherited trait.

Considering the current benefit of organism function is critical. Usually, what is implied is that such a benefit is accrued by an individual. And yet, behaviors that are beneficial for the lineage or colony but not for the individual who produces them are an apparent exception to the rule that current selected effects were previously beneficial to the parent organism. An example is the self-sacrifice of a worker bee that is beneficial to the lineage at the cost of that individual. By invoking evolutionary “conflicts”, the worker bee’s self-sacrifice allows biologists to distinguish between levels of functional benefit. So, a trait can be considered functional or dysfunctional depending on the level of analysis. But this demonstrates that function is defined by the contribution to a beneficiary, not merely by its presence or absence in a given generation.

The second way to deflate the benefit criticism is to restrict the scope of normativity. In this vein, Neander describes “minimal functions” (2017, p. 1151) as “mere activities”: that which an organism does irrespective of whether it benefits the organism or not. Of course, it is implied that “mere activities” lack any normative connotations. Implicit in this logic is the idea that the so-called “normal-proper functions”, that

is “the ones that underwrite talk of normal function” (Neander, 2017, p. 1151) cannot be “mere activities” so long as they result in the trait’s inheritance (Neander, 2017, p. 1156). So even if biological contingencies cause a selected trait to fail to produce that for which it was selected, its selective retention must preserve its normativity and proper function. In this way, since only historical selection warrants normative assessment, from the perspective of the examined variants of the SE theory a person’s impacted or degenerate wisdom teeth should be regarded as functional.

The third way is to argue that when etiological theories say natural selection selects for a trait, they refer to the specific feature of the organism that causes a positive fitness difference compared to organisms without this feature—see e.g. J. Beatty’s notion of trait fitness. While disposition or propensity theories incorporate the idea that selection is entirely reliant on “positive fitness difference”, once again such difference cannot be understood without some prior axiological assumption concerning benefit. In other words, we see positive fitness as implicitly endorsing the claim that beneficial consequences are explanatorily prior.

Ultimately, whether to the individual or to the lineage,<sup>5</sup> the SE theory deems organism benefit to be marginally relevant. While marginalising talk of benefits or beneficiaries successfully avoids using teleological vocabulary, most worryingly, it also eliminates any hint of causal efficacy. Although this argument will be made more explicit in the next section, if proper functions were causally inefficacious, functional ascriptions would just be rhetorical biological glosses without any significant causal role to play. This further reinforces the often-made critique that proper functions are epiphenomenal, as MacLaughlin (2001) and Christensen and Bickhard (2002) argued, for reasons very similar to the ones expressed here.

Finally, there is a more generic issue concerning functionality versus neutrality implicit in the very notion of differential selection of traits. A strict SE logic assumes that all beneficial traits are passed. However, this assumption disregards the utility of what we might describe as runner-up traits, i.e. traits that while beneficial, are out-reproduced by more beneficial alternatives. It is the essence of natural selection theory that differences in the relative contribution of variants of a trait to survival and reproduction enable the most effective variant to outcompete the others for representation in future generations. So it is not just that beneficial traits replace non-beneficial traits, but rather that in succeeding generations beneficial traits become prevalent over slightly less beneficial traits. Indeed, natural selection assumes the functionality of many selectively eliminated traits. Darwin’s scenario for the step-by-step evolution of image-forming eyes, for example, assumed that primitive precursors to eyes were all functional in their own right, being replaced over the course of evolution by slightly more efficient forms. Natural selection assumes gradients of functional variation, not just selection of functional versus nonfunctional variants. So, to attribute function to a selectively favoured trait does not necessarily imply that traits once present but now eliminated from a population lacked function; only that relative abundance of a given variant of a trait likely correlates with a relative difference in relative functionality within that context.

Let us know turn to the location problem.

### (iii) Natural selection does no physical work

The location problem concerns all SE theory variants, including the so-called “strong theory” advocated by Godfrey-Smith (1994) as well as the GSE. This argument advances the idea that natural selection is a population-level theory that explains statistical changes, rather than a

<sup>5</sup> Lineage should not be ambiguously confused with “species”. To claim that a trait can be beneficial is not the same as claiming it is beneficial to the species. It is just beneficial to a lineage, as well as to an individual’s genetics.

causal theory of force, from which it follows that the theory cannot account for the physical work that enables the persistence and reproduction of living organisations that is key to function.

