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In What Sense Can There Be Evolution by Natural Selection Without Perfect Inheritance?

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ABSTRACT

In *Darwinian Population and Natural Selection*, Peter Godfrey-Smith brought the topic of natural selection back to the forefront of philosophy of biology, highlighting different issues surrounding this concept. One such issue is whether the perfect transmission of characters from parent(s) to offspring is necessary for evolution by natural selection (ENS). Drawing on the classical summaries for ENS, Godfrey-Smith's answer is that it is not, and opposes his view to the replicator framework. In this paper, I show that Godfrey-Smith's approach to ENS is only one of two legitimate perspective on ENS. One focuses on natural selection in the context of other evolutionary processes, while the other assumes their absence. After having presented these two perspectives, which I call the 'contextual' and the 'pure' perspective respectively, I draw on a framework which conceptualises the difference between natural selection, drift, and mutation in a causal rather than statistical fashion developed elsewhere. From there, I show that following the pure rather than the contextual perspective, perfect inheritance of characters is a necessary condition for ENS. This is because, I argue, imperfect inheritance is inevitably associated with an evolutionary process conceptually distinct from natural selection, namely mutation. I conclude by proposing that the classical summaries for ENS correspond more to the contextual perspective and the replicator framework more to the pure perspective.

1. Introduction

Ever since Darwin (1859), numerous authors have proposed summaries for evolution by natural selection (ENS), all of which roughly have the following tripartite formulation: for ENS to occur, a population should exhibit (1) variation in character, (2) leading to differences in fitness, and (3) which is heritable to some extent (e.g. Lewontin 1970, 1985; Endler 1986; Brandon 1990; Ridley 1996; Bourrat 2014; see Godfrey-Smith 2007, 2009 for the subtle differences between each of these summaries). One remarkable point about those summaries also referred to as the 'classical' approach to ENS, is that they do not postulate *perfect inheritance*¹ of characters from parent(s) to offspring. This led Godfrey-Smith to

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the conclusion that ENS is possible even if ‘everywhere we look there are degrees of similarity but no variation “faithfully transmitted”’ (Godfrey-Smith 2009, 33). In other words, this position, which Godfrey-Smith calls a form of ‘evolutionary nominalism’, holds that ‘the grouping of entities into types is in no way essential to Darwinian explanation’ (Godfrey-Smith 2009, 35). According to Godfrey-Smith, evolutionary nominalism is in sharp contrast with an alternative approach to ENS, namely the replicator framework (Dawkins 1976; Hull 1980; Dennett 1995; Haig 2012; Lu and Bourrat 2018; Wilkins and Bourrat 2018), which posits the perfect inheritance of types at some level (often the genetic one) for ENS to occur. Replicators, according to this view, are transmitted without changes across generations except for some errors (mutations).

In consequence, these two ways of approaching natural selection seem to conflict with one another regarding the question of inheritance. This difference leads naturally to the question of whether the classical approach has the edge over the replicator framework. Godfrey-Smith (2009, 34–35) thinks it does because considering ENS without replication is more general than assuming that it requires it. In this article I take a different position from that of Godfrey-Smith. I show that depending on what one means by ‘ENS’, the perfect transmission of characters across generations can be regarded as a necessary or an unnecessary condition. Under what I call the ‘pure’ perspective on ENS, namely when natural selection is considered in isolation from any other evolutionary factors, the perfect inheritance is required for ENS to occur. However, when natural selection is considered in the context of populations in which different evolutionary factors are contributing to an evolutionary outcome—an approach favoured by Godfrey-Smith, which I call the ‘contextual’ perspective on ENS—then perfect inheritance is not necessary for ENS to occur.

To reach this conclusion, in the next section, I recognise that Godfrey-Smith’s version of the contextual perspective is quite successful at delimitating a class of populations in which part of the evolutionary change can occur as a result of natural selection and produce complex adaptations. However, this approach, I argue, does not permit to delimit specifically the outcome of the process of natural selection when no other evolutionary process is present. To do so, one must switch to the pure perspective and delimit a class of populations in which natural selection is the *only* evolutionary process occurring. But specifying the properties of this class of population requires first to have some criteria at hand for distinguishing the process of natural selection from other evolutionary processes, especially drift and mutation. Natural selection and drift are classically characterised in statistical terms (Millstein 2016). This is problematic because a statistical interpretation always has more than one compatible causal interpretations. In section 3, relying on previous work, I propose an alternative way of distinguishing natural selection from drift starting from one of Godfrey-Smith’s distinction based on intrinsic and extrinsic properties (Godfrey-Smith 2009, 53–57) and previous work of mine (see Bourrat 2015a, 2017).

From there, I show in section 4 that evolutionary change resulting solely from the process of natural selection over more than one generation requires perfect inheritance at some level. This is because, I argue, when ENS is associated with imperfect inheritance, at least another evolutionary process—mutation—which is conceptually distinct from natural selection is at work in the population considered and explains the imperfect transmission of characters across generations. To make this latter point, I start from two toy

examples, which I subsequently generalise. I conclude that the pure and the contextual perspective on ENS need not be opposed: they represent two complementary forms of evolutionary explanations.

2. The Contextual and the Pure Perspective on Evolution by Natural Selection

At the core of Godfrey-Smith's take on ENS is the notion of a 'Darwinian population'. A Darwinian population is 'a population—a collection of particular things—that has the capacity to undergo evolution by natural selection' (Godfrey-Smith 2009, 6). From there Godfrey-Smith proposes the concept of a 'minimal Darwinian population'. A minimal Darwinian population is a population that features the classical three properties of variation in character, difference in fitness and inheritance (Godfrey-Smith 2009, 39). Fitness for Godfrey-Smith is understood fundamentally as resulting from differences in reproductive outputs.

