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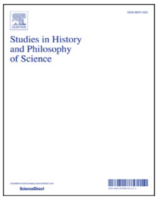

Function, persistence, and selection: Generalizing the selected-effect account of function adequately

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ABSTRACT

The selected effect account is regarded by many as one of the most attractive accounts of function. This account assumes that the function of a trait is what it has been selected for. Recently, it has been generalized by Justin Garson to include cases in which selection is understood as a simple sorting process, i.e., a selection process between entities that do not reproduce. However, once extended, this generalized selected effect account seems to ascribe functions to entities for which it looks unintuitive to do so. For instance, the hardness of rocks on a beach being differentially eroded by waves would be ascribed the function of resisting erosion. Garson provides one central argument why, despite appearance, one should not ascribe functions in cases of such sorting processes. In this paper, I start by presenting his argument, which hinges on whether a collection of entities form a population. I find it wanting. I argue instead that some selection processes are evolutionarily more or less interesting and that when a selection process is regarded as evolutionarily uninteresting, it will yield an uninteresting form of function rather than a reason for withholding the concept of function altogether.

1. Introduction

The Selected Effect (SE) account of function is one among several major accounts of biological function. Following this account, the function of *X* is *F*, if *F* has been selected in the (not too distant) evolutionary past of the organism bearing *X*. Said slightly more accurately by one of the major advocates of this account, Karen Neander[1]:

> It is a/the proper function of an item (*X*) of an organism (*O*) to do that which items of *X*'s type did to contribute to the inclusive fitness of *O*'s ancestors, and which caused the genotype, of which *X* is the phenotypic expression, to be selected by natural selection (Neander, 1991, p. 74).

Neander uses here ‘inclusive fitness’ instead of ‘fitness’ simpliciter, to include cases of selected traits that decrease the *direct* fitness of an organism bearing it but increase that of their relatives or organisms with the same genotype as them (Bourke, 2011; Gardner et al., 2011; Hamilton, 1963). A classic example is altruism. Following Neander's version of the SE account, it is the function of a worker bee's stinger to defend the hive (an altruistic behaviour), even though this trait does not generally increase a worker's direct number of offspring produced, only that of its mother (the queen) with which it shares part of its genotype.

Neander's inclusive fitness extension of the SE account is one of many ways to broaden its applicability. As of today, however, it is unclear whether and to what extent the SE theory can be extended to more complex selection scenarios involving frequency- and density-dependent selection. A preliminary review of the problem by Christie et al. (forthcoming) suggests that it might be more difficult than anticipated. There are both epistemic and theoretical reasons for that. In this paper, I will leave these complications aside, focusing instead on the bare bones of the theory. That being said, even in its simplest form, the SE account is faced with several criticisms. The account has been accused, among other things, of being neither genuinely explanatory nor normative, of being unfaithful to what biologists mean when they use the word “function”, and of being prey to a host of counterexamples. For a short review of these criticisms with rebuttals, see Garson (2016, pp. 46–55). I will also bracket these problems off here.

Instead, I will consider that the strengths of this account outweigh its problems. In particular, one advantage of the SE account over its rivals (for a review of the different accounts, see Garson, 2016) is that it enables us (1) to make a distinction between function and accidental benefits, (2) in principle to explain why one trait rather than another is observed in today's organisms, and (3) to distinguish whether an observed trait is dysfunctional (see Garson, 2016, pp. 35, 2019, Chapter 2).

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[1] For other versions of the account see for instance Millikan (1989), Griffiths (1993), Godfrey-Smith (1994), and Shea (2007).

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Recently, Justin Garson has proposed to generalize the SE account beyond its natural home, namely, the selection processes between reproducing organisms.[2] He summarises his account as follows:

> GSE: The function of a trait consists in the activity that contributed to its differential reproduction, or to its differential retention, within a population (Garson, 2017, p. 523).