Of the six characteristics of an ideal theory of biological functions spelt out in section 1, this criticism concerns (6), which is probably the most critical of all. In the SE theory, a trait derives its proper function from its selection history. So far, all SE variants have stressed the importance of a trait’s history to assess its reproductive value. This is also done by saying that a trait T increased its frequency in a population over some alternative because it had some effect F (Sober, 1984, p. 100). In so doing, the theory passes the explanatory burden of function attribution on to natural selection, which in turn attributes a trait’s functionality to having been selectively reproduced. But to explain the kind of functional work that organisms do to stay alive and reproduce it is insufficient to merely trace the causal history of the trait to some distant or recent past. Rather it is necessary to identify a current source of physical work that can account for the thermodynamic “cost” of its maintenance and reproduction. Otherwise this simply begs the question: how did an inherited trait contribute to its own reproduction? Specifically, to what extent has a selectively favoured trait contributed toward the work that prevented its selective elimination?

For heuristic purposes, we will distinguish two overarching stances to the problem of how natural selection operates. One is representationalist. The representationalist stance takes its inspiration in the artifact model (Lewens, 2007, pp. 527–8). In the representationalist stance, selection is inspired by an analogy to intelligent design. Following Darwin’s initial inspiration, natural selection has often been analogised to artificial selection, e.g., the selective breeding of domesticated species. Breeders are interested in generating specific outcomes based on a preconceived goal, on the basis of which the selection processes are designed. The breeder’s goal provides the normative determination of what is and is not a useful trait. Wimsatt (1972) and Griffiths (1993) endorsed this interpretation. They compare natural selection to a human agent who actively selects breeding stock in order to increase the probability of a desired trait.

Yet the analogy between natural and artificial selection is problematic. In an 1866 letter to Darwin, Alfred Russel Wallace (1916, pp. 140–143)—the co-discoverer of natural selection—criticised it for the way it implied that nature actively selects traits, regarded as functional. Taken too literally it provides an incorrect construal of Darwin’s theory. The “natural” analogue to the breeder in this analogy is the ecosystem within which an animal or plant develops. Yet the ecosystem has no goal to achieve, nor does it “prefer” one form over another. It neither actively “eliminates” less adaptive life forms nor actively “promotes” the reproduction of better adapted forms; it merely provides affordances and limitations.

By contrast, the non-representationalist view rejects the breeder/designer analogy (Reiss, 2009) and interprets natural selection in statistical terms as a distributional consequence of many potentially diverse causal processes, rather than a distinctive cause in itself. In this view, natural selection names a distinct causal principle that “acts” over and above the mere collection of dynamical processes that constitute metabolism and reproduction. For example, Neander claims that traits are “selected for, adapted for and in that sense designed for” their corresponding functions (Neander, 2004/2012). The non-representationalist camp is divided on whether the statement that a trait is “selected for” reveals a specific causal form that is only visible when natural selection is analysed (Garson, 2019, p. 26). What seems unquestionable, though, is the existence of “forces of mutation, migration, selection and drift” (Sober, 1984, p. 141) in natural selection that explain trait distribution and variation. For one thing, Godfrey-Smith (1994, p. 356) argues that “functions are dispositions and powers which explain the recent maintenance of a trait in a selective context.” Only by assuming a specific “disposition” or “power” that produces a physical effect that contributed to successful reproduction are we justified in believing that this disposition is functional. Because trait preservation or maintenance is entirely

general and abstract it does not discriminate between the vast web of organism mechanisms that influence this result. In this respect, from a causal perspective retrodicting the actual physical efficacy of a particular trait is entirely obscured. All functional traits presumably have this same generic consequence. When this is further framed in population terms, even this generic level of physicality is obscured and any reference to specific thermodynamic work is lost.

As Walsh et al., 2002 remark, “The only genuine forces going on in evolution are those taking place at the level of individuals (or lower) and none of these (and no aggregate of these) can be identified with either selection or drift” (p. 453). In other words, natural selection theory is agnostic with respect to the energetic work that generates and reproduces those traits that pass through the sieving process of selection. It is this agnosticism about causal mechanism—its generality—that enables the SE theory to sidestep any consideration of organism work, and thus to define function irrespective of what it does. For instance, Neander (2012/2020) argues that the statement “beavers build dams” describes something true independently of whether particular beavers are doing it at this point in time. But this nevertheless assumes that at least at some point dam-building work was done that contributed to its persistence among beavers. So, does Neander’s tenseless strategy resolve the problem of defining the function irrespective of work?