One important feature of Godfrey-Smith's set-up for minimal Darwinian populations is that perfect inheritance from parents to offspring is unnecessary. This feature is typical of the summary approach to ENS of which perhaps the most famous exemplar is proposed by Lewontin (1970). Because in most real populations the perfect or quasi-perfect inheritance of characters seems to be the exception rather than the rule, this feature of minimal Darwinian populations seems quite a reasonable one. Thus, following Godfrey-Smith, a population in which there is perfect inheritance from parents to offspring should be regarded as a special case of minimal Darwinian population in which not only do parents cause their offspring to resemble them—there is some fidelity in the inheritance pattern—but also the pattern is such that inheritance is perfect.

It is undeniable that this approach to ENS and Godfrey-Smith's version of it particularly (which involves several important refinements I will not expose here) is a very useful one. Perhaps its main benefit is that it allows assessing cases in which natural selection is an important 'driver' of evolution and among them those that will lead to the evolution of complex structures. In other words, it permits us to identify cases in which natural selection translates into complex adaptations.

That said, despite its benefits, the approach has some limits. One of them, relevant for my purpose, is that because it approaches natural selection from the structures it produces rather than from the process itself, it hinders the exact causal role that each evolutionary process, and more particularly natural selection, plays in a given evolutionary outcome. Godfrey-Smith (2007, 2009) is certainly aware of this limitation since he reviews a number of cases satisfying the criteria of a minimal Darwinian population in which no evolutionary change is observed. In those cases, Godfrey-Smith argues, natural selection and at least another evolutionary force or process 'push' in opposite directions leading the population to exhibit no evolutionary change (see also Godfrey-Smith and Lewontin 1993). But his reasoning involves stepping aside from his framework and to assess what causal role each evolutionary process role is playing in the evolutionary change observed (or lack thereof).

The same limitation is visible from one semantic slip Godfrey-Smith makes when he criticises the replicator framework (Godfrey-Smith 2009, 31–36). As I mentioned earlier, the replicator framework presupposes the (quasi-)perfect transmission of types

Table 1. The difference between the contextual and the pure perspective on ENS.

	Contextual perspective	Pure perspective
Corresponding Darwinian population	Minimal Darwinian population	Pure Darwinian population
Evolutionary force(s) present in the population exhibiting ENS	Natural selection and possibly other evolutionary forces	Natural selection strictly
Targeted explanation	What the minimal properties of a population to exhibit <i>some</i> ENS (contextual ENS) are	What the only properties of a population for it to exhibit <i>strictly</i> ENS (pure ENS) are

across generations in cases involving natural selection, an assumption Godfrey-Smith rejects. Although Godfrey-Smith's criticism is initially targeted to the idea that *natural selection* does not require perfect transmission, he ends up claiming that perfect inheritance is not necessary for *evolution* (Godfrey-Smith 2009, 33) to occur.

Considering these remarks, I propose that the question of whether ENS requires perfect transmission across generations can be answered in two different ways. First one can ask whether the outcome of ENS when natural selection is only one of the evolutionary processes undergone by the population requires perfect transmission of characters from parents to offspring. This type of answer fits well with Godfrey-Smith's approach in which natural selection is contextualised within total evolutionary change. I call this approach the *contextual* perspective on ENS. From this perspective, one is generally interested in whether and to what extent natural selection plays *some* role in evolutionary explanations. This is a perfectly legitimate perspective, but it is not adequate for fulfilling an equally legitimate aim, namely understanding the nature of evolutionary change due *solely* to the process of natural selection. To that effect, another perspective or approach is required, one I call the *pure* perspective on ENS. As I show below, each perspective responds differently to the question of whether ENS requires perfect inheritance.

Answering the question of whether ENS requires perfect transmission of character from parents to offspring from a pure rather than a contextual perspective involves considering a case of population in which natural selection is the only evolutionary process at play in transgenerational evolutionary change. To do so in a way analogous to what Godfrey-Smith (2009) did from the contextual perspective, one can consider a class of populations of entities—albeit highly idealised ones²—in which all the evolutionary forces (i.e. mutation, migration, and drift) with the exception of natural selection have been eliminated so that any evolutionary change observed in this population can only be attributed to natural selection. I call this class of populations *pure Darwinian populations*.

Table 1 summarises the differences between the contextual and pure perspective on ENS. My aim in the remainder of this article is to show that the perfect transmission of character from parents to offspring is necessary if one approaches ENS from a pure rather than a contextual perspective.

3. Separating the Effects of Natural Selection on Reproductive Output From the Effects of Drift

So far, I have shown that one legitimate way to answer the question of whether perfect inheritance is necessary for ENS is to consider that 'ENS' means 'pure ENS'. But I have

yet to propose tools that will allow me to distinguish natural selection from the other evolutionary processes, namely mutation and drift.³ In this section, relying on an analysis provided elsewhere (Bourrat 2015a, 2017, 2018), I partially undertake this task by proposing some tools to distinguish the concept of natural selection from the concept of drift, the latter of which is classically opposed to natural selection.⁴ I leave mutation for Section 4.

The notion of drift is often associated with the notions of ‘sampling error’, ‘indiscriminate sampling’ or ‘random sampling’ (e.g. Crow and Kimura 1970; Beatty 1984; Hartl and Clark 1997; Millstein 2002, 2016; Gillespie 2004; Plutynski 2007; Hamilton 2009). In population genetics, differences in reproductive output occurring by chance or accident between entities of a population and leading to evolutionary change are often considered as synonyms for evolution due to drift. Although a statistical description of drift as resulting from the deviation from expected values of reproductive output is pragmatically useful in evolutionary theory, it remains insufficient to capture its underlying causal processes unless one supposes that fitness is a propensity. This interpretation of fitness is endorsed by numerous authors (see, for instance, Brandon 1978; Mills and Beatty 1979; Beatty and Finsen 1989; Sober 2001; Pence and Ramsey 2013). It tells us that fitness is a tendency or disposition comparable to familiar examples like fragility. Entities are ‘expected’ to produce a certain number of offspring in a given environment in the same way that a glass is expected to break under certain conditions.

