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# Natural selection and the reference grain problem

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## HIGHLIGHTS

- One classical definition of fitness depends on the notion of transmission of types between generations.
- This dependence on type means this definition cannot be description independent.
- If it is not description independent, this casts some doubt on the status of natural selection as being mind-independent.
- I call this problem the 'reference grain problem'.
- I show that it can be linked to the reference class problem in probability theory.
- I tentatively propose two solutions to it.

## ARTICLE INFO

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## ABSTRACT

Over the last 20 years, the concept of natural selection has been highly debated in the philosophy of biology. Yet, most discussions on this topic have focused on the questions of whether natural selection is a causal process and whether it can be distinguished from drift. In this paper, I identify another sort of problem with respect to natural selection. I show that, in so far as a classical definition of fitness includes the transmission of a type between generations as part of the definition, it seems difficult to see how the fitness of an entity, following this definition, could be description independent. In fact, I show that by including type transmission as part of the definition of fitness, changing the grain at which the type of an entity is described can change the fitness of that entity. If fitness is not grain-of-description independent, this further propagates to the process of natural selection itself. I call this problem the 'reference grain problem'. I show that it can be linked to the reference class problem in probability theory. I tentatively propose two solutions to it.

## 1. Introduction

The philosophical literature on natural selection is dense and often entangled with issues surrounding the concept of fitness (for an overview see Rosenberg & Bouchard, 2010). Most of this literature has revolved around two related topics. The first one amounts to establishing whether natural selection can reasonably be considered as a 'force' or cause of evolutionary change. The second one amounts to distinguishing natural selection from drift. There is much disagreement over these two questions. Some authors have argued that natural selection is a force or cause of evolutionary change (e.g., Bouchard & Rosenberg, 2004; Millstein, 2006; Otsuka, 2016, 2016; Reisman & Forber, 2005; Rosenberg & Bouchard, 2005; Shapiro & Sober, 2007; Sober, 1984; Stephens, 2004) and that natural selection and drift are distinct causal processes, while others, the 'statisticalists', disagree (e.g., Matthen & Ariew, 2002, 2009; Walsh, 2007; Walsh, Ariew, & Matthen, 2017; Walsh, Lewens, & Ariew, 2002). The statisticalists argue that natural selection is fundamentally a statistical process and that drift and natural selection should not be separated.[1] There also exists disagreement among the 'causalists'. While some have argued that natural selection results from individual-level causes (Bouchard & Rosenberg, 2004; Bourrat, 2018; Glennan, 2009; Otsuka, 2016), others have argued that natural selection and drift are population-level causes (Millstein, 2006; Reisman & Forber, 2005; Stephens, 2004).

I have my own view on these questions. Elsewhere (see Bourrat, 2014b; 2015a, 2017, 2018), I argue that natural selection and drift are distinct causal processes and that, at least in some cases, they can be regarded as resulting from individual-level causes in a particular

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[1] Some also argue that drift is an error term (e.g., Brandon, 2005) or that it is a useful fiction (e.g, Rosenberg, 1994). For a review of the debate see Huneman (2012).

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context given by the population and its environmental setting. Although the question of the causal status of natural selection and whether it can be distinguished from other evolutionary forces are important questions, I turn here to a different problem associated with the concepts of natural selection and drift, which, as far as I am aware, has hardly been noticed in the literature.

A striking fact among the protagonists in this literature is that nearly all seem to accept that the process of natural selection and its product, namely evolution by natural selection, are to some extent independent from the grain at which they are described. There are two important exceptions to this general trend. First, some work stresses the point that whether natural selection occurs in a particular setting depends on the way the environment is described (e.g., Abrams, 2009, 2014; Brandon, 1990, Chapter 2, 2005). Second, the statisticalists, as portrayed in Walsh (2007; see also Walsh et al., 2017), argue that whether natural selection and drift occur is not description independent. Walsh shows that the way one describes a cause can influence the way in which the strength of a particular evolutionary cause is interpreted. Although I agree with Walsh that his argument shows that the notion of causes used in evolutionary theory are not description-independent, following Northcott (2010, pp. 462–463), I do not embrace his view that difference makers ought to be description independent to count as causes.

In this paper, I argue that there is yet another way in which natural selection is a process that is not description independent besides the two mentioned above. In Section 2, I show that one classical definition of fitness in evolutionary theory is associated with the notion of type transmission. From there, I argue, it follows that one should typically expect different answers about the fitness of and entity when the grain of description used to describe this entity's type is different. This leads me to the conclusion, in Section 3, that whether and the extent to which evolution by natural selection occurs in a population, is also grain-of-description dependent: Natural selection can be both regarded as occurring and not occurring – though on different grains of description – in a given population. I call this problem the 'reference grain problem', and compare it to the reference class problem in probability theory by pointing to the similarity and common origin between these two problems. Although I do not provide a complete and definitive solution to this problem, I briefly propose two ways in which the problem could be addressed in Section 4. First, I suggest that natural selection could be considered as a model of a process rather than a physical process and that this model might bear some similarities with its target system (a population) *at a particular grain of description*. Second, I argue that one could narrow down the concept of what a type in evolutionary theory is and I show how this could resolve the problem.