Unquestionably, natural selection theory does *explanatory* work. It has been remarkably successful at explaining change and variation at the population level. But the problem for a theory of function is that selection in any form (SE or GSE) is implicitly defined with respect to organism work. Natural selection theory describes the contextual conditions that affect how organism work differentially influences the transmission of traits, but only provides generic hints about the mechanisms involved. And it is not just the work of producing the selectively favoured effect that must be taken into account. With respect to selection processes taking place within the organism such as antibody production or the fine-tuning of neural connections in the developing brain, the process of selection also depends on surplus. Without a surplus of options—many varying offspring, antibodies, synapses, etc., many or most of which can be treated as expendable—there can be no selection. So, unless the work that generates this surplus is accounted for, natural selection remains a descriptive theory (Havstad, 2011, Al-Shawaf, Zreik, & Buss, 2021), not a causal one.

If the logic of natural selection simply describes what occurs when organism processes interact with a given environment in a way that affects the probability that this way of interacting will or will not be passed to future progeny, natural selection is best conceptualised as the imposition of a passive environmental filter or *sieve* through which some traits can pass and others cannot (e.g., Haldane, 1927; Dawkins, 1986; Futuyama, 2009; Havstad, 2011, Al-Shawaf et al., 2021). Traits go through a winnowing process that tends to minimise the transmission of less adaptive or *less functional* traits to progeny. Because it is passive, the only source of efficient causality in this process is the thermodynamic work that an organism engages in to persist and reproduce. It is the backdrop against which all processes of selection take place. As a result, it may be said that natural selection<sup>6</sup> *assumes* function rather than

<sup>6</sup> While there is nothing wrong with natural selection theory and its account of the evolution of function, its use as a criterion for defining function is misplaced. The theory of natural selection was not originally intended as a theory of function. It was rather, a way to account for the relative fit of organism functions to their ecological context, irrespective of the causal processes responsible. Additionally, selection does not have to do so much with whether a trait has a beneficial contribution to fitness as with whether a trait contributes more to fitness than do alternative traits. To show through an optimality model, or some other analysis, how a trait contributes to fitness is not sufficient to explain its prevalence. Selection comes into play only when there are differences in fitness. The authors are thankful to one anonymous reviewer for highlighting the importance of fitness differences.

explains it in the full sense of saying how it arises.

In summary, then, both the representationalist and the non-representationalist stances to function statements in the SE theory fail to identify the locus of the work that underwrites selective retention. But it is not just the work of producing the selectively favoured effect that must be taken into account. As noted above, with respect to selection processes taking place within the organism such as antibody production or the fine-tuning or neural connections in the developing brain, the process of selection depends on surplus. Without a surplus of options in excess of just the work required for persistence and reproduction there can be no selection. The very logic of selection depends on the production of surplus of options. As a result, the very possibility of selection in any form (SE or GSE) is implicitly defined with respect to organism work, something that SE theories expect to be explained by selection.

(iv) The SE theory falls into a vicious regress

If (iii) is true and, as argued, natural selection does no work to produce or reproduce a functional trait, then the SE theory risks falling into a vicious regress. On the one hand, it defines the function of the heart in terms of its successful selection history, but on the other, successful selection and reproduction of hearts requires living systems that generate the work to produce heart forms that contribute to survival and reproduction of the organisms in which they are produced. Those heart forms that more efficiently or more effectively perform the distribution of oxygen and nutrients will be more likely to be selected and reproduced. So, to avoid circularity, the family of theories that integrate the SE theory need to account for the biological work that hearts do to enable biological organism to survive and reproduce. Since natural selection and the selection processes that undergird differential persistence do not describe any individual-level causal mechanism, merely appealing to past instances of selected effects or generic “powers” fails to identify this source. And given that no prior selected effect is deemed functional except with respect to a prior selected effect, the SE theory leads into a vicious regress. The only way out of this quandary appears to be to make function epiphenomenal. But of course, this move undermines the effort to naturalise biological function and avoid the most common pitfalls of teleological explanation.