But as is emphasised by Godfrey-Smith (2009, 29) and others, this interpretation is problematic (see for instance Drouet and Merlin 2015). One reason is that interpreting fitness in terms of propensity must necessarily rely on one of the different propensity interpretations of probability. Unfortunately, these interpretations are very controversial. In particular, they suffer from the charge of being empty accounts of probability (Eagle 2004; Hájek 2012). Furthermore, single-case probabilities, when interpreted as propensities—which for many represent the least controversial accounts of propensity—rely on the assumption of a fundamentally indeterministic world. This is quite problematic since some have been argued that indeterminism is eliminable from evolutionary theory (Horan 1994; Graves, Horan, and Rosenberg 1999; Rosenberg 2001; Weber 2001; Bouchard and Rosenberg 2004). Arguably, our concept of fitness should be orthogonal to the question of whether the world is determinist or indeterministic (Millstein 2003; Bourrat 2017). Thus, to capture more substantially the notion of drift, we need conceptual tools which do not rely on one particular—and controversial—interpretation of probability, and are compatible with a fully deterministic world.

Godfrey-Smith (2009, 53–63) precisely develops tools which are compatible with these two requirements. He holds the view that the distinction between natural selection and drift has something to do with the notions of intrinsic and extrinsic properties of entities forming populations. Although this distinction has some problems, I think it is on the right track.

Godfrey-Smith’s distinction is the following. He argues that, everything else being equal, when there is variation in *intrinsic* properties between the members of a population that leads them to have different reproductive outputs, the resulting evolutionary change should be attributed to natural selection. In contrast, when this difference in reproductive output is due to differences in *extrinsic* properties, the resulting evolutionary change should be attributed to drift. He defines an intrinsic property as a property which, in contrast with an extrinsic one, does not depend on the existence and arrangement of other

objects. This is also the working definition I will use here. Good examples of intrinsic properties are the chemical composition of an organism, having eyes of a particular colour or having a particular mass. Examples of extrinsic properties are being at a particular location, having a particular weight (which contrary to mass depends on the gravitational force an object is subjected to) or being someone's cousin.

The rationale behind this view is that when extrinsic properties are causally responsible for differences in reproductive outputs, these cannot be systematically attributed to the bearers of those properties. In some sense, intrinsic properties are constitutive of an entity while extrinsic properties are not. Another way to understand this distinction is in terms of counterfactual dependencies. When evolutionary change is due to drift, had the circumstances been otherwise, some extrinsic properties of their bearers would have been different and led to a different evolutionary outcome.⁵

Although I regard Godfrey-Smith's framework as a valuable one to separate natural selection from drift, it is incomplete. One way to appreciate this incompleteness is by remarking that any biological property, say for instance 'height', is diachronically the result of the interaction between the bearer of the property and its environment. Had an organism been put in a different environment from birth, its height may have been very different. Godfrey-Smith's distinction between intrinsic and extrinsic properties only accounts for 'synchronic' dependences on reproductive output leaving out 'diachronic' ones. Classically the intrinsic/extrinsic distinction is one of metaphysical dependence (synchronic), not of causal dependence, the latter of which requires time (diachronic). Yet, the distinction between natural selection and drift cannot be fully drawn without taking diachronic dependences on reproductive output into consideration. To see this, take the following case presented in Bourrat:

Suppose that ... two organisms have the same susceptibility to a disease *D*. Yet, for some reason one gets *D* and has to spend more energy to eliminate it. To do so it burns a larger amount of fat than the other organism. As a result, the two organisms have different amounts of fat and produce different numbers of offspring. (Bourrat 2017, 33)

Because an organism's amount of fat is one of its intrinsic property and that the two organisms have some variation in this property which ultimately leads to differences in reproductive output, then one could argue following Godfrey-Smith's analysis, that this represents a case of natural selection. But obviously any evolutionary biologist would recognise in this case the hallmark of drift. What does this show us? As argued in Bourrat (2017), using a number of other examples, it demonstrates that although some properties like 'having a disease' are intrinsic properties—they do not depend on the existence or configuration of other objects at the time they are measured—the fact that they are the result of chance events in the past of the entities makes them events that ought to be associated with drift rather than natural selection.

From there, one might consider that Godfrey-Smith's approach is doomed to failing to discriminate cases of drift from cases of natural selection in general, and more particularly when the properties involved can vary during the lifetime of an organism. However, as shown in Bourrat (2017), the account can be supplemented to make it consistent with such cases. I argue that not only should a property causing a difference in reproductive output be intrinsic to be associated with natural selection, it should be also invariable. The property for an individual of having a given amount of resources to spend for the

production of offspring which is less than that of another individual *because* of a disease that is ultimately the result of some chance event, in spite of being an intrinsic property, is ultimately caused by some differences on extrinsic properties. Had the circumstances been different, this intrinsic property would have been different. The difference in intrinsic property here is just redundant with some difference in extrinsic properties. In causal terms, differences in intrinsic-variable properties here *screen off*⁶ differences in extrinsic properties with respect to differences in reproductive output. For that reason, they should not be associated with natural selection but rather with another evolutionary processes, which I argue, is either drift or belongs to the same family of evolutionary processes as drift (see Bourrat 2015a, 2017). This implies that only intrinsic properties which do not causally depend on extrinsic properties—they do not screen off extrinsic properties—can confidently be associated with natural selection.