### *1.1. On fitness and the transmission of types between generations*

One useful way to characterise natural selection is to start from the following Principle of Natural Selection (PNS), inspired by Brandon (1990, see also 2014):

> **(PNS)** Natural selection will occur in a population if and only if there is at least one difference in fitness, in a common environment, between two or more individual entities of a population.

There are different ways in which fitness can be characterised. To name a few, Bouchard and Rosenberg (2004), for instance, following others before them, propose the notion of 'solution to design problems' that leads to differences in reproductive output. Brandon (1990, 2014) prefers the notion of 'adaptedness', which means 'better able to survive and/or reproduce in a given environment' and might be regarded as tendency or propensity (Mills & Beatty, 1979; Pence & Ramsey, 2013). Godfrey-Smith (2009b, pp. 53–59) defends the view of fitness as amounting to differences in intrinsic properties leading to differences in reproductive output. According to him, intrinsic properties are the kind of properties that should be associated with natural selection. An object's intrinsic property for Godfrey-Smith is a property that does not depend on the existence or particular arrangement of other objects, while an extrinsic property does depend on the existence or particular arrangement of other objects (Godfrey-Smith, 2009b, p. 53). Elsewhere (see Bourrat, 2015a, 2017), I have proposed a refinement of Godfrey-Smith's account by stressing that to be successful in characterising natural selection, not only should a difference in property be intrinsic, but also invariable.

So far so good. But the PNS as stated and the notions of fitness mentioned above that can underpin it only permit us to account for the success of an entity (or its type) within one generation. To account for the evolutionary success of an entity over more than one generation, some conditions over the inheritance of the trait responsible for the difference in fitness must be met.[2] In other words, the PNS, in and of itself, will not permit us to distinguish whether natural selection is responsible for some observed evolutionary change. Suppose a population reproducing in discrete generations in which two types (**B** and **R**) do not reproduce with perfect fidelity. Although each type produces some offspring of the same type, it also produces some offspring of a different type, say type **G**. Let us also assume that **B** and **R** produce offspring of type **G** with a different rate in a given environment supposed constant over time. With type **B**, for each four offspring produced, three are of type **B** and one of type **G**. With type **R,** two are of type **R** and two are of type **G** (see Fig. 1). Is the fitness of type **B** and type **R** the same? If not, how should we infer the fitness after one generation of these two types from their reproductive outputs?

Following the PNS proposed above, the fitness of the two types is the same, since they both produce four offspring. Therefore, it seems reasonable to assume that there is no natural selection occurring in this population. Although this is strictly speaking correct, when providing an evolutionary explanation, we typically want to know whether an evolutionary change observed (or lack thereof) between two or more generations is *due to* natural selection or to another evolutionary process. By evolutionary change, following standard textbooks, I mean a change in frequency of types across generation or average change in character if the trait is a quantitative one. It might be the case that two types have vast differences in fitness *qua* adaptedness and if these differences are not passed on to the next generation, then natural selection will not be the reason why evolutionary change, if any occurs, is observed. In the case presented in Fig. 1, there is an interaction between natural selection and inheritance, so that adaptedness does not capture all there is about natural selection (for a similar point given in the context of the Price equation see Okasha (2011, pp. 246–248)). This type of interaction between natural selection and inheritance led Michod (1999, p. 176) to argue that a concept of fitness which does not take inheritance into account will be dynamically insufficient to predict evolutionary change. In fact, in the example depicted in Fig. 1, a measure of adaptedness, would not permit us to tell whether natural selection is responsible for the **B** type success.

To predict the evolutionary dynamics, and more particularly the role of natural selection in it (an intragenerational measure of success, and the interaction between this measure and inheritance), it thus seems that a different notion of fitness *qua* adaptedness is required; one that takes the transmission of types into consideration. This is indeed

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[2] To see this notice that in quantitative genetics, following the so called 'breeder's equation' (for an introduction see Falconer & Mackay, 1996, Chapter 11), the extent to which natural selection is responsible for the evolutionary change observed can be approached by measuring the heritability of a trait under selection. The more the trait is heritable, the more natural selection will have, with some caveats that cannot be developed here, been causally responsible for the difference in the composition of the population at a later generation (assuming the population size is infinite) of this trait. For more on the concept of heritability see Jacquard (1983), Godfrey-Smith (2007, 2009b, pp. 168–172), Okasha (2006, Chapter 1), Downes (2009), Bourrat (2015a), and some of its caveats see Lewontin (1974; see also K. E. Lynch & Bourrat, 2017; Bourrat & Lu, 2017; Bourrat, Lu, & Jablonka, 2017).