According to Garson (2019, pp. 74–77), a number of authors before him (e.g., Godfrey-Smith, 1993; Griffiths, 1993; Millikan, 1984; Papineau, 1984) have attempted to generalize the SE account beyond biological organisms, and in particular to propose that learning produces new functions. However, he notes that all these accounts assume that, for new functions to be produced, the selection process causally responsible for the new functions ought to involve entities that reproduce in the same way organisms reproduce. One exception to this requirement is Wimsatt (1972). However, while for Wimsatt natural selection and function have a deep connection, he does not go as far as to propose an SE account of function. Garson, in contrast, aims to generalize the SE account beyond populations of reproducing entities. This extension is a welcome one. To do so, Garson follows a trend in evolutionary theory to extend the concept of natural selection. Over the last 30 years or so, and even before that, several attempts have been made to extend the concept of natural selection to other domains, such as culture, origins of life, and major transitions (Bourrat, 2014). Bouchard (2014) proposes to extend the concept of selection to ecosystems.[3]

Despite this welcome extension, I believe that Garson's proposal is problematic. In particular, one of Garson's implications is that entities that do not reproduce can be attributed functions. Garson argues that, in some cases, however, those entities should not be ascribed functions because they belong to sets that do not exhibit a sufficient level of fitness interaction between their members. Fitness interactions between the members of a set are, according to Garson and following recent analyses of the concept of population (e.g., Godfrey-Smith, 2009; Matthewson, 2015; Millstein, 2009), an important feature of biological populations. Without (enough of) them, these objects do not form a population. Since selection processes generating functions always occur in populations, there can be no functions in the absence of a population. I show that this argument does not succeed. I argue that, in some cases, natural selection produces some evolutionarily uninteresting outcomes. In other cases, the outcomes are much more interesting from an evolutionary perspective. ‘Interesting’ and ‘uninteresting’ should not be understood in absolute terms but rather relative to particular explanatory contexts and interests. However, whether an outcome is deemed interesting has nothing to do with whether the set of entities in which a selection process occurs exhibits a sufficient level of fitness interaction. I argue that this feature is also inherited by GSE functions. When the entities of a population do not reproduce or grow, the selected effects in this population are uninteresting, in the same way the evolutionary outcomes of selection without reproduction leads to some uninteresting outcomes (Bourrat, 2014). However, there is no reason to argue that uninteresting outcomes do not represent *bona fide* functions of the entities bearing those traits.

The paper will run as follows. In Section 2, I start by presenting the link between natural selection, adaptation, and SE function. I then briefly introduce the idea, proposed by several authors in recent years, that the process of natural selection, in its generalized form, does not need to occur between reproducing entities and that it can lead to simple, uninteresting forms of evolution by natural selection (ENS). In Section 3, I turn to Garson's main argument for considering that sets of entities that do not exhibit enough fitness interactions between their members, should not be regarded as populations. I show why this argument does not succeed. Finally, in Section 4, I propose a solution to the problem of liberality that my account might be accused of falling prey to.

2. Function, adaptation, and evolution by natural selection

A crucial point to note for my analysis is that there exists a link between the concept of function *qua* selected effects and the concept of adaptation (this point concerning ENS was made, although in different terms by Pittendrigh, 1958). As succinctly put by Sterelny and Griffiths (1999, p. 221), “[t]he [SE] functions of a biological trait are those effects for which it is an adaptation.”[4] Note here that the term ‘adaptation’ is understood as an outcome of the process of selection, not as the process of adaptation to the environment. Futuyma (2005, p. 260) refers to these two ideas as historical and ahistorical definitions of adaptation, respectively. Thus ‘adaptation’ for Sterelny and Griffiths refers to traits that have been—and might still be, but not necessarily so—adaptive for a substantial period of time in the evolutionary history of the members that bear them.

If one examines further the links between the concepts of SE function and adaptation, one will conclude that an adaptation is nothing more than a phenotype that is the outcome of the process of natural selection going in the same direction[5] for some time, assuming the organisms bearing those traits are able to pass them on reliably between generations, or in other words a form of ENS. Thus, SE functions result from the process of ENS. With a link between SE function and ENS established, we can now ask under what conditions ENS is observed. This will permit us, by transitivity, to establish the conditions under which SE functions can be observed, for if ENS is observed in such conditions, then following the above reasoning, it should yield adaptations with some effects that are SE functions.

A starting point in the literature on ENS is Lewontin's three conditions. There are several versions. I present here the 1985 version. In this version, Lewontin tells us that:

> A sufficient mechanism for evolution by natural selection is contained in three propositions:
>
> 1. There is variation in morphological, physiological, and behavioral traits among members of a species (the principle of variation).
>
> 2. The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents (the principle of heredity).
>
> 3. Different variants leave different numbers of offspring either in immediate or remote generations (the principle of differential fitness) (Lewontin, 1985, p. 76).