#### 4. Dispositional theories

An alternative way for SE theories to avoid vicious regress is to conceive functional work in terms of dispositions. Because standard dispositional approaches such as the systemic approach (Cummins, 1975) or the goal-directedness approach (Adams, 1979; Boorse, 2002) are rival accounts to the SE theory and their concepts of function are incompatible with it, we will not review them. Instead, we will briefly discuss Mills and Beatty’s (1979) propensity interpretation, the most distinctive attempt to break the alleged circularity of the concept of natural selection by providing a less generic source of organism work. Mills and Beatty’s (1979) propensity view described fitness as “a complex dispositional property of organisms” that shows their “propensity to survive and reproduce in a particularly specified environment and population” (1979, p. 270). Could this interpretation provide the SE theory with what it needs?

When Mills and Beatty further elaborated this notion, they argued that “when we say that an entity has a propensity (disposition, tendency, capability) to behave in a particular way, we mean that certain physical properties of the entity determine, or are causally relevant to, the particular behavior whenever the entity is subjected to appropriate ‘triggering conditions’” (1979, pp. 270–1). In this way, the effect of a particular trait is made more likely by such conditions. When these conditions obtain, they increase the chances that a certain trait becomes functional.

The appeal to individual causes is usually interpreted as a way of detaching fitness—the central concept in natural selection theory—from

reproductive success, and hence, of allowing for the possibility that fitness may not be what distinguishes those who reproduce. As Beatty remarked, fitter organisms have “greater ability to leave offspring, and not just (and not even necessarily) greater success in that regard” (Beatty & Finsen, 1989, p. 17). So, rather than passing the buck on to previous generations, this move finally stops it at the organism level.

Insofar as the propensity interpretation provides a forward-looking theory of function, it is apt to stop the vicious regress. Nevertheless, their proponents admit that “the propensity interpretation leaves much to be desired” (Beatty & Finsen, 1989, p. 18), for which the view has been many times reviewed and alternative, more satisfying criteria of fitness been put forward. An additional complaint is that the propensity interpretation fails to specify what determines that the particular physical transformation produced by a given disposition is truly beneficial, except in hindsight. In this respect, it could be said to replace selected effects with selected propensities, while failing to provide a causal account of what makes a particular pairing of disposition and triggering context beneficial. To simply posit that a disposition is beneficial reintroduces a predictive perspective that SE theories tried to elude.

An alternative way to avoid both the SE retrospective assessment and any teleological predictive framing of the concept of disposition is to abandon a strict temporal sequence conception of causality and to envisage processes that have simultaneous beneficial consequences. Of course, such a move risks introducing an irreducible processual element in which the temporal priority of cause over effect becomes ambiguous. But this is neither exceptional in physical theory nor necessarily problematic.

## 5. An atemporal alternative

To elucidate how beneficial consequences can be simultaneous with their cause, consider the analogy to instantaneous velocity in the calculus. Velocity is defined in terms of a finite distance covered in a finite time. If there is no temporal duration or spatial distance covered the concept of velocity has no meaning. And yet, at each point along a projectile’s trajectory it is obvious that the projectile does have a definite velocity. The calculus resolves this apparent paradox by defining the concept of an instantaneous velocity, the value of which can be calculated by the values of velocity measured at successively smaller distances and times converging toward a finite value. So, despite the appearance of paradox (à la Zeno), precisely determining a scalar value and direction of an “instantaneous velocity” is not in any way controversial or logically problematic in physics. These properties are precisely calculable by reference to the physically measurable continuities exhibited by the overall trajectory of the object moving in space.

The analogy to biological dispositions as trajectories of change is straightforward, but it requires one additional factor: reference to a ubiquitous background disposition, the relentless increase in thermodynamic entropy. Organisms are dynamical open systems that maintain themselves far-from-equilibrium, and life takes place against the constant tendency for organism processes to spontaneously degrade and breakdown. To the extent that an organism persists and reproduces, it is because it is engaged in work to offset the effects of the relentless increase of entropy. This perspective is not entirely new. Many other authors have emphasised the importance of the thermodynamic grounding of living organisations to understand their distinctiveness (Kauffman, 2019; Moreno and Mossio, 2015; Nicholson, 2018). What is new is the use of this insight to develop a concept of instantaneous functional effect.