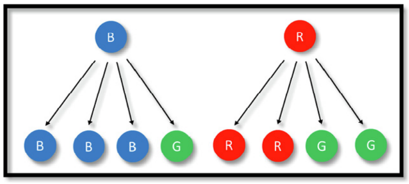

**Fig. 1.** Two types of entity with different transmission patterns.

the view taken from the perspective of a prominent account of evolutionary theory, namely the replicator approach, or gene-eye's view (Dawkins, 1976; Hamilton, 1964; Hull, 1980; Wilkins & Bourrat, 2018; Williams, 1966). This view stresses that the *faithful* transmission of types from parents to offspring is an important aspect of evolution by natural selection. I have shown elsewhere that *faithful* transmission is not as important as stressed by the replicator approach, since it can rather be seen as a product of natural selection itself (Bourrat, 2014a; 2015b). Yet, I believe that the *transmission of type* – whether with high faithfulness as stressed by the replicator approach or not – is fundamental to the idea of evolution by natural selection.

And this conception of fitness has indeed been integrated in the formalism originating from the gene's-eye view, namely kin selection, which is perhaps the most celebrated theoretical development in evolutionary theory. In a classical paper on this topic fitness is defined as:

> [Fitness[3]] in relative terms, [is] the number of copies of [an entity]'s genes expected to be found in the population in the very distant future. (Gardner, West, & Wild, 2011, p. 1027)

We can see in this quote that the notion of copy, which implies transmission of type across time, is fundamental to the definition. I want to stress that this definition is not a marginal one. It is the result of a long tradition starting from Fisher (1930) who defined the fitness of a type as an intrinsic growth rate of that type. All this means that, besides a definition of fitness tied to differences in reproductive output proposed above, in tracking the *adaptedness* of an organism (or type) to its environment, we also need a notion of fitness that tracks the role of selection over time across generations to assess evolutionary success.[4] Fitness with this latter conception not only measures the differences in properties between entities that have consequences for reproductive output, but also the extent to which the entity's type is able to be transmitted faithfully over time, and consequently its evolutionary success. Note also that the ‘type’ of entity could be defined over multiple traits, for example, a member of type X could represent an organism with a size Y and a colour Z. Note also that I will not consider cases in which traits are continuous. The argument considered here only applies to nominal traits. It is unclear whether a continuous treatment would lead to the same conclusions.[5]

To be clear, there are difficulties with all definitions of fitness, some of which are directly related to the one used by Gardner et al. or Fisher (for a review of some difficulties faced by different concepts of fitness, see Ariew & Lewontin, 2004), but it is fair to say that the transmission of type between generations is an integral part of a conception of fitness in some important areas of evolutionary theory.[6] In these areas, if one is to infer fitness from reproductive output and associate fitness with natural selection and evolutionary success due to natural selection only, they must take into account the degree of transmission of types between generations. The notion of fitness proposed by Gardner et al. is the one I will refer to in the reminder of this paper.

It should be noted at this point that whether individuals reproduce faithfully or not does not matter as much when they have the same transmission pattern. This is the case, for example, with sexual organisms with fair meiosis in which, at the phenotypic level, offspring are not perfect copies of their parents. To see why and yet remain with our example of asexual organisms in Fig. 1, suppose the case depicted in Fig. 2 where three types **B**, **R** and **Y** reproducing in discrete generations, produce respectively 2, 4 and 6 offspring of their type and type **G** with the same transmission pattern in a homogenous environment. More specifically half of the time they produce offspring of type **G**, while the other half of the time they produce offspring of their own type. In this case, whether one infers the fitness of each type from the total number of offspring or only the offspring of their type, the relative difference in the production of offspring of their type will be the same. The fitness of type **R** is twice the fitness of type **B** and the fitness of type **Y** is three times the fitness of **B**. Note that this will be the case so long as the transmission pattern is the same across the different types (and that at least some offspring have the parental type). Of course, one difference between a case in which individuals reproduce with perfect fidelity and a case in which individuals produce types different from themselves is that natural selection might explain more of the evolutionary change observed in the former case and less the latter case. But, if considering only the fitness across generations of the types, manipulating the transmission pattern *while keeping it the same across all types* of the population will have no fitness effect.

Consequently, in cases in which the transmission pattern across the different types in the population is the same, inferring fitness directly from reproductive output, without considering the type of offspring produced, does not constitute a problem for establishing in the long run the relative success of an initial type when compared to other types. However, in cases in which the transmission pattern is different between the entities being compared (e.g., if meiosis is not fair in the case of sexual organisms i.e., when there is some meiotic drive)[7] estimates of fitness based on the number of offspring produced will become inadequate to predict the evolutionary success of each type. This is because, taking the example of meiotic drive, comparing the reproductive output of two individuals will not be a reliable proxy for the number of copies of a given allele transmitted to the next generation, while in the case of fair meiosis, one can expect that half of the offspring of an individual will have a copy of any given allele, independently of the allele considered (expect for sexual chromosomes).

