Two kinds of drift?

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Abstract

Philosophers of biology have recently been debating about whether or not random genetic drift is a distinct process from that of natural selection. One camp argues that drift is a process of "indiscriminate sampling" that is logically and ontologically distinct from the "discriminate sampling" process that is natural selection. The other camp argues that, rather than being two autonomous processes, natural selection and drift are just two aspects or facets of a single process. I argue that the two positions involved in this dispute are not mutually exclusive. Indeed, by explicitly taking into account its sources, I argue that two kinds of drift are theoretically possible. The first kind – that I call circumstantial-drift – involves a process of its own, separate from the process of natural selection, or, more specifically, it requires that differences in a circumstantial trait cause differences in reproductive output of biological entities. The second kind – that I label probabilistic-drift – requires no other process than a probabilistic causal relation between a heritable physical trait and reproductive output, i.e. requires only the causal relation on which the work of natural selection could also depend. If both of these kinds of drift are theoretically possible, then neither defining, nor empirically identifying drift need to be zero-sum games.

Keywords: philosophy of biology; genetic drift; natural selection; fitness.

1. Introduction

A philosopher who is just becoming acquainted with evolutionary biology might be forgiven for thinking that random genetic drift is to natural selection what, in Plato's work, the sophist is to the philosopher. As in the case of the philosopher, the realm of natural selection seems to be that of necessity, of those relations between beings that are grounded in their very

nature. On the other hand, much like the sophist, random genetic drift seems to belong to the realm of the accidental, of the aimless and fleeting relations established between the superficial attributes of beings.

But a minimal reading of population genetics textbooks will show the philosopher that, instead of rejecting or minimizing random genetic drift, biologists consider it one of the main factors controlling evolution and have thus transformed it into a pillar of evolutionary theory. That drift is ubiquitous in nature is still something that may be incorporated into a Platonic view of the world. Indeed, drift is taken to affect all finite populations because any finite population is prone to sampling error: if, from a pool of parents or gametes, we pick only a finite subset with which to form the next generation, it is very likely that this sample will not be perfectly representative of the initial population and deviations in frequency of traits or types might thus ensue. The negative connotations of these terms (sampling *error*, *unrepresentative* sample, *finitude* of the population) might still seem to betray some form of Platonism: by necessity, this earthly, hopelessly finite existence cannot live up to the requirements of an ideal reality, and the ubiquity of drift may simply be explained as an artifact of this unbridgeable ontological gap. But the unsuspecting philosopher gets into an even bigger difficulty upon discovering that the effects of drift are not as unpredictable and inconstant as one might think, as biologists show (e.g. Gillespie 1998) with some pieces of disarmingly simple mathematics: the likelihood of a type drifting to fixation in a population where no other evolutionary factors act is equal to the proportion of that type in the population; the number of generations it will take for drift to halve the genetic variation of a population is a function of population size, and so on. Thus, there is much more necessity to drift than our unsuspecting philosopher might have initially thought.

To some extent, the puzzlement of this hypothetical philosopher over drift seems to subsist even in today's highly specialized discussions between philosophers of biology. Ontological issues seem to have taken the front row in these debates. Could we not simply explain drift away as an artifact of our ignorance (Rosenberg 1994)? Or is it such a necessary part of biological evolution that it could give rise to something like a first law of biology (Brandon 2006)? Does it make any sense to claim that, in a given population, drift dominates or is stronger than natural selection (Clatterbuck, Sober and Lewontin 2013; Brandon and Fleming 2014)?

I cannot delve here into these interesting questions. Instead, in this paper, I will tackle another recently debated issue that concerns the manner in which the distinction between drift and natural selection should be understood. More specifically, this issue concerns whether genetic drift is a distinct process from that of natural selection. According to one side of the dispute, drift should be seen as a particular type of process, namely "indiscriminate sampling" (Beatty 1984; Hodge, 1987; Millstein 2002, 2005, 2006, 2021) that is logically and ontologically distinct from the process of "discriminate sampling" that is natural selection.[1] The other side of the dispute maintains that drift and natural selection are not "separate" processes: in cases where both selection and drift are present, "there is a single process, sampling" (Brandon 2005, 167) and, Brandon argues, trying to disentangle two different processes here is a futile endeavor; similarly, Abrams (2007a) argues that drift and natural selection are aspects of a single process, while Clatterbuck, Sober and Lewontin (2013, 590) argue against seeing selection and drift as "autonomous processes" and claim that they are just two "facets" of a single "process of evolution."