The asymmetric directionality and magnitude of the background thermodynamic disposition provides the context with respect to which a vector of organism work can be assessed moment-by-moment. Like the vector of instantaneous velocity, the vector of instantaneous organismic work is measurable—at least in principle (e.g., metabolically, with respect to energy use per time). The dispositional nature of biological

function thus has both directionality, specified with respect to its opposition to local entropy increase, and magnitude, specified by the work that is expended in this process. This instantaneous vector of organism work can be defined both with respect to the whole organism as well as with respect to some specific consequence like reproduction. For example, the function of the rate of metabolic work required to maintain body heat in a mammal can be assessed with respect to its dissipation rate from the body surface.

This way of identifying function has many features in common with the systemic definition of function such as originally proposed by Cummins (1975). Systemic definitions of function treat a trait as functional if it benefits the system of which it is a part. Using the maintenance of the stable far-from-equilibrium state of the organism as a generic surrogate for whole system benefit is of course a crude measure, but it can be fractionated into specific contributions, as is demonstrated by the case of heat dissipation described above. In addition, this proposal overcomes many of the difficulties we identify above that have been identified as problematic for selected effects approaches, because it is neither retrospective nor predictive.

Dispositional theories based on propensity must include some implicit recognition of this vector of organism work. Just appealing to selection processes, which occur under the backdrop of entropy-resisting tendencies that are directional, is simply not enough. Thus, if the family of SE theories could be supplemented with a refined version of the propensity theory, to avoid circularity it should deal with the problem of the vector of work—the asymmetric directionality of the background disposition to become stabilised in far-from-equilibrium conditions. The directionality of organism processes is synonymous with saying that these tendencies are inherently end-directed. But if the SE theory was devised to skirt around the use of teleological vocabulary, how could it address the limits of the propensity interpretation to account for organism work?

## 6. Conclusion

Of the six characteristics of a successful theory of function listed in section 1, section 4 has sketched (6) a causal theory of the work that organisms must do to stay alive and reproduce in the context of the second law of thermodynamics. While this theory is apt to deal with the rest of desiderata (1–5) further analysis may be required to counter the possible objections that have been levelled against Cummins’ systemic view and other theories of function that try to account for organism benefit. This work should be undertaken separately. So far, the analysis of the ills of the SE and GSE theory has established that these exhibit two kinds of problems.

The classification and location-related problems of SE theories suggest that, despite their popularity, SE theories face renewed challenges that touch on central aspects. They (i) fail to distinguish proper or proximal functions from incidental functions; (ii) fail to distinguish between neutral, incidental, and malfunctioning traits, thereby treating organism benefit as irrelevant; (iii) fail to account for the physical work that enables the persistence and reproduction that selection depends on, and (iv) in so doing, are trapped in a vicious regress.

These ills also affect the GSE theory.<sup>7</sup> By generalising the concept of selected effects, it expanded the scope of selection to include nonreproductive processes. Yet in so doing, the GSE theory simply replaces the subtractive logic of cross-generational selection with a subtractive logic taking place within a lifespan, while still remaining agnostic to the work

<sup>7</sup> Incidentally: the irrelevance of reproduction and the critical role of surplus options are implicit in Campbell, 1960 “blind variation and selective retention” famous characterization of selection logic. This implicit agnosticism with respect to causal mechanism is the basis for the power of the SE logic to successfully apply across so different domains. But as we have also argued it is also what underlies each of the critical failings of its theory of function.



that makes selection possible. As we saw, it takes work to produce the surplus options that selection is defined with respect to, whether in terms of many variant offspring, immunoglobulins, or synapses. So although this generalisation of the selected effects logic cannot account for function irrespective of reproduction, it also fails to attribute causal efficacy to the work that produces its necessary preconditions. Consequently, it too fails to break the circularity implicit in SE theories.

In the last analysis, most of the ills that beleaguer the family of SE theories arise from its attempt to avoid the aporia of backward causality by starting from the perspective of the consequence and retrodicting its antecedent. In so doing, however, the theory falls prey to another equally problematic aporia: its functional ascriptions fail to describe genuine causal relations. While Mills and Beatty's propensity view can break this circularity, it is still agnostic with respect to how to specify these causal relations. All these ills can be traced to the way that the retrospective logic of selected effects ignores work that makes organism persistence and reproduction possible. At best, SE theories ultimately demote functional ascriptions to merely heuristic status. At worst, they eliminate any possible causal basis for defining functional normativity. Finally, we argue that a retrospective appeal to the temporal persistence of a trait is unnecessary for an account of function. A function can be identified in terms of a particular direction and magnitude of work expended moment by moment to maintain and reproduce the organism of which it is a part.