Thus, this leads to a picture in which intrinsic properties must be decomposed into two subcategories, namely, on the one hand, *intrinsic-invariable* properties, such as having a particular gene, and on the other hand, *intrinsic-variable* properties, such as a particular height due to a particular life history causally independent from any intrinsic-invariable properties of the entity. From there one can define the population differences in intrinsic-invariable properties within an environmental background leading to some differences in reproductive outputs as the ones to be attributed to natural selection, while the population differences in intrinsic-variable and extrinsic properties within an environmental background leading to differences in reproductive output as the one to be attributed to drift.⁷

At that point the reader might have several objections to the framework presented here, such as the fact that there are no absolutely invariable properties in nature except perhaps genes, the objection that in many cases natural selection select for variable properties, or again that following my framework, the view that extrinsic properties and intrinsic-variable should be associated with drift leaves out a very important aspect of this notion namely its association with randomness. To avoid too much repetition, I refer the reader to the analysis given in Bourrat (2017) where I deal with all these objections in detail, starting with a discussion of the conditions under which extrinsic and intrinsic properties can be associated with the notion of randomness including in a deterministic setting.

With respect to the first objection, all I will say here is that natural selection is a process that can only be described at a particular grain of description—that is the extent to which one zooms in and out when providing a description. By changing the grain of description at which an evolutionary sequence is given, one can describe a situation in which an object does not vary in time or produce offspring which are perfectly identical to it, while a finer grain of description would have led to the conclusion that the object varies or that it has produced offspring different from it. Thus, it does not make sense to claim that natural selection occurs in a particular population if one does not also refer to a particular grain of description. The implications of these remarks on grains of description in regard to the nature of the process of natural selection are explored in depth in Bourrat (2019). With respect to the second objection, if it is true that natural selection sometimes selects for variable properties such as, for instance, some species of fish changing sex during their lifetime, or many life-history traits, invariance is nevertheless recovered at some level. In fact, the relevant intrinsic-invariable property in such cases is the particular trajectory or pattern underlying the change over time. A salmon failing to change sex at a

particular time in its life is what could make this individual failing to maximise its reproductive output, and thereby what should be associated with natural selection, rather than variation on this property were it the same for two salmons.⁸

The attentive reader will notice that Godfrey-Smith's concept of minimal Darwinian population presented earlier does not permit us to distinguish cases in which differences in reproductive output are due to differences in extrinsic and/or intrinsic-variable properties from those that are due to differences in intrinsic-invariable properties. Recall that in this definition only variation in *character* is mentioned. The distinction Godfrey-Smith makes between differences in intrinsic and extrinsic properties—which I modified—is thus an elaboration on his concept of minimal Darwinian population, which he incorporates as part of what he calls a 'Darwinian space' of which the full exposition would go beyond the scope of this paper. In order to remain consistent and for the purpose of the paper only, suffice for me to refine here the notion of a minimal Darwinian population and assume that a minimal Darwinian population is a population in which at least part of the differences in reproductive output between the members of the population are due to differences in intrinsic-invariable properties. This is to avoid classifying cases in which *all* the differences in reproductive output would be ultimately due to differences in extrinsic properties as Darwinian populations. To be consistent these populations should be considered as non-Darwinian populations.

4. Different Cases of Evolution and Their Causal Interpretation

With these distinctions and definitions in place, we now have at hand all the necessary tools to evaluate whether the perfect transmission of characters is necessary for ENS once it is understood from a pure rather than a contextual perspective. Starting from an underspecified toy model (Figure 1) in which there is imperfect inheritance of character (height), I show that under two causal interpretations of this model, natural selection is

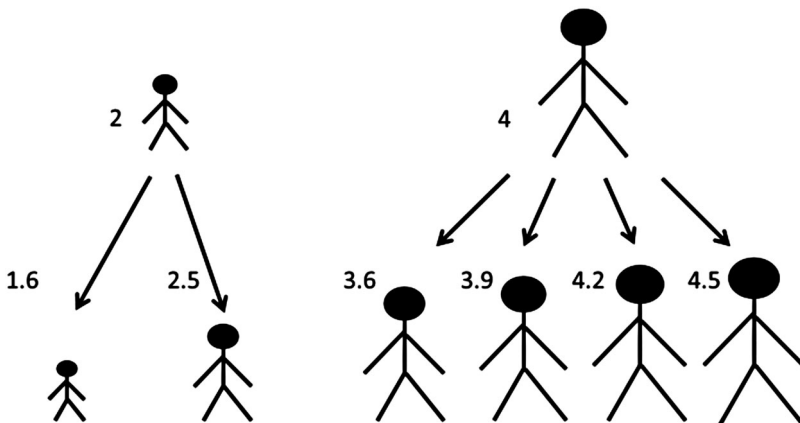


Figure 1. Case 1. Two individuals of different heights producing offspring that resemble them more than they resemble the other parental individual (there is heritability on height) without being perfect copies of their parent. Numbers represent heights.

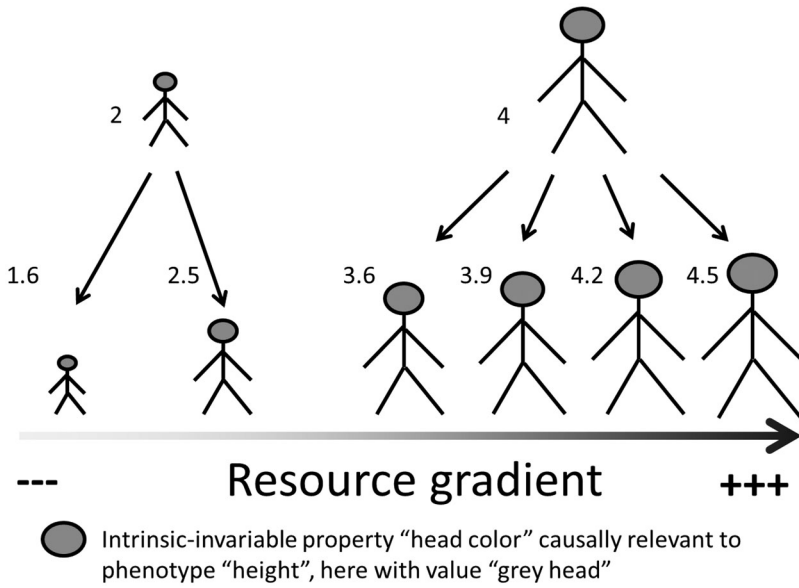


Figure 2. Case 2. Situation identical to Case 1 but in which all the differences in height between the individuals are due to some differences in intrinsic-variable properties. See main text for description.