As shown by Godfrey-Smith (2007), this tripartite characterization of ENS is part of a long history since Darwin (1859) of summaries or ‘recipes’ for ENS. In the next sentence following the conditions, Lewontin claims that they are necessary and sufficient conditions for ENS. This is clearly false: the conditions are, in fact, neither necessary nor sufficient.

First, it is easy to see that they are not sufficient, as shown by Godfrey-Smith (2007). Suppose, for instance, a population in which individuals reproduce asexually and in discrete generations. Assume that the population is made of three individuals, two small and one tall (there is variation). Assume that one small individual produces a single offspring while the other has no offspring and the tall individual produces two (there is differential fitness). Finally, assume that the small individual breeds true, while the large one produces one small and one

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[2] See Garson (2011, 2012, 2014, 2016, 2017, 2019).

[3] See also Dussault and Bouchard (2017) and Bouchard (2013) for an account of function applied to ecosystem derived from this idea. Note that Dussault and Bouchard's accounts support (forward-looking) fitness-contribution functions rather than SE functions.

[4] See also Huneman (2010).

[5] Or selecting for the same value of a trait for some time if selection is non-directional.

tall individual (there is heredity though imperfect, but this satisfies Lewontin's principle of heredity).[6] Despite this population satisfying the three conditions, no evolution is observed. In the next generation, the population is composed of two small individuals and one large, like in the parental generation. This lack of change can be explained by the fact that two evolutionary processes are at play in the population: natural selection embodied by differences in fitness, and mutation embodied by a lack of perfect transmission. The two processes have opposite effects. Natural selection eliminates small individuals over time, while mutations recreate them due to the perfect inheritance of large individuals. The net change is nil. Note that in response to this and similar examples it is possible to tweak the conditions slightly to make them sufficient conditions. To do so, one just needs to add the extra assumption that the pattern of inheritance is the same for every individual of the population. With this in place, it follows that if the three conditions are satisfied, then ENS will occur.

However, it can also be shown that Lewontin's three conditions are not *necessary* for ENS. This is so because the definitions of fitness and heredity[7] used by Lewontin are too restrictive. A number of philosophers, including myself, have indeed recently put some pressure on these two concepts.[8] Starting with the concept of heredity, suppose as before a population of small and tall individuals, but assume that tall and small individuals produce equal proportions of offspring of both types, say one small and one tall for the small individuals, and two small and two tall for the large individuals. In this situation, offspring do not resemble their parents more than they resemble other parental individuals in the population, which seems to violate Lewontin's condition of heredity. Crucially, assume now that the population does not reproduce in discrete generations. In particular, individuals can survive after they reproduce and large individuals have a higher viability than small ones. In those conditions, we will observe an increase in the frequency of large individuals in the population (Bourrat, 2015b; Earnshaw-Whyte, 2012). By the standard definition of evolution, this change in frequency constitutes an evolutionary change. Furthermore, because it is due to a difference in survival between the two types, which is a component of fitness (Sober, 2001), then it must be due to natural selection. This means that ENS can be observed even if there is no heredity in the classical sense of heredity.

In Bourrat (2015b), using the Price equation, I showed that this phenomenon can be explained by the fact that a general concept of heritability (a quantitative measure of heredity), in line with evolutionary theorizing, should take into account a parental individual persisting (and remaining of the same type over time) in situations of non-overlapping generations. An intuitive way to see why this is so, is to note that a large individual producing one large and one small offspring *and* surviving is numerically equivalent to this individual producing three offspring, two large and one small, *and* dying at the same time it reproduces.[9] *Mutatis mutandis*, the same is true for a small individual. If this latter perspective is adopted, heritability as it is classically defined (in terms of parent-offspring resemblance), is restored, and the problem of ENS seemingly occurring without heredity disappears.