### Ethical statement

- Funding: this article has not been funded by any specific research project.
- Conflict of Interest: the authors declare not to have any conflicts of interest.
- Ethical approval: n/a.
- Informed consent: n/a.
- Author contribution: n/a.

### References

- Adams, F. (1979). A goal-state theory of function attribution. *Canadian Journal of Philosophy*, 9, 493–518.
- Al-Shawaf, L., Zreik, K., & Buss, D. M. (2021). Thirteen misunderstandings about natural selection. *Encyclopedia of evolutionary psychological science*, 8162–8174.
- Beatty, J., & Finsen, S. (1989). In M. Ruse (Ed.), *What philosophy of biology is. Essays dedicated to David Hull/Rethinking the propensity interpretation: A peek inside Pandora's box*. Dordrecht: Kluwer.
- Boorse, C. (1976). Wright on functions. *Philosophical Review*, 85, 70–86.
- Boorse, C. (2002). In A. Ariew, R. Cummins, & M. Perlman (Eds.), *Functions: New essays in the philosophy of psychology and biology/A rebuttal on Functions* (pp. 63–112). Oxford: Oxford University Press.
- Bouchard, F. (2013). How ecosystem evolution strengthens the case for function pluralism. In P. Huneman (Ed.), *Function: Selection and mechanisms* (pp. 83–95). Dordrecht: Springer.
- Brandon, R. N. (1990). *Adaptation and environment*. Princeton: Princeton University Press.
- Buller, D. J. (1998). Etiological theories of function: A geographical survey. *Biology and Philosophy*, 13(4), 505–527.
- Campbell, D. T. (1960). Blind variation and selective retentions in creative thought as in other knowledge processes. *Psychological Review*, 67(6), 380–400.
- Christensen, W. D., & Bickhard, M. H. (2002). The process dynamics of normative function. *The Monist*, 85(3), 3–28.
- Cummins, R. (1975). Functional analysis. *Journal of Philosophy*, 72, 741–765.
- Cummins, R. (2002). Neo-teleology. In A. Ariew, R. Cummins, & M. Perlman (Eds.), *Functions: New essays in the philosophy of psychology and biology* (pp. 157–172). Oxford: Oxford University Press.
- Darwin, C. (1859). *On the origin of species*. London: John Murray.
- Davies, P. S. (1994). *Evolutionary functions and philosophy of mind*. Dissertation. Chapel Hill, NC: The University of North Carolina.
- Davies, P. S. (2000). The nature of natural norms: Why selected functions are systemic capacity functions. *Noûs*, 34(1), 85–107.
- Dawkins, R. (1986). *The blind watchmaker*. New York: W.W. Norton & Co.
- Edelman, G. M. (1987). *Neural darwinism – the theory of neuronal group selection*. New York: Basic Books.