The two sides engaged in this dispute assume that, when it comes to distinguishing it from natural selection, drift is just *one* thing[2] and that, therefore, only one side could be right about it: the spirited exchange between Millstein (2002, 2005) and Brandon (2005) is a clear indication of this. My approach here challenges this assumption. I argue that, instead of being mutually exclusive, these two views may very well coexist. More precisely, I will argue that, by taking as a criterion the *sources* of drift, we may distinguish between two theoretically possible kinds of drift – that I label circumstantial-drift and probabilistic-drift – and I will detail how the former type of drift relies on a process that is distinct from that of natural selection, while the latter does not (Sections 3 and 4). If both of these kinds of drift are theoretically possible, then neither defining, nor empirically identifying drift need to be zero-sum games. Finally, a brief discussion in Section 5 will show why the received philosophical view of natural selection, based on the propensity interpretation of fitness, is not helpful when someone is trying – as I am here – to distinguish between the sources of drift.

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[1] In a different formulation of this conception, drift may be traced back to non-interactive, non-pervasive, indiscriminate causes (Gildenhuys 2009) which are, again, distinct from the interactive or discriminate causes involved in the process of natural selection.

[2] Various authors have shown that a variety of biological phenomena are usually subsumed under the label of "drift" (Beatty 1992; Plutynski 2007; see also Millstein 2011). I have no quarrel with this point. But what I am arguing against here is the idea that there is a single general way in which such phenomena differ from natural selection.

Before we get to these issues, a few terminological and conceptual assumptions need to be made explicit.

2. Assumptions and terminology

The causal view of natural selection. In this paper, I will adopt what might be called, for lack of a better word, a "causal view of natural selection" (Glymour 2011). According to this increasingly popular view, one may claim that natural selection is acting between the biological entities[3] of a population only if phenotypic differences between these entities cause differences in their reproductive output (for various versions of this causal condition, see Hodge 1987; Glymour 2006, 2011; Okasha 2006; Godfrey-Smith 2007; Otsuka 2016; Jeler 2017).[4] Furthermore, for the purposes of this paper, I will follow Millstein (2002) in identifying these "phenotypic differences" with differences in heritable physical traits.[5] Of course, this basic causal condition would have to be supplemented with a thick network of conceptual links and clarifications in order to yield a comprehensive causal view of selection. I will not pursue this legitimate task in this paper. But I do see my discussion here as contributing to the formulation of a causal view of drift, i.e. a view of drift that would be compatible with and complementary to the causal view of selection.

Let me briefly discuss two differences between this causal view and the mainstream view of natural selection that derives from the propensity interpretation of fitness (Brandon 1978, 1990; Mills and Beatty 1979). First, according to some of its defenders (e.g. Hodge 1987; Otsuka 2016; Jeler 2017), the causal view I adopt here maintains that it is the differences in *actual* reproductive output that are relevant for selection, and not the differences in *expected* reproductive output (i.e. expected fitness or adaptedness) as per the propensionist view.[6]

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[3] The term "biological entities" is meant to convey the fact that not just organisms, but biological individuals at multiple levels of organization – potentially ranging from genes to species – might be seen as undergoing selection.
[4] I do not assume a particular account of causation here (for a classification of views of causation employed in the literature concerning natural selection and drift, see Pence 2017).
[5] If someone disagrees with Millstein's identification of traits that may be subjected to selection with "heritable physical traits," one may simply replace this term with one's preferred definition of selectable traits. I believe that, apart from this replacement, the points I make in this paper will still stand.
[6] As Hodge (1987) and Otsuka (2016) have argued, against an old philosophical worry (see e.g. Mills and Beatty 1979), this assumption of the causal view does not render natural selection tautological. Indeed, whether or not there is a causal relation between phenotypic differences and differences in actual reproductive output between the members of a population is an empirical fact, and not an analytic truth. Thus, the tautology issue has no bite against the causal view of selection. Let me add that I do not see balancing selection as contradicting the idea that selection requires differences in reproductive output. Balancing selection covers situations in which, over a longer time

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However, on the one hand, according to supporters of the propensionist view, propensities are properties that hold causal efficacy, and propensities can thus be seen as causes of actual reproductive output. Indeed, as per the classical formulation of the propensionist view provided by Brandon (1990, 11-12) "natural selection is not just differential reproduction, but rather it is the differential reproduction that is *due* to differential adaptedness."[7]. Moreover, as I will argue in Section 4, in a particular type of case, the idea that it is differences in actual reproductive output that are relevant for selection can become problematic for the causal view of selection. Therefore, this first difference between the two views of selection might be smaller than it seems.