Fitness in Lewontin's three conditions is defined in terms of the number of offspring (either in the next or remote generations). However, there is no reason to assume that reproduction is necessary for ENS. ENS can result from differential persistence only, with fitness measured in terms of persistence. This point has recently been made by a number of authors both in philosophy of biology and evolutionary biology (e.g., Bouchard, 2008, 2011; Bourrat, 2014; Doolittle, 2014, 2016; Lenton et al., 2021; Papale, 2020). Even Godfrey-Smith (2009), who regards reproduction as an essential feature of Darwinian populations, i.e., populations able to undergo ENS, concedes so when he claims that "[i]t is *possible* to bend a partially Darwinian description around change in collections of things lacking reproduction, but this is a very artificial extension of the theory." (Godfrey-Smith, 2009, p. 40, his emphasis). One possible response to that remark is that although it might seem an artificial way to extend the theory, one should not prejudge the fruitfulness of the extension of a theory beyond its original scope. The history of science is full of cases where extensions of a theory, appearing initially artificial, have yielded high returns.

One essential point emphasized by Godfrey-Smith, however, is that in collections of things in which there is no reproduction, then there is no *multiplication* of this population's entities. This means that the population is doomed to reduce its size over time and potentially go extinct. As claimed by Godfrey-Smith, "[i]ts evolutionary possibilities are very limited" (Godfrey-Smith, 2009, p. 104). That they are limited does not mean that they are non-existent, however. This point will turn out to be crucial.

Why is multiplication,[10] which is a term used by Maynard Smith (1983; see also Griesemer, 2000), an important feature of ENS? It is so because if we assume that different individuals of a population reproduce differentially, then it is possible for them to produce complex structures such as a heart or an eye. In such a population, the background against which new variation occurs (by mutation) changes over time. As an individual dies, a new one with traits that have been selected in the past replaces it (at least in expectation). This new individual, in turn, has a small probability of mutating which might lead to a fitness benefit for its carrier. And if a mutation is beneficial, it will have a higher-than-average probability of spreading in the population and change this population's phenotypic background. By repeating this process over and over, following Darwinian orthodoxy, complex structures can be produced over evolutionary time. This is what Godfrey-Smith (2009, pp. 49–50) calls the "'creative' role of selection" and which underlies the distinction between interesting and uninteresting evolutionary outcomes made in the introduction. This point is the same as the one made by Okasha (2006, p. 214) in his discussion of clade selection, where he concedes that one can conceive of the differential persistence of clades (which do not reproduce in any obvious way) as a form of selection. However, he notes laconically that this form of selection is "not very interesting."

To see this point in more depth, contrast the orthodox situation of a population of reproducing organisms with a situation in which there is only differential persistence in the collection of entities. We could even imagine that, over time, these entities can change (or mutate) randomly. In this situation, however, the probability that the mutations lead to a complex adaptation is much less likely (to the point where we can say it is probabilistically impossible). This is so because, in this population, beneficial mutations cannot spread (by multiplication) in the population. The background against which new mutations can arise always remains the same, thereby highly constraining the possibility to see emerging complex structures from such a population. This represents the main reason why Godfrey-Smith and Okasha consider that selection processes in sets of merely persisting entities are artificial or uninteresting. That complex structures cannot arise from populations of persisting entities is one thing. However, the claim that such a process should be denied the status of ENS is another entirely.

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[6] Godfrey-Smith (2007, p. 503, see also 2014, p. 32) provides different versions of this example.

[7] Or more precisely heritability, which is the quantitative measure of heredity that Lewontin defines in his three conditions.

[8] For pressure on the concept of fitness *qua* reproductive output see Bouchard (2008, 2011; see also Bourrat, 2014; Doolittle, 2014, 2016). For pressure on the concepts of heredity and heritability see Earnshaw-Whyte (2012), Bourrat (2015b), and Charbonneau (2014). Papale (2020) provides a synthesis of this work.

[9] This conventionalist move raises questions about identity which have interesting biological implications. Some of them have recently been explored by Babcock (2020).

[10] Multiplication encompasses cases of reproduction and developmental growth, the latter of which refers to situations of single organism becoming bigger over time, without separation between its different parts. Modular organisms are a prime example of this phenomenon.

There is nothing in the classical model of evolutionary theory that tells us that ENS *ought* to produce complex adaptations. An adaptation, in its simplest form, is just one variant that is represented in a high frequency in a population. Complex structures are undoubtedly more interesting than simpler ones from an evolutionary perspective, but 'interesting' is not a feature of the world. Furthermore, it is not unlikely that ENS started from merely persisting entities that subsequently acquired the capacity to reproduce and ultimately replicate because it was advantageous (Bourrat, 2014; Wilkins et al., 2012). From that perspective, reproduction, or more generally multiplication, are derived properties of a lower-powered process of ENS.