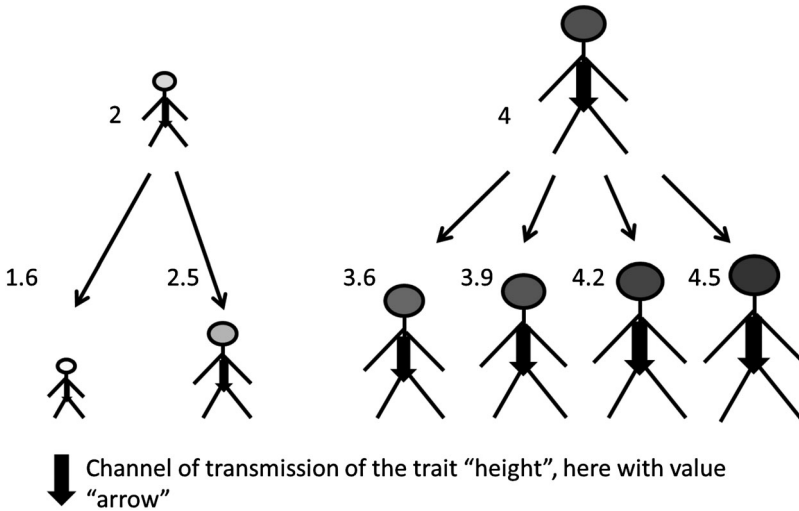


Figure 3. Case 3. Situation identical to Case 1 but in which all the differences in height between parents and offspring are due to the channel of transmission being imperfect. See main text for description.

either absent in the population—the population is thus a non-Darwinian population; Case 2 and Figure 2—or it is present but mixed with another evolutionary factor which I associate with the evolutionary process of mutation—the population is thus a minimal Darwinian population, not a pure Darwinian population. Further on, I establish more systematically that imperfect inheritance of character is incompatible with pure Darwinian populations.

To start off, let us imagine a population of individuals in a deterministic world (or sufficiently close to one) in which every individual has a different height. Suppose that all the individuals reproduce asexually, simultaneously and that generations are non-overlapping (when an individual reproduces it immediately ceases to exist). Suppose also that each individual produces a number of offspring that is a linear function of its height (or any other character): the taller the individual, the higher the number of offspring it produces. Finally, suppose that there is heritability⁹ on height in the sense that offspring resemble on average more their parent than they resemble other individuals of the parental generation (positive slope of regression line). Let us call this case ‘Case 1’.¹⁰ For simplicity, imagine that the parental generation of the population is composed of only two individuals with different heights (say 2 units and 4 units respectively).¹¹ Suppose also that the short individual has two offspring, while the tall one has four offspring and that each offspring is of a height different both from its parent and any of its siblings.¹² Although this setting is clearly unrealistic, this does not undermine the conceptual point I want to make.

Figure 1 is an illustration of Case 1. A simple calculus using the value of heights presented in Figure 1 leads to the conclusion that the population is evolving because the average height at the parental generation is 3 units while it is 3.38 units at the offspring generation. Although the population is evolving, can we confidently assume that this is a case of minimal Darwinian Population, that is, a case in which natural selection is causally involved in the evolutionary change observed? And if this case is a case of minimal Darwinian Population, should we ascribe *all* the evolutionary change to natural selection, or should we ascribe to it only part of it? In other words, is the population a *pure* Darwinian population? As it stands Case 1 is underdetermined and answers to these questions cannot be given. Cases 2 and 3 presented below are possible (but not exhaustive) underlying causal interpretations of Case 1, one of which (Case 2), I will show, is not a case of Darwinian population, following the terminology given in the previous section, while the other (Case 3) is a case of minimal Darwinian population but not a pure Darwinian population.

4.1. Case 2: Evolution Due to Differences in Intrinsic-variable Properties

One possible causal interpretation of the difference in height in Case 1 is that each individual of the population is in a different environmental context (i.e. has different extrinsic properties) which is causally relevant for height yet correlated between parents and offspring. Apart from this difference, we can suppose no other difference between the individuals of the population. Had each individual of the population been in the same environmental context, they would have had the same height. Let us call this case ‘Case 2’.

Figure 2 illustrates Case 2. Imagine that the property ‘head colour’ is causally involved in determining the height of each individual and is intrinsic-invariable within the range of possible environmental states so that two perfect clones growing in any two different states of the environment have the same value for the property ‘head colour’. Let us also assume that ‘head colour’ is the only intrinsic-invariable property involved in the determination of height and that each parent has the value ‘grey head’ so that there is no variation in intrinsic-invariable properties between the individuals of the population. Suppose also that each individual transmits its intrinsic-invariable properties (the value ‘grey head’) perfectly to

its offspring. Suppose finally that the level of resource received by an individual is causally involved in determining the height of each individual and that there is a gradient of resources in the population (as shown in Figure 2): the higher the amount the resource received, the taller the individual. Each offspring, once it is born, moves away from its parent but remains close to it. Because each individual is at a different position along the resource gradient, they all are different from each other. Yet, because each offspring remains located close to its parents, offspring resemble on average more their parent than other parental individuals.