- Futuyama, D. J. (2009). *Evolution*. Sunderland, MA: Sinauer Associates.
- Garson, J. (2011). Selected effects functions and causal role functions in the brain: The cause for a causal approach to neuroscience. *Biology and Philosophy*, 26, 547–565.
- Garson, J. (2016). *A critical overview of biological functions. SpringerBriefs in philosophy*. Cham: Springer.
- Garson, J. (2019). *What biological functions are and why they matter*. Cambridge: Cambridge University Press.
- Godfrey-Smith, P. (1994). A modern history theory of functions. *Noûs*, 28, 344–362.
- Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford: Oxford University Press.
- Gould, S. J., & Lewontin, R. (1979). The spandrels of san marco and the panglossian paradigm. *Proceedings of the Royal Society of London*, 205, 281–288.
- Gould, S. J., & Vrba, E. S. (1982). Exaptation—a missing term in the science of form. *Paleobiology*, 8(1), 4–15.
- Griffiths, P. E. (1992). Adaptive explanation and the concept of a vestige. In P. Griffiths (Ed.), *Trees of life: Essays in philosophy of biology* (pp. 111–131). Dordrecht: Kluwer.
- Griffiths, P. E. (1993). Functional analysis and proper function. *The British Journal for the Philosophy of Science*, 44, 409–422.
- Haldane, J. B. S. (1927). A mathematical theory of natural and artificial selection, part V: Selection and mutation. *Mathematical Proceedings of the Cambridge Philosophical Society*, 23(7), 838–844. Cambridge University Press.
- Havstad, J. C. (2011). Problems for natural selection as a mechanism. *Philosophy of Science*, 78(3), 512–523.
- Kauffman, S. A. (2019). *A world beyond physics: The emergence and evolution of life*. Oxford: Oxford University Press.
- Kurten, B. (1983). Variation and dynamics of a fossil antelope population. *Paleobiology*, 9(1), 62–69.
- Lewens, T. (2007). Functions. In M. Matthen, & C. Stephens (Eds.), *Philosophy of biology* (pp. 537–559). New York: Elsevier.
- MacLaughlin, P. (2001). *What functions explain*. Cambridge: Cambridge University Press.
- Millikan, R. G. (1984). *Language, thought, and other biological categories*. Cambridge, MA: MIT Press.
- Millikan, R. G. (1989a). An ambiguity in the notion “function”. *Biology and Philosophy*, 4, 172–176.
- Millikan, R. G. (1989b). In defense of proper functions. *Philosophy of Science*, 56, 288–302.
- Millikan, R. G. (1993). *White queen psychology and other essays for Alice*. Cambridge, MA: MIT Press.
- Mills, S., & Beatty, J. H. (1979). The propensity interpretation of fitness. *Philosophy of Science*, 46, 263–286.
- Moreno, A., & Mossio, M. (2015). *Biological autonomy. History, philosophy and theory of the life sciences* (Vol. 12). Dordrecht: Springer.
- Moreno, A., & Mossio, M. (2015). *Biological autonomy: A philosophical and theoretical enquiry*. Dordrecht: Springer.
- Neander, K. (1983). *Abnormal psychobiology. Dissertation*. Bundoora, Australia: La Trobe University.
- Neander, K. (1991). Functions as selected effects: The conceptual analyst's defense. *Philosophy of Science*, 58, 168–184.
- Neander, K. (2004/2012). Teleological theories of mental content. *Stanford Encyclopedia of Philosophy* <https://stanford.library.sydney.edu.au/archives/spr2013/entries/content-teleological/>.
- Neander, K. (2012/2020). Teleosemantic theories of mental content. *Stanford Encyclopedia of Philosophy* <https://plato.stanford.edu/entries/content-teleological/>.
- Neander, K. (2017). Functional analysis and the species design. *Synthese*, 194, 1147–1168.
- Nicholson, D. J. (2018). Reconceptualizing the organism: From complex machine to flowing stream. In J. Dupré, & D. Nicholson (Eds.), *Everything flows: Towards a processual philosophy of biology* (pp. 139–166). Oxford: Oxford University Press.
- Oeschger, E. S., Kanavakis, G., Halazonetis, D. J., et al. (2020). Number of teeth is associated with facial size in humans. *Scientific Reports*, 10, 1820.
- Papineau, D. (1987). *Reality and representation*. Oxford: Blackwell.
- Papineau, D. (1993). *Philosophical naturalism*. Oxford: Blackwell.
- Reiss, J. (2009). *Not by design: Retiring Darwin's watchmaker*. UC Press.
- Sober, E. (1984). *The nature of selection: Evolutionary theory in philosophical focus*. Chicago: The University of Chicago Press.
- Thorndike, E. L. (1905). *The elements of psychology*. New York: A. G. Seiler.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410–433.
- Wallace, A. R. (1916). *Letters and reminiscences*. New York: Harper & Brothers.
- Walsh, D. M., Lewens, T., & Ariew, A. (2002). The trials of life: Natural selection and random drift. *Philosophy of Science*, 69(3), 429–446.
- Wimsatt, W. C. (1972). Teleology and the logical structure of function statements. *Studies in the History and Philosophy of Science*, 3, 1–80.
- Wouters, A. (2003). Four notions of biological function. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 34, 633–668.
- Wouters, A. (2005). The functional perspective in organismic biology. In T. Reydon, C. A., & L. Hemerik (Eds.), *Current themes in theoretical biology* (pp. 33–69). Dordrecht: Springer.
- Wright, L. (1973). Functions. *Philosophical Review*, 82, 139–168.
- Wright, L. (1976). *Teleological explanations*. Berkeley: University of California Press.