## 2. Fitness and the reference grain problem

I have shown so far that operationalising fitness in terms of relative number of descendants *of the same type* is important in some areas of evolutionary theory (see also the discussion in Godfrey-Smith, 2009b, pp. 31–39). In doing so, I have implicitly assumed that the notion of type identity between parent and offspring is unproblematic. Yet, although the notion of transmission of types in relation to evolution has been discussed in the philosophical literature (e.g., Abrams, 2009, 2012, 2014; Brandon, 1990; Godfrey-Smith, 2009b; Griesemer, 2000; Mameli, 2005; Pence & Ramsey, 2015) there is, as far as I am aware, no discussion in the philosophy of biology on its relationship with the notion of grain of description.[8] However, as I will show in this section, if one accepts a definition or concept of fitness which depends on the notion of type identity across generations, a problem soon emerges. To

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[3] In the terminology of Gardner, West, & Wild, ‘reproductive value’ is a synonym for ‘fitness’ in the sense I am using it here.

[4] There is a multipronged controversy over whether fitness is a useful concept in evolutionary theory when it refers to organisms (entities) as opposed to traits (types) (see Sober (2001), and the debate between Sober (2013) and Pence and Ramsey (2015)). Following Pence and Ramsey, I will consider that trait fitness is derivative of an organism's fitness and leave this controversy aside.

[5] I thank Arnaud Pocheville for raising this point to me.

[6] For a view that the notion of type is optional for evolutionary theory see Godfrey-Smith (2009b, 33–36) on what he calls ‘evolutionary nominalism.’

[7] See Burt and Trivers (2006) for more on the concept of meiotic drive.

[8] For an exception to this see Charbonneau (in press) which deals with long-standing issues on ‘the metrics of similarity’ in the field of cultural evolution.

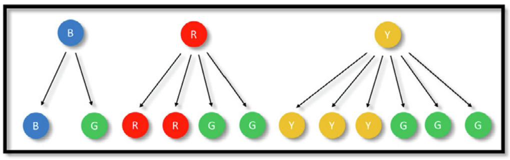

**Fig. 2.** Three types of entity with the same transmission pattern.

see this, I first show in what sense the claim that two objects belong to the same type is a claim that depends on the grain of description one uses.

A type is classically defined as an entity's property or set of properties that can be shared by other entities. For instance, all red entities belong to the type ‘red’. Although the notion of type used in evolutionary theory is quite straightforward, its relation to the notion of identity is complex. In fact, assessing whether two objects are identical presupposes that one has chosen a particular *grain of description*,[9] that is, the amount of zooming in or out made when the system is observed. At a fine-grained description for instance, even two replicated sequences of DNA are never perfectly identical and will thus be members of two different types for some properties. If this is true for DNA, this is even more relevant for two organisms or two groups of organisms. And this fact is not solely a biological one. At a fine-grained description, there are no two identical snow-flakes. Depending on which properties are measured and with what precision, two individual atoms of carbons of the same isotope might have different properties (e.g., different spins on their electrons). Because identity is grain-of-description relative, it means ultimately that in the context of evolutionary theory, producing offspring *of the same type* is not grain-of-description independent. By ‘grain of description’ I mean here both the way in which the domain of a variable is carved up (e.g., a given shade of red such as scarlet or ruby as opposed to the colour red) but also the temporal scale used to measure each value of the domain (e.g., how long has the object remained exactly red or this particular shade), so the zooming in or out is both spatial and temporal. In fact, if two entities vary slightly in colour over time, measured over a short timescale, the two entities might appear as different, while over a longer timescale they might appear as identical because over that longer timescale they have on average the same value.[10] In the reminder, I will focus on cases in which the same timescale is always the same, although I will come back the problem of timescale toward the end of the paper when I discuss what I call ‘evolutionary types.’

If type-identity between two objects depends on the grain of description used and that assessing fitness depends on the notion of parent-offspring type-identity, it follows that differences in fitness are not grain-of-description independent. As I show below, this can lead to conflicting views as to whether a particular case of evolutionary change is due to natural selection or other evolutionary processes. More specifically, one immediate consequence of the grain-of-description dependence of fitness is that one given entity, once examined from different grains of description, should, in some cases at least, be considered as having different fitnesses.

To see this, assume a population of entities that can be categorised as members of distinct types from a given perspective and produce asexually, on average, a different number of offspring of their own type. Because of this difference in number of offspring of the same type, we claim that the population evolves by natural selection, following the considerations of the previous section. But this conclusion might be altered if we change the grain of description. Imagine now that we decide to be less coarse and introduce more details in our description. To do that, we separate members of a given type we previously delineated into members of subtypes. As a result, it might be the case that because of this different way of characterising the entities of the population, the conclusion is now that each subtype has a different fitness from the one established with the coarser-grained description and consequently that natural selection has not the same magnitude when this description is used.