3. Of rocks and beaches

In the previous section, I made two points. First, I showed that strong links between ENS, adaptation, and SE function, exist. A trait's SE function just is the effects of an adaptation, and ENS, when inheritance is well behaved, just results in adaptation. Second, I claimed, following a number of authors, that the concept of ENS can be straightforwardly extended to entities that do not reproduce but merely persist.

One logical conclusion from this reasoning is that a form of adaptation results from differential persistence only, and consequently, that individuals in populations of merely persisting objects can be ascribed SE functions. Although Garson does not exactly use this reasoning, he gets to the same conclusion. Selective retention or mere sorting processes alone can yield (G)SE functions. Thus, he argues that in a population of objects that persist differently, the function of a trait is that for which it has been selected, where selection only consists of differential persistence, i.e., with no multiplication. One example used by Garson is synapse selection.

Synapse selection, of which Garson (2011, 2014, 2019) proposes a detailed account, occurs following the formation of the brain in mammals, including humans, and certain other animals. The idea is that some, if not the majority, of the synapses produced during brain formation, are eliminated over time by a process of selection. Whether a synapse is eliminated depends on whether it is activated frequently enough. If it is not activated frequently enough, it is eliminated. Garson argues that there is furthermore a form of competition between synapses: the activation of some synapses can trigger the elimination of others. Synapse selection fits a process of selection without reproduction squarely. There is no reproduction in this example because one synapse being activated does not lead this synapse to produce more synapses or even lead to the production of more synapses altogether. From there, because some synapses are associated with different behaviours or abilities, their function is that for which they have been retained over an organism's life. This leads Garson to conclude that synapses can acquire new functions over time, depending on the environment and condition of the organism.

I am broadly on board with Garson's project. However, stated as I did, it may seem that one implication of Garson's account is that *any* sorting process will yield functions. This would be so because any sorting process can be regarded as a selection process that leads to a weak form of adaptation. This includes the case of rocks on a beach being differentially eroded by the waves because some rocks are harder than others, an example Garson borrows from Kingsbury (2008, p. 496).[11] As a result, one would have to conclude that at least one function of a rock on the beach is to resist erosion. This is Lewens' (2004) conclusion when discussing function attribution in cases of inorganic sorting processes. Lewens furthermore explains that it would be a futile exercise to attempt distinguishing functions originating from simple sorting processes such as the differential erosion of rocks on a beach from what might be deemed 'genuine' functions originating from processes involving multiplication (like natural selection between organisms).

> One might think that the kinds of functions possessed by items that survive sorting processes are mock functions, or "as-if" functions at best. […] Trying to discriminate between "real" and merely "as-if" functions is probably a waste of time. Here I want to argue that there is no nonarbitrary way for the proponent of the SE account to say why sorted functions are any less genuine than biological functions (Lewens, 2004, p. 128).

Lewens point should be in accordance with Garson's aim in developing the GSE account when he says that "[m]y main argument for GSE is that it solves all the puzzles of function, without pointless restrictions. Parity of reasoning demands that we accept it" (Garson, 2019, p. 101). However, Garson refuses Lewens' conclusion, which would imply ascribing functions to rocks on a beach. Why? Because according to him, a set of rocks on a beach is not a *population*. In contrast, synapses form a population (Garson, 2019, p. 108). GSE, he argues, does not apply to *any* set of objects; it only applies to *populations* of objects by virtue of a selection process always occurring in a population (Garson, 2019, p. 104). Thus, one can reconstruct Garson's argument as follows:

***P1**: If X has a GSE function, then it is the result of a selection process.*

***P2**: If X is the result of a selection process, then it occurs in a population.*

***P3**: Mere sorting processes, like differential erosion of rocks on the beach, do not occur in a population*

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***Cl**: Mere sorting processes do not yield GSE functions*

As I show below, his argument does precisely what he intends to move away from when developing the GSE, namely, avoiding adding arbitrary restrictions. There are multiple arguments for why I think so. First, there is no consensus about the concept of population in evolutionary biology and philosophy of biology. Garson relies on the analyses of the concept of population from Godfrey-Smith (2009), Millstein (2009), and Matthewson (2015). Following these analyses, fitness interactions between the entities of the set is an important feature of a population. In the case of rocks on the beach, there are no fitness-like interactions, while there are in the cases of antibody and synapse selection. For that reason, we should conclude that the former is not a process of selection yielding functions while the latter are. I do not deny that fitness interaction[12] might be an important aspect of (biological) populations in that it can speed up the processes of adaptation. However, claiming that this is a defining feature of a population and consequently of natural selection—if we agree that natural selection always occurs in a population—is far from an "emerging consensus" (2019, p. 103) as Garson claims.