In this case, we have variation in height, that leads to differences in reproductive outputs and that is heritable (using the standard regression notion of heritability).¹³ Yet the population here is clearly not a minimal—let alone a pure—Darwinian population. In fact, all the differences between individuals are *ultimately* differences in extrinsic properties (their parent's position and their own position). There is no population variation in intrinsic-invariable properties (only in intrinsic-variable properties due to differences in extrinsic properties), thus these differences cannot be attributed to natural selection.

This case, although not original (see the very similar although less detailed case 9 in Godfrey-Smith 2007), is useful for our purpose for three reasons. First, it shows us that underlying a continuous trait such as height, there *can* be perfect inheritance of intrinsic-invariable factors (in our case the head colour) within the range of possible states of the environment. Observing a continuous trait is thus insufficient to claim that ENS does not require perfect inheritance to occur. This is a fairly obvious point, but it is worth mentioning. Second, it illustrates, following the analysis provided above, that unless the different values of a given trait are intrinsic-invariable—or at least depend partly on intrinsic-invariable properties—within a specified range of environmental conditions, natural selection cannot be invoked as a cause of evolutionary change on this phenotype. If height is a variable trait within the different environmental states over a given period of time in a given population, and that there is no variation in the population on at least one intrinsic-invariable property causally involved in determining the height of individuals, then height is not a trait subjected to natural selection. This is because whether individuals survive or reproduce depends ultimately entirely on differences in extrinsic properties. This point is important for our purpose because the fact that a trait studied is continuous or discrete is relevant for ENS only if this trait is intrinsic-invariable that is, insensitive to differences in extrinsic properties.

Finally, this case points out that even if in a population there is a positive heritability (using the regression approach, see Note 7) and differences in reproductive outputs between the different individuals, this does not necessarily make this population a minimal Darwinian population, since the resemblance between parents and offspring can be due to a correlation between the environment of parents that is not explained by intrinsic-invariable properties of individuals.¹⁴

4.2. Case 3: Evolution Due to Unreliable Channels of Transmission

Another possible explanation accounting for the different individual heights in Case 1 is invoking the unreliable transmission from parents to offspring of an intrinsic-invariable factor involved in the determination of height. To see this, imagine a case in which, within the parental generation of the population, individuals have differences in

intrinsic-invariable properties that are causally involved in differences in height. In this particular case, any extrinsic or intrinsic-variable properties causally involved in individuals' heights is kept constant across the population so that any difference in reproductive output is due to the differences in intrinsic-invariable property in relation to height. Imagine now that because of the nature of the channel of transmission of height (with the channel of transmission supposed to be an intrinsic-invariable property and identical for all the individuals of the population), each offspring produced is both different from its parents and from its siblings, but resembles its relatives more than other individuals; in other words the channel of transmission for height is not perfectly reliable. Let us call this case 'Case 3'.

Figure 3 illustrates this case in a simplified way. Suppose, as in Case 2, that the trait 'head colour' is the only intrinsic-invariable property causally relevant in the determination of an individual's height. By 'causally', I mean here that this property is a difference maker for reproductive output in the population. But contrary to Case 2, each individual in the parental generation has a different height because they have a different head colour. Let us postulate that, *ceteris paribus*, height depends additively on head colour: the darker the colour, the proportionally taller the individual. Because the two parental individuals in Figure 3 have different head colours, both have a different height. Suppose also that, contrary to the previous case, there is no resource gradient in the population and that all other extrinsic and intrinsic-variable properties have the same evolutionary consequences on height (or any other phenotype) and reproduction. Although the amount of resources received by an individual might be causally involved in its height, this is not an *actual* difference maker in this population, only a *potential* one to use the distinction of Waters (2007). Finally, suppose that each individual has the same channel of transmission across generations for height (represented by the value 'arrow' in Figure 3), which is supposed to be an intrinsic-invariable property of individuals on which there is no variation in the population (another potential difference maker), and that leads them to produce offspring similar but typically not identical to them (for some complex deterministic reasons). As with Case 2, there is variation in height which leads to differences in reproductive output and which is heritable. Does this represent a case of ENS?

To answer this question, we only need to know whether the differences in reproductive output between the individuals are due to some difference(s) in intrinsic-invariable property. The difference between the reproductive outputs of the two parental individuals is fully accounted for by a difference in height which differs only because of some difference in the intrinsic-invariable property 'head colour'. This population is thus a minimal Darwinian population and natural selection is causally responsible for at least some of the evolutionary change. With this established, we can now ask whether natural selection is the only causal factor that explains the evolutionary change observed across generations in this population or in other words whether the population is a pure Darwinian one.

Because the channel of transmission for height does not have a high fidelity, new variation is produced in the population at each generation by modification of the offspring's intrinsic-invariable characters (head color) when compared to the parent.¹⁵ The production of new variation from existing variation by changing an otherwise intrinsic-invariable character represents clearly an evolutionary process distinct from both natural selection and drift. In fact, production of new intrinsic-invariable properties between two generations does not match either of the two definitions, namely in terms of differences in intrinsic-

invariable properties for natural selection, and in terms differences in extrinsic or intrinsic-variable properties for drift. Thus, if the evolution of height described by our Case 3 depends on both natural selection and the production of new variation at the time of reproduction, it is not a pure case of ENS. This is a case of ENS with production of new variation at each generation. Although some production of new variation is necessary for complex adaptations to arise but also necessary for perpetual evolution to occur, it is conceptually distinct from natural selection (and drift). Below, I propose that this evolutionary process can be associated with the notion of ‘mutation’, which is one of several possible evolutionary factors besides natural selection, drift, and migration.