Fig. 3 and Table 1 provide an extreme case in which natural selection simply vanishes when one changes the grain of description. In this example, depending on what perspective we take, there are either two types of entities, namely red (**R**) and blue (**B**) or four types, namely **R1**, **R2**, **B1** and **B2**. From a coarse-grained perspective (P1), **R** entities deterministically[11] produce 4 **R** offspring at each discrete generation, while **B** entities produce only 3 **B** offspring. Everything else being equal, from that perspective, it seems that natural selection is responsible from the evolutionary change observed because there is a difference in fitness between the two types (4 for **R** and 3 for **B**). Now, taking a finer perspective (P2), we categorise entities with shades of colours and observe that the **R** and **B** parents, when we were assessing their colour from P1, are respectively of the type **R1** and **B1** when assessing their colour from P2. Furthermore, we notice that half of the offspring of **R1** are **R1** and the other half are **R2** while two third of the offspring of **B1** are **B1** and the remaining third are **B2** (see Fig. 3). From that perspective, the fitness of **R1** and **B1** are identical since only the offspring of their types are incorporated into the measure of fitness and thus the evolutionary change observed is not due to natural selection, because types do not vary in fitness. Incidentally, the two types have different transmission patterns, which is an analogous case to the case of unfair meiosis mentioned earlier. The concern here is thus that evolution by natural selection can at the same time occur and not occur, though on different grains of description.

The problem illustrated in Fig. 3 and Table 1 is important because nothing from the theory provides a guide for choosing the most appropriate grain of description for a particular situation. This is unwelcome for several reasons. First, a scientific realist might want to argue that one desideratum for a property such as fitness is that it remains invariant and thus independent from the grain of description, or in other words, be scale-invariant. From that perspective if evolution by natural selection is found at a particular grain of description, it should also be found at a finer-grained description.

Second, obtaining a finer grained description over the same temporal scale will in many cases lead to a higher level of empirical content about a system and should allow us to potentially identify a higher number of relevant difference makers, which is one desideratum for both prediction and explanation. This conclusion might be regarded by some as contentious. I believe it is not since assuming the exact same system, described with a different grain of description, will typically lead the finer description to contain more information than the coarser one. Yet, this leads to the worrying conclusion that, if one were to choose the finest possible grain of description to describe evolutionary change, they would most likely have to claim that the difference in fitness between the different entities is nil. This is because from the finest possible grain of description, none of the parental entities would be able to produce *perfectly* identical offspring to themselves with respect to the focal (determinable) property and thus the evolutionary

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[9] I consider the notion of ‘grain of description’ to be different from that of ‘level’ in the following sense. Considering a phenomenon occurring at one level of organization (say the organism or the cell level), one can give different amounts of details about this phenomenon. This difference in amount of details concerns the grain of description, not the level of organization at which the description is given. Of course, in many cases changing the level of organization, also changes our grain of description, but this need not be. For a discussion on grain of description see Abrams (2014, especially Fig. 1).

[10] See Pocheville (2010) which provides a nice treatment of the question of timescales in evolutionary theory. See also Bourrat (2015c, 2015d) on the relevance of timescales for the levels-of-selection problem.

[11] A similar demonstration could be made without the assumption of determinism.

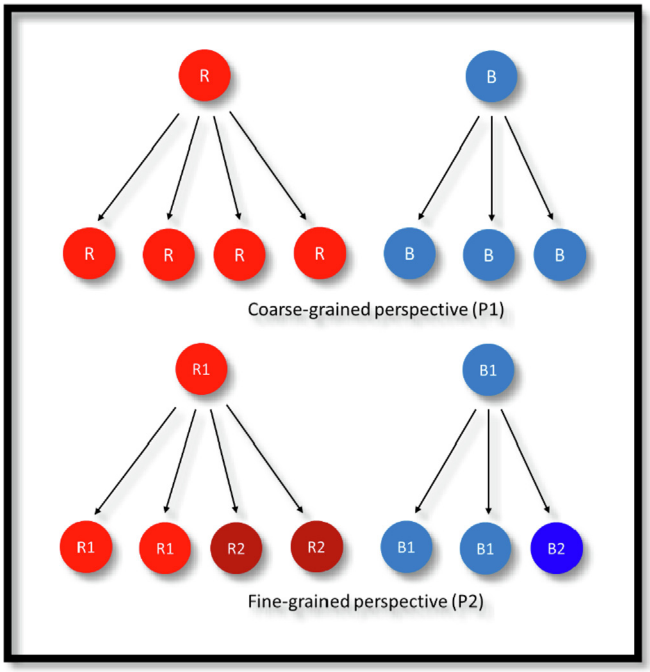

**Fig. 3.** Reproductive outputs of two types of entities seen from two different perspectives with different grains of description.

**Table 1**
Conflicting views on whether there are differences in fitness between two entities and consequences for natural selection.

| Perspective | Parental types | Reproductive output of the same type | Is the evolutionary change observed due to natural selection? |
|---|---|---|---|
| (P1) Coarse-grained | R | 4 | Yes because of differences in fitness |
| | B | 3 | |
| (P2) Fine-grained | R1 | 2 | No because no difference in fitness |
| | B1 | 2 | |

change observed would not be attributed to natural selection. One would have to conclude that every evolutionary change observed is due to a form of transgenerational mutation. Note that this question is different from asking what grain evolutionary biologists should choose in practice, which is a methodological question raising epistemic issues.