Other philosophers of biology have explicitly endorsed the view that there *need not* be fitness interactions between organisms to produce genuine ENS. For instance, Sober (1984, p. 17), when discussing the sense one should give to the notion of "struggle for existence" one can find in Darwin (1859), argues that "[t]wo plants at the edge of the desert may differ in their abilities to withstand the drought. They thereby struggle against each other, but not in the Malthusian sense." This contradicts the picture that interactions between individuals need to occur so that a selection process can occur. Two plants at the edge of the desert belong to a population in an abstract sense, and this is enough to apply Lewontin's three conditions and yield adaptation. Another example comes from Brandon (1990, p. 71), who, discussing whether for two individuals to be in the *same* selective environment they must literally be interacting with the same features of the environment, and thus ultimately with one another, answers that "for our purposes, selective environments can be characterized in terms of the patterns of relative fitnesses without regard to the sources of that pattern." This is consistent with Sober's view (and Darwin's view, following Sober's argument) that if

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[11] We will see, in Section 4, that this type of example has some precedence in the evolutionary literature.

[12] Or something equivalent for non-biological entities.

the sources of the pattern can be considered as similar, even if this means two individuals are separated, there is no reason to consider that they would not undergo a process of selection. Similarly, Lewens (2007, p. 60) notes that the modern understanding of selection does not require any scarcity of resources—which would lead to fitness interactions—between organisms.

Second, the simplest models of population genetics illustrating how natural selection operates in a population are frequency- and density-independent selection models (see Hamilton, 2009, Chapters 6 and 7). In those models, classically, no factors, including the environment (which is considered absent, or more accurately infinite), the frequency of other alleles, or the density of the population, can impact fitness. The fitness of a genotype is considered invariant; the lack of fitness interactions between the genotypes of the population are thus explicitly built into those models. These models might not realistically represent their target system(s), but that is not the point here. Instead, the point is that it is doubtful they would be so often used to present the process by which natural selection operates if interactions between the members of a population were such an important feature for understanding ENS and adaptation. As Lewontin (1970, p. 1) wrote, “natural selection occurs even when two bacterial strains are growing logarithmically in an excess of nutrient broth if they have different division times” which is in line with the point made in the previous paragraph.

Bouchard (2011, 2014) went as far as denying that a population is necessary for ENS to occur. By saying that, I am not endorsing Bouchard's view on this particular matter, but this shows that it is unclear that any consensus exists on the definition of a population.

These three lines of argument represent good evidence that trying to put some restrictions on what counts as a GSE function by relying on such an ambiguous concept as ‘population’ seems at best contentious and at worse doomed to failure.

There is yet another argument against Garson's unwillingness to ascribe functions to rocks on the beach being differentially eroded because they do not belong to a population. The argument goes as follows: Even if we were accepting that the presence of fitness interactions between the entities of a set is a defining feature of a population in which ENS can occur, the examples in which the entities of a set do not appear to have functions—such as rocks on the beach being differential eroded—can easily be tweaked so that the entities of the set have fitness interactions without this changing our intuitions that they do not have functions. Garson is well aware of this. He presents a modified case of the rocks on the beach discussed above he owes to Karen Neander. In this example, the rocks are organized in a pile and jostle each other as the waves crash on the pile. In the jostling process, the softer rocks erode faster than the hard ones. This example—and the many others one can create at will—would appear to be a lethal argument against Garson's proposal, but Garson claims that this is not so. He argues that the fitness interaction requirement, in and of itself, is not enough. Not only must entities of a population interact with one another, but they must do so in the right way. In particular, based on Matthewson’s (2015) analysis, he argues that “roughly […], on average, each member of the population must have fitness-relevant interactions with several other members of their group—not just a few” (Garson, 2019, p. 106). He then proceeds to show that in a pile of rocks, one rock only interacts with a *few* other rocks, and thus does not have the right level of connectedness or “linkage.” For that reason, a pile of rocks is not a population.