4.3. No Pure ENS Without Perfect Inheritance Across Generations

So far, I have established that two cases of populations in which there are differences in reproductive output between the different types of a population and heritability for the trait causally involved in the differences in reproductive output are not cases of pure Darwinian population. One—Case 2—is a non-Darwinian Population, because no evolutionary change is due to variation in intrinsic-invariable properties between the individuals of the population (natural selection is not responsible for the evolutionary change observed). The other—Case 3—is a minimal Darwinian population, but not a pure Darwinian population since the evolutionary change observed is due partly to natural selection and partly to the production of new variation through an unfaithful channel of transmission for height. Yet, as such, these two cases do not demonstrate that imperfect inheritance is incompatible with a population being a pure Darwinian population. In fact, one might argue that a subclass of pure Darwinian populations different from Case 3 exhibits imperfect inheritance of characters from parents to offspring. To address this concern, instead of finding new cases exhibiting imperfect inheritance across generations and then further establish that natural selection is not the sole evolutionary process responsible for the evolutionary change observed, one must provide a demonstration that *any* case in which there is no perfect transmission from parent to offspring necessarily involves an evolutionary force conceptually distinct from natural selection and is therefore incompatible with a pure Darwinian population.

To do so, let us summarise the conditions for a population to be a pure Darwinian population.

For a population to evolve *solely* by natural selection—that is to be a pure Darwinian population—the three following conditions must be fulfilled:

Condition 1. Natural selection, i.e. there should be existing variation in intrinsic-invariable characters within the population that leads to differences in reproductive output;

Condition 2. No drift (or correlated response), i.e. there should be no existing variation in extrinsic and/or intrinsic-variable characters within the population that leads to differences in reproductive output. If there is drift together with natural selection, we have a case of minimal Darwinian population, not pure Darwinian population;

Condition 3. No mutation (i.e. no production of new variation) in the population, which represents an evolutionary processes distinct from natural selection. If there is production of new variation together with natural selection, we have a case minimal Darwinian population, not pure Darwinian population.

Demonstrating that at least one of the three conditions above is incompatible with imperfect inheritance will be sufficient to show that imperfect inheritance is incompatible with a pure Darwinian population. The demonstration is quite straightforward. Conditions 1 and 2 are compatible with imperfect inheritance of intrinsic-invariable properties. In fact, there is nothing in the three conditions preventing an offspring to differ from its parent. Existing differences in intrinsic-invariable properties—Condition 1—and no existing differences in intrinsic-variable or extrinsic properties—Condition 2—are logically compatible with imperfect transmission of those differences. However, requirement 3 is incompatible. In fact, all conceivable cases with imperfect transmission of intrinsic-invariable properties will necessary lead to the production of *new* differences of intrinsic-invariable properties in the population. Yet, the consequences of the process of natural selection on an evolutionary trajectory come from differences in reproductive output, not from the production of new variation.

Because Condition 3 cannot be reconciled with the unfaithful transmission of characters across generations, we have here the demonstration that ENS, when interpreted from the pure perspective on ENS, requires the perfect transmission of traits across generations.

Before concluding this section, I would like to defend the view that the production of new variation during an act of imperfect transmission from parents to offspring should be associated with the evolutionary process of mutation as understood in population genetics. Although mutations are classically thought as occurring randomly, I follow Godfrey-Smith (2007) and Mamei (2004) in their views that there are no fundamental reasons to consider so. As Godfrey-Smith puts it, ‘Darwinian evolution can occur on variation that is *directional*, even adaptively “directed”’. In these cases, natural selection may have less explanatory importance than it has when variation is random, but it can still exist’ (Godfrey-Smith 2007, 493, my emphasis).

A textbook definition of mutation process in population genetics is ‘the permanent incorporation of random errors in DNA that results in differences between ancestral and descendant copies of DNA sequences [. It] is the ultimate source of all genetic variation’ (Hamilton 2009, 154). This definition is compatible with Godfrey-Smith’s definition which reads as ‘[m]utation processes subtly change intrinsic character’ (Godfrey-Smith 2009, 55). If one replaces ‘intrinsic’ by ‘intrinsic-invariable’ in my framework and do not pay attention to the requirement that the errors are ‘random’ (see the paragraph above), we can see that the imperfect transmission of character satisfies his definition of mutation for it subtly changes the intrinsic-invariable properties that the offspring would have had, had the transmission been perfect.¹⁶

At that point, one could argue that because I *stipulate* that imperfect transmission of characters across generations represents an evolutionary process different from natural selection, the result found here is trivial or just definitional fiat. But that would unfair. In fact, it would miss the point that by providing a reasonable attempt to make sense of the evolutionary processes of natural selection, drift, and mutation in causal terms using the intrinsic-variable or extrinsic/intrinsic-invariable distinction, I *did not stipulate* a priori that imperfect transmission over generations should be associated with mutation. It is only because imperfect transmission necessarily leads to the production of new intrinsic-invariable properties—which can more naturally be associated to mutation than natural selection or drift—that I was able to claim that from a pure-ENS perspective perfect transmission is required. Furthermore, without making the

distinction between natural selection, drift, and mutation in terms of intrinsic-variable, extrinsic and intrinsic-invariable properties in the way I did, it would be impossible to conceptually separate Case 2 from Case 3. Yet, the difference between the two cases is plainly obvious.

5. Conclusion: The Replicator and Classical Approaches to Evolution by Natural Selection Reconsidered

In this paper, I have distinguished two legitimate perspectives on ENS. One—the pure perspective—focuses strictly on the evolutionary outcome of the process of natural selection when no other evolutionary process is involved. I have shown that for this to occur, the perfect transmission of traits between generations is necessary. Under the other—contextual—perspective, the process of natural selection is considered in settings in which it is one evolutionary process among other processes, most notably drift and mutation. From that perspective, ENS is compatible with the unfaithful transmission of traits between generations.

Returning to the opposition presented in the introduction between the replicator framework and the classical approach, one can now more clearly see that this opposition may result more from a difference in the type of evolutionary explanation targeted by each approach rather than from something more fundamental.