This point is strengthened by the supervenience assumption which is widely accepted by scientists and philosophers of science. It follows from this assumption that a physical property (and any process(es) depending on this property) existing at a coarse grain of description should also exist at the finest possible grain of description (even if it might be very difficult to describe), assuming that both descriptions are *faithful* (i.e., there are no biases in the way they are described) from their respective grain of description. This is because any two descriptions supervene on the same target system. However, as I showed above this is not necessarily the case for evolution by natural selection, if it is considered as being description independent, since some evolutionary change attributed to natural selection at a coarser grain of description will rather be understood as mutation when assessed from a finer grain of description. As a result, if taken at face value, problem I present questions the status of evolution due to natural selection as an outcome originating from a process which is mind-independent. Importantly, note that it is possible for a physical property to be only detectable at a finer-grain of description. In such cases, it is perfectly reasonable to consider that different grains of description lead us to change our mind about whether an entity has a given property and whether a process occurs. That said, this should only happen when one moves from a coarser to a finer grain description, not from a finer to a coarser grain of description (once again and this is important, assuming descriptions are faithful and refer to the exact same object). This is because, over the same timescale coarser-grained descriptions typically have less empirical content than finer-grained descriptions, not the contrary, assuming once again they describe faithfully the exact same physical object in both space and time.

To be sure, I want to stress again that I am not discussing what in practice scientists would do. In fact, as Rueger and McGivern (2010) have shown using simple models in physics, describing a phenomenon with a fine-grained model does not necessarily imply that it will describe the phenomenon better than using a coarser-grained model. Furthermore, some questions might best be dealt with at a particular level and/or grain of description. Yet, the point I make still stands whether an evolutionary process can be described and the case can be dealt with both equally well from a fine-grained and coarse-grained perspective.

Taking all this into consideration the reader might still consider that the type of problem illustrated in Fig. 3 and Table 1 is far removed from any practical problem a biologist could encounter with a real population. This is not so, for without a clear methodology to distinguish types within a population at hand, one might be accused of gerrymanderring types in order to show what he or she intends to show. Furthermore, I believe that recognizing this problem might be useful in the context of the debate between (nearly) neutralists, of which one of the strongest proponent is Michael Lynch (see M. Lynch, 2007) and adaptationists of which Dawkins is an emblematic figure. The nearly neutral theory of molecular evolution, as its name indicates, looks at evolution from a molecular perspective, that is, a fine-grained one. Under this view, evolution is mostly driven by mutation and drift, with selection playing a minor role. Adaptationists, on the other hand, look at evolution from the perspective of the organism in its environment. The notion of the gene they use in this context is different (Griffiths & Neumann-Held, 1999; Lu & Bourrat, 2018). From this perspective, evolution is mostly driven by natural selection. It is fair to say that the grain of description used to characterise evolution is much finer (both spatially and temporally) for neutralists than for adaptationists. If the nature of evolutionary processes is sensitive to the grain of description used, as I suggest it is, it might be possible to regard mutation and/or drift at the molecular level as selection at the level of the organism merely by changing perspective. This difference could indeed be driven by an implicit change in level of description given about the system when the level of description is changed. I will not attempt an analysis here, but I think it is a promising line of research.

The grain-of-description dependence of fitness and evolution by natural selection seems to be, in some respects, a similar problem to the well-known reference class problem in probabilities. If someone tells us that “you” have nine chances out of ten to die before the age of 100 years, this information will not make any sense if we do not know which reference class has been delimited to obtain this probability. Is the class ‘all humans on Earth’, ‘humans in your country’, ‘humans of your gender’, ‘humans living in the same city as you’, ‘humans with the same life-style as you’, ‘humans of the same age as yours’, etc.? Because you belong to an infinite number of classes at the same time, one could say that you have an indefinite probability of dying before the age of 100 years, which represents a problem if probabilities are unconditional ‘guides to life’ (Hájek, 2007) where ‘unconditional’ means ‘independent from any reference class.’ Although the reference class problem is classically thought to be only a problem for a frequentist interpretation of probability, Hájek (2007) convincingly demonstrates that each interpretation of probability theory has its own reference class problem. Problem I have presented with fitness has a common origin with the reference class problem.[12]

The common origin of these two problems lies in the fact that as recognised by Venn in 1866 "every single thing or event has an indefinite number of properties or attributes observable in it, and might therefore be considered as belonging to an indefinite number of different classes of things" (Venn, 1876). In the case of the reference class problem in probability, because an event can be considered as belonging to many different classes, it is problematic to know what class should be used to predict it. In the case of fitness, since different grains of description will lead to one class of objects (say **R**) to be made of a multitude of subclasses (say **R1**, **R2**, **R3**, etc.), it will be problematic to know which one of these different (sub)classes should be used to describe an event of evolutionary change. This problem widens the scope of the reference class problem beyond probability theory and independently from it. In fact, all it requires for occurring is that the number of offspring of the same type produced is different when the grain of description is altered. Probabilities do not have to be mentioned for it to occur. To distinguish the reference class problem in probability, which occurs at any given grain of description, from the reference class problem I identified in evolutionary theory, I name the latter the 'reference *grain* problem.'