This argument is unconvincing. As a preliminary remark, I note that Matthewson's account is tailored to *biological* populations, not their geological analogs (and beyond). Second, one response to Garson's argument is that a pile of rocks is not the only situation in which rocks can jostle each other. Take another example of rocks not organized in a pile, but small enough to be displaced by each wave. In this situation, each time a wave slams the beach, the small rocks become suspended in the water and jostle each other when the wave retreats. Because the wave mixes the rocks, there are fitness interactions between the rocks and a high degree of connectedness. Following Garson's argument, one would then have to regard a set of small rocks that are suspended in water as a population, but not a pile of larger rocks! I believe that this is enough to show that one can strip connectedness altogether as an essential property of populations that can undergo ENS (for convergent points see Colombo, 2020; Conley, 2020). Once again, that does not contradict the point that in paradigmatic cases of ENS, which I take to be cases in which selection is particularly conducive to cumulative adaptations, connectedness is an important feature of a population.

The above point is reinforced, once again, by classical models in evolutionary theory. A large number of models assume that an individual only interacts with its neighbours (or more generally locally) and *not* potentially with any other member of the population they belong to. This feature results in what is called ‘population structure’ in population genetics (see, for instance, Hamilton, 2009, Chapter 4). This is also a widespread assumption in some evolutionary games (see Nowak, 2006, Chapter 9). In both population genetics and evolutionary game theory, population structure is a fundamental feature to understand some evolutionary phenomena. For instance, if a population is well-mixed (maximal degree of connectedness), altruism cannot evolve while it can in some situations of local interactions (Bourrat, 2015a; Fletcher & Doebeli, 2009). As with frequency- and density-independent selection, some might complain that these models are highly idealized. However, models in which there *is* some population structure are typically more realistic than frequency- and density-independent selection models, and more generally, models in which the individuals are well-mixed.

4. Strength of selection and GSE function: separating the wheat from the chaff

I started this paper by untangling the links between natural selection, evolution, adaptation, and SE function. I claimed, following others, that the SE functions of a trait are the selected effects for which it is an adaptation in the evolutionary sense. I then briefly reviewed the literature showing that ENS does not require the existence of reproduction or multiplication. If this is so, there is no need to invoke these features to talk about functions. I then showed that this ought to be Garson's conclusion, since he proposes a generalized account of SE function in which reproduction is not an essential feature of the entities forming a population. However, when dealing with situations that do not intuitively seem to yield any function, such as a set of rocks on the beach becoming harder over time as a result of differential erosion, Garson refuses to bite the bullet. Instead, he argues that a set of rocks on the beach is not a population and consequently cannot be considered to exhibit GSE functions since ENS always involves a population. However, as I have shown, such an argument fails for two main reasons: a) defining a population on the basis of fitness interactions remains contentious, and b) connectedness or linkage does not appear to do the work intended by Garson.

I should note that I remain open to the possibility that an objective criterion permitting us to separate genuine from “mock” functions exists. However, insofar as Garson's ‘population’ argument is his master argument, I remain pessimistic that such a criterion exists. I tend to agree with Lewens (2007, p. 130) who, when referring to organic selection processes (but this can be extended to any other selection process in which there is no multiplication), claims that:

> If we feel that they are more genuine, then we can best explain that by pointing to the simple fact of historical habit (we are used to using teleological language in this domain), and to the fact that natural selection, operating over organisms, tends to give rise to entities that look more like designed items than do inorganic sorting processes operating over physical entities.

Where does this leave us? It is interesting here to set side by side Lewens's quote and a quote from Van Valen, who, more than 30 years ago, was already talking about ENS of rocks. The case he presents is slightly different, for it concerns the hardness of different *grains of* *minerals* composing granite, but Van Valen's and Kingsbury's examples are strikingly similar. Van Valen's example is worth quoting in full.

> Then again, look at the rock called granite. It is composed mostly of grains of feldspars and quartz, with some mica and other minerals inserted among them. When granite weathers, the feldspars and micas become clays but nothing much happens to the quartz grains. They are more resistant and get transported down streams or along shores. Thus most beaches are the result of differentially eroded granite.
>
> This is an example of natural selection in the nonliving world. Quartz grains survive longer than feldspar grains, and there is a progressive increase in the average resistance to weathering, of the set of grains that have still survived. This action of natural selection is even creative, as we see by the formation of a beach.
>
> The lack of reproduction imposes constraints on the flexibility of evolution here, but one shouldn't confuse that with the selection itself. We do have here a common sort of evolution by natural selection, and there are many other nonliving examples. (Try to think of some. Being irreversible, they provide at least local arrows for the direction of time.)
>
> So we should try to relax the constraints that channel our thoughts toward the ways we have thought before (Van Valen, 1989, p. 2).