The classical approach—of which some formalism exists (see Okasha 2006, ch. 1)—permits us to explain the role played by natural selection in the evolutionary trajectory of a population in the context where other evolutionary processes exist. Invoking replication for such explanations is not necessary because natural selection *can* play an evolutionary role without any individual ever being replicated. In that sense, as mentioned early on, the classical approach provides a more contextual perspective on ENS. In contrast, the replicator framework focuses more on the bare bones of the process of natural selection and the sort of evolutionary outcomes it produces—mutations are in the background and are regarded as providing a raw substrate for natural selection to do its work. As such this framework is more in line with the pure perspective on ENS.¹⁷

Notes

1. By ‘perfect’ I mean here ‘exact copying most of the time’. Note that recently Earnshaw-Whyte (2012) has claimed, using a simple verbal model, that ENS does not even require stronger degrees of similarities between parents and offspring—that is it does not require heritability between parental and offspring characters. However, as shown in Bourrat (2015b), this claim relies on an imprecision surrounding the concept of heritability. When understood in its most abstract form, even in the model presented by Earnshaw-Whyte, I show using a version of the Price equation (see Okasha 2006, chap. 1), that there is some heritability between parent and offspring. The upshot of my analysis is that an individual persisting without change in character over time should account for part of the heritability observed in a population exhibiting variation between two times.
2. Note importantly that whether such populations exist in nature should not be regarded as more problematic for the soundness of the pure perspective on ENS than imagining a body being subjected to a given Newtonian force without frictions.
3. The evolutionary force known as ‘migration’ will not be treated here since I suppose a population isolated from any other population.

4. In a series of papers, Grant Ramsey (2006, 2013, 2016; Pence and Ramsey 2013) develops of a convergent framework. One difference though is that his approach relies on the propensity interpretation of fitness while mine does not.
5. Godfrey-Smith's view on drift is actually more complex. However, the extrinsic/intrinsic distinction is the only part of his account I need for the purpose of this article. In Bourrat (2017), I criticize his view that drift also results from what he calls 'low continuity', that is, when small differences in individual properties (whether intrinsic or extrinsic) have large effects on reproductive outputs.
6. For an introduction to the notion of 'screening off' see Brandon (1990, 83–84).
7. Note that drift is defined here very broadly. It entails what is known as 'correlated responses', i.e. evolutionary changes which are not causally due to the trait under scrutiny but to another known cause.
8. This assumes here that the failure does not depend on changes in extrinsic properties within the range of the extrinsic properties encountered by the species, otherwise the pattern of change is itself an intrinsic-variable property.
9. Heritability is a population level measure of inheritance from parent to offspring. There are roughly two notions of heritability used in the literature, namely broad-sense heritability (H^2) and narrow-sense heritability (h^2). In evolutionary theory only narrow-sense heritability is of interest and it can be defined in two different ways. Under one, h^2 is the ratio of additive genetic variance to phenotypic variance (Falconer and Mackay 1996). A less biologically centered definition would be 'the ratio of intrinsic-invariable phenotypic variance in a given environment and at a particular grain of description to phenotypic variance'. Under the other, more abstract, but formally linked to the first one, h^2 represents the slope of regression of average offspring character on parental or mid parental character (Falconer and Mackay 1996; Rice 2004; Okasha 2006). This latter definition has been favored by many authors. I follow suit, although see notes 13 and 14. The concept of heritability is associated with a number of philosophical issues (for more details see Sesardic 2005; Godfrey-Smith 2007; Downes 2009, 2017; Bourrat and Lu 2017; Bourrat, Lu, and Jablonka 2017; Lynch and Bourrat 2017).
10. This is a more detailed version of Godfrey-Smith's (2009, 24) model.
11. The fact I use only two individuals in my figures instead of a population composed of a higher number of individuals is for illustrative purpose only and has no consequences on the conclusions drawn later on.
12. In Case 1 there is no difference in viability between the individuals: they all die simultaneously after a unique reproductive event. That makes of Case 1 a 'fertility selection' example, i.e. in which selection comes primarily from difference in fertility between some individuals of the population. Yet, all the reasoning involved could have been made using a 'viability type' example, i.e. in which selection comes primarily from differences in viability.
13. Note here, that some have argued that the regression definition of heritability (see note 7) should not be regarded as a definition but rather as a method of estimation of heritability (e.g. Lynch and Walsh 1998, 171). In fact, arguably, because all the variation in character is due to variation in the environment of organisms in the Case 2, it should not be associated with heritability. This is a similar case to the ones of gene-environment covariance discussed in Lynch and Bourrat (2017).
14. Following on from notes 7 and 13, this suggests that the variance approach to heritability might, in some respects, be superior to the regression approach to discriminate the effects of natural selection from those of drift or correlated responses. This is mainly because the variance approach takes the independent population variable to be an intrinsic-invariable property of individuals (most of the time genes) while the regression approach takes any property (extrinsic, intrinsic-invariable or intrinsic-variable, i.e. any phenotype) as an independent variable. As such the regression approach to heritability is blind to the causes that produce resemblance.
15. 'New' should be understood here from the point of view the parental individuals. Unfaithful transmissions produce characters that are new and different from that of their parents. These

new differences might also be new with respect to the whole population, but this is not the sense in which I am using the word ‘new’ here.

16. The idea that an intrinsic-invariable property can change by mutation might appear as contradictory. However, by ‘invariable’ one should understand here ‘invariable given a range of environmental conditions in which events changing the property are so rare that they are considered as exogenous to the environment’. This means that the relevance of making explicit the grain of description—which will fix what is meant by ‘rare’—is not limited to natural selection and drift, as argued in Section 2 and Bourrat (2019), but also to mutation.
17. It goes without saying that each approach can be used for both perspectives on ENS. I am only suggesting here that they respectively fit better with one perspective rather than the other.

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