One should note that the reference grain problem in evolutionary theory and the reference class problem in probability, although they overlap, are nevertheless slightly different, or more accurately, the former is a special case of the latter which justifies the different label. In fact, in the traditional reference class problem, the heart of the problem is to assess which one of an infinity of classes is the correct one for a given event. But the different possible classes an object belongs to *can be* independent from the grain of description used to delimit each class and depend only on different properties of the object (e.g., male, French, 30 years old). Contrast this with the evolutionary problem I have presented above. Although the problem here is also to choose the relevant class, this is not because one and the same entity belongs to an infinity of classes *that can represent different properties*. Rather, it is because this entity can belong to an infinity of classes merely by changing the grain of description for one and the same property such as colour (e.g., being red or being scarlet) and that there seems to be no way to decide, beyond our intuitions, which grain of description and thus which class is best to use. Thus, if 'colour', to take the theoretical example in Fig. 3, is causally linked to fitness, claiming that evolution by natural selection has occurred in a population between entities of different colours is not more meaningful than claiming you have 9 chances of 10 to die before the age of 100 years. One must first stipulate which grain of description one has used to make this assertion.

## 3. Solving the reference grain problem?

As already noted, Hájek (2007) demonstrates convincingly that the reference class problem is pervasive in probability theory and that all major probability interpretations face the problem in one form or another. Attempts to solve this problem have been made by arguing that one should use probabilities only over the narrowest class(es) for which reliable statistics can be compiled. However, this solution is unsatisfactory. In fact, it is not clear what 'reliable statistics' means (Hájek, 2012), and using the narrowest possible class would ultimately lead to the use of classes made of single events in which case probabilities would become dispensable, unless the world is fundamentally indeterministic. Thus, although one might be tempted to give an analogous solution to the reference grain problem by using the finest possible grain of description one has at their disposal, not surprisingly this solution will suffer from the same problem. As I mentioned earlier, at the smallest possible grain of description, every entity (such as an organism) is unique and thus any mention of evolution by natural selection at one grain of description would correspond to mutation at the finest possible one. This solution seems an undesirable one.

Because the solution of narrowing down the reference class is unsatisfactory, Hájek (2007) proposes to abandon the idea that events have unconditional probabilities and rather embrace the idea that any probability is relative to a reference class that must be specified to be meaningful. Although this solution is somewhat difficult to reconcile with the view that unconditional or single-event probabilities are a 'guide to life', this might be the only pragmatic solution to what seems otherwise to be insoluble. Concerning the reference grain problem in relation to natural selection, Hájek's conclusion might also be the only reasonable one. One could in fact argue that because any notion of fitness tied to the notion type will face a reference grain problem, we should abandon the idea that fitness is an objective or unconditional property of the entities forming a population. Rather, the argument runs, fitness should be seen as a property that is relative to the grain of description chosen (and therefore at least partly subjective) and natural selection, mutation and drift processes can only be characterised at a particular grain of description.

At this point one could interpret this proposal in two different ways. One could consider that fitness is just an instrumental property given the degree of knowledge one has and that entities do not literally have any fitness at all independent from a given grain of description. Or one could consider that a given entity has an indefinite number of fitnesses at the same time. I have no particular view over which one of these two options is more preferable. The main issue here is to reconcile the fact that the concepts of fitness and natural selection are very useful and successful tools for thinking about evolution (especially with respect to adaptations) with the idea that the presence/absence of natural selection will depend on what grain of description is used, and thus does not represent objective facts about the world.

Considering this, one way the reference grain problem might be resolved is by applying an account of models such as the ones proposed by Godfrey-Smith (2006, 2009a, 2009c) or Weisberg (2013) to the concept of natural selection. It would consist in considering that natural selection is not a physical process, but rather the model of a process that bears some resemblance with a particular target system at a particular grain of description. Although in principle quite straightforward, it should be stressed that choosing the grain(s) of description at which to apply the model might be a difficult task in practice.

Another partial solution to the reference grain problem, perhaps more palatable than the previous one, might lie in restricting what sort of types count as *relevant for evolutionary theory*. I call types relevant for evolutionary theory 'evolutionary types'. The solution would be the following. If two different members of two different subtypes at a given grain of description belong to the same type at a coarser grain of description, and have the same composition of offspring (or later-generation descendants) at the fine-grained description (i.e., same of offspring of each subtype), then it might be argued that they belong to the same evolutionary type, in spite of being two different subtypes. An evolutionary type defined as such would be *less* description dependent than a type in the way it was defined so far. As such, it might permit privileged grains of description for evolutionary theory. The reason that this is the relevant type for evolutionary theory, one might argue, is that *recurrence over time* of a structure/function is what matters evolutionarily, not that the structure reappearing at each generation. This is very well demonstrated by a number of species (e.g., ferns) which exhibit what is known as 'alternation of generations', in which A produces B, which can produce B or A (for a recent history of the concept see Nyhart & Lidgard, 2017). In spite of an alternation of generations these

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[12] Note that the reference class problem is not unrelated to Walsh's (2007; see also Walsh et al., 2017) point that natural selection and drift are not description independent phenomena mentioned in the Introduction.