Van Valen tells us that it would be a mistake to consider that the differential persistence of grains does not constitute ENS. It is just a very constrained type of evolution. To go back to Lewens' quote, it is *not* our historical habit to see it that way and a beach does not seem to be designed as a heart does. However, we should not be prejudiced against seeing this type of case as evolution. Constrained evolution is still evolution and the same goes for GSE functions. In some cases, it is relevant to apply the concept of SE function to merely persisting entities or entities that do not reproduce in obvious ways; in other cases, it is much less so. However, that should not lead us to conclude that a rock has no GSE function. The function of resisting erosion in the example of the rocks on the beach is simply much less interesting or relevant than when the entities of a set are multiplying.

Context and interests can partly explain what one will deem interesting or uninteresting cases of ENS but one might want to pin down the distinction more objectively. One way to do so is to go back to the distinction between ENS of persisting entities and ENS of multiplying entities. As we have seen, what permits one to separate interesting from uninteresting cases of ENS is the possibility of cumulative adaptive evolution. However, cumulative adaptive evolution is not an all or nothing matter. It comes in degrees. Under some restrictive assumptions, part or total evolutionary change between two times can be regarded as the degree to which a trait has become more adapted to its environment. Assuming a strong link between natural selection (including cases of differential persistence) and adaptation exists,[13] it would, in principle, be possible to provide standardized measures of the change due to natural selection in a given set and over a given period of time and, in doing so, compare different degrees of adaptation and consequently of GSE function in different situations. The Price equation, which is a very general tool used in evolutionary theory that can accommodate any assumption about the entities of a set (see Luque, 2017; Okasha, 2006; Price, 1970) would be a natural starting point for this project. In situations of differential persistence, the standardized measure would generally appear much weaker than in situations in which multiplication occurs, all else being equal. Whether a situation is deemed interesting from the perspective of GSE functions would thus amount to the value of this measure. In situations where the value obtained would be small, as, in most situations of persistence, the amount of functionality yielded by the traits selected would also be small when compared to situations in which reproduction occurs. That would represent a basis for the claim that such situations are uninteresting or marginal cases of function.

Quantifying the degree of function in a given situation could also be the answer to a potential worry, namely, that ascribing functions to the entities of any sorting process renders my version of the GSE account overly liberal. It should not be forgotten that the notion of biological function plays an important role in a number of domains, for instance, the naturalization of mental representations and the concept of mental disorder. For Dretske (1988, Chapter 3), representations have the function to carry information about the world. For Wakefield (1992), a mental disorder is a harmful dysfunction. Providing an account of function in which any sorting process can yield functions could imply that too many mental states are representations and too many conditions are disorders.[14] Garson's restriction that the GSE account only applies to *populations* (that is, for him, sets of entities in which there are sufficient fitness interactions) is precisely designed to avoid this type of liberality problem. Quantifying degrees of function would also permit us to bypass this problem. Since in situations of mere persistence, the measure would generally produce lower values than in situations of biological organisms, one could simply say that the function of a rock's hardness to resist erosion is much weaker than the function of a heart to pump blood. By transitivity, this view could lead to a graded account of representations and disorders. This line of thought is convergent with Matthewson's (2020) recent proposal that proper functions come in degrees. Arnold (1983) provides a starting point in the quantitative measure of functions which he calls "performance." Arnold does not have in mind the SE account when discussing performance. His account would be closer to the propensity account of function (see Bigelow & Pargetter, 1987), which states that a trait has a function if it provides a fitness benefit to its bearer. However, the quantitative-genetics formalism Arnold uses has straightforward links with the Price equation (see Queller, 1992) and it could be developed to suit the requirements that the GSE account demands.

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[13] Some have questioned the idea that natural selection necessarily leads to increased adaptation (for reviews, see Birch, 2016; Okasha, 2018). This has implications for the (G)SE account, but as we saw in the introduction, I will bracket this problem off here.

[14] I thank an anonymous reviewer for prompting me to discuss this problem.

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