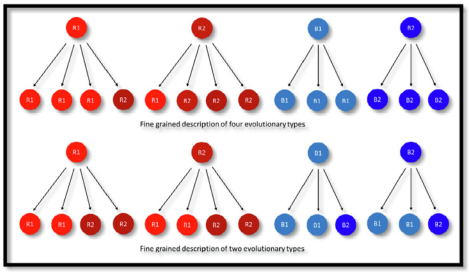

**Fig. 4.** Two fine-grained descriptions of evolutionary change compatible with the same coarse-grained description as in Fig. 3.

organisms are considered as belonging to the same type, which is here the life cycle of an individual.

To see how defining evolutionary types as I did represents a partial solution to the reference grain problem, suppose we are in the case presented in Fig. 4. This case is derived from the case presented in Fig. 3. As with the case presented in Fig. 3, we suppose entities that can be described from two perspectives (coarse and fine). From the coarse-grained perspective, the types are **R** and **B**. They produce 4 and 3 offspring of their type respectively (not represented in Fig. 4, see Fig. 3). From the finer-grained perspective, the types are **R1**, **R2**, **B1**, and **B2**.

We now suppose two situations. In one case (Fig. 4, top), **R1** produces 3 **R1** and 1 **R2**, **R2** produces 3 **R2** and 1 **R1**, **B1** produces 3 **B1**, and **B2** produces 3 **B2**. This fine-grained description is compatible with the coarse-grained description. It seems in this case that there are four different evolutionary types since each one of these types has its own distinctive transmission pattern. Contrast this with the case of the finer-grained description at the bottom of Fig. 4 in which **R1** and **R2**, on the one hand, and **B1** and **B2**, on the other hand, have the same offspring composition respectively. Namely, **R1** and **R2** both produce 3 **R1** and 1 **R2**, and **B1** and **B2** both produce 2 **B1** and 1 **B2**. In this case, whether the parental type is **R1** or **R2**, on the one hand, or **B1** or **B2**, on the other hand, this does not make a difference in what type of offspring is produced at the next generation (One could imagine situations where the same composition in descendants does not occur at the next, but at later generations). For that reason, one might argue that **R1** and **R2** are one single type in virtue of having the same transmission pattern, in the same way the alternation of generations in some species is considered as belonging to a single life cycle. The same reasoning can be shown with **B1** and **B2**.

Using the notion of evolutionary change as I defined it, the interpretation is that there is no evolution by natural selection occurring at that grain of description for the fine-grained description on the top of Fig. 4.[13] Using the coarse-grained perspective (on the one hand **R1** and **R2** lumped together, and on the other hand **B1** and **B2** lumped together) in this case would misidentify (due to a lack of information) two evolutionary types, while there are in fact four. In the case of the fine-grained description at the bottom of Fig. 4, the interpretation, would be that **R1** and **R2**, on the one hand, and **B1** and **B2**, on the other hand, belong to the same evolutionary type because each subtype produces the same proportion of offspring of each subtype. Applying this method provides us with a privileged grain for describing evolutionary change when two or more possible grain of description are available. This grain is the coarsest possible one for which giving a finer description yields the same offspring (or descendants at a later generation) composition for some the different subtype identified, and that there are in this offspring composition members of all the parental subtypes leading to this offspring composition.[14] Applying this algorithm in our example, the privileged grain is thus the fine-grained description for the case at the top of Fig. 4, while it would be the coarse-grained one for the case at the bottom of Fig. 4 in which **R1** and **R2** on the one hand, and **B1** and **B2** on the other hand, are lumped together.

## 4. Conclusion

In this paper, I have shown that one way to approach the concept of fitness in evolutionary theory suffers from a similar problem to the reference class problem in probability. This problem originates from the fact that this approach to fitness and the conception of evolution by natural selection that follows from it both depend on the notion of type identity. The problem boils down to the point that different grains of description will sometimes lead to the conclusion that one and the same entity can belong to different types and produces offspring which are either of the same type or of different types from their parent. This, in turn, can lead to conflicting views as to whether natural selection or (an)other evolutionary process(es) are responsible for the evolutionary change observed. I labelled this the *reference grain problem*. Far from having proposed a definitive solution to this problem, I have suggested that one way to dissolve the problem is to consider natural selection as the model of a process rather than a physical process. Another quite different solution, perhaps more promising, and certainly more pragmatic, is to put some constraints on the kind of type that is relevant for evolutionary theory in the context where different grains of description are available.

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[13] Note that **R1** and **R2** would increase in frequency over **B1** and **B2**, but that would be due to the mutation not natural selection. In fact following the Ariew and Lewontin’s (2004) distinction between reproduction *of* and reproduction *by*, the increase in frequency of **R1** and **R2** is a case of reproduction *of* these types, not reproduction *by* (for instance, reproduction *of* **R1**, but not *by* a **R1** parent), only the latter of which, they argue and I agree with them, should be associated with fitness (and consequently natural selection).

[14] In practice, it would just suffice that members of two subtypes produce *on average* the same proportion of members of different subtypes, and that there are in this average offspring composition members of all the parental subtypes leading to this offspring composition, for the subtypes to be considered as belonging to the same evolutionary type.

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