But a second difference stems from the fact that the propensionist view holds – as testified by the above quotation from Brandon – that selection is defined with respect to an *overall* propensity to survive and reproduce of an individual or type of individual in its environment (i.e. "fitness" or "adaptedness"). A global property of this sort – that supervenes on all the other properties of the individuals or types in question – is not necessary for defining selection according to supporters of the causal view. For the latter, selection occurs if there is a difference in reproductive output between individuals that is caused by a difference in *a* trait. To put it otherwise, there is selection if the difference in a trait (or trait value) between individuals causes a difference between the magnitudes of the component of their reproductive output that is causally determined by that trait. As I will detail in Section 5, this difference provides the main reason why I did not adopt the propensionist view in this paper.[8]

Circumstantial traits. One of the central notions for what follows is that of "circumstantial trait." In this paper, "circumstantial traits" should be taken to mean extrinsic properties that are not caused by intrinsic properties and that do not supervene on internal relations. Following Godfrey-Smith (2009, 53), I assume that an extrinsic property of a biological entity is a property that logically depends on the existence and arrangement of other

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interval or larger region of space, genetic variation is maintained due to selection (Hedrick 2009; Charlesworth 2006). Therefore, over these larger intervals/regions, alleles or traits have similar reproductive output. However, this pattern is the result of fluctuating differences in reproductive output over shorter periods of time or within smaller regions (negative frequency-dependent selection or selection varying in space and time so that different variants are favored at different times or locations) or the result of the reproductive advantage of heterozygotes.

[7] Brandon (2005, 169) provides a similar, though subtly different definition: "Selection is differential reproduction that is due to (and in accord with) expected differences in reproductive success."

[8] Let me add that my discussion in Section 5 is not meant to provide a complete clarification of the complex relationship – involving a number of shared assumptions and subtle differences – between the causal and the propensionist views of selection. At least a stand-alone paper would be required for this.

objects or biological entities. Think of an example Futuyma (2005, 227) uses to introduce drift: a population of brown and yellow snails live on a cow pasture and some of them get stepped on by cows for reasons that have nothing to do with their color (this example has been widely discussed in the philosophical literature on drift, see Millstein 2002; Millstein, Skipper and Dietrich 2009; Matthen 2010). Here, being in one of the places where cow hoofs touch the ground is an extrinsic property for a snail, while being yellow or having a particular allele are not. But not all extrinsic properties are "circumstantial traits" in the sense adopted here. First, possessing an extrinsic property may be causally determined by the possession of an intrinsic property. As per Brandon's (1990) classical example, a class of individuals may be found more often in a better-quality environmental patch because those individuals have a preference for that type of patch. And, as Brandon argued, it is sensible to assume that in such cases we are dealing with selection for tendencies to choose habitats, rather than with drift. (This is in line with Futuyma's reasoning, who assumes, in his snail example, that the snails are stepped on by cows for reasons that have nothing to do with their color.) So, an extrinsic property that is causally determined by an intrinsic one will not count as a circumstantial trait here.

There is a second class of extrinsic properties that will not count as circumstantial ones. For an individual with a given color pattern, the fact that it finds itself in a population in which the individuals with its color pattern are infrequent is an extrinsic property (i.e. "being rare with respect to one's color pattern"). And, crucially, such extrinsic properties may be subjected to selection: indeed, frequency-dependent selection is precisely the kind of selection in which being "rare" (with respect to a particular aspect, like color pattern) increases or decreases the reproductive output of an individual.[9] But traits like "rarity" belong to a particular class of extrinsic properties, the ones that, according to Langton and Lewis (1996), supervene on internal relations between the relata, i.e. on relations (e.g. match, difference etc.) that hold between the intrinsic properties of their relata. Indeed, the color pattern of the individuals of a population is an intrinsic property of these individuals, and an individual's being rare with respect to its color pattern is a property that supervenes on the intrinsic properties (color patterns) of the other members of the population. And, according to biologists, such extrinsic properties may be subjected to selection (for more details on this, see my recent discussion in Jeler 2024). To sum

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[9] This is one of the reasons why I disagree with the distinctions between natural selection and drift proposed by Godfrey-Smith (2009) and Bourrat (2015, 2017).

up, my "circumstantial traits" are not equivalent to extrinsic properties, but to extrinsic properties that are not caused by intrinsic ones and that do not supervene on internal relations between the biological entities of the focal population.

Let me note that Abrams (2007b; 2014) has also used the term "circumstances" and, to avoid confusion, I should spell out the differences between our meanings for the term. Abrams' circumstances are "extremely specific subenvironments" – i.e. environmental features or combinations of environmental features described in an extremely fine-grained manner – that are "unlikely to be experienced more than once" (Abrams 2014, 132). There are two points that distinguish my take on circumstances from Abrams'. First, I am more flexible with respect to the grain of description of these circumstantial traits. One of Abrams' unlikely to be repeated circumstances is, for a sparrow, being spotted by a predatory bird because the wind blew a leaf in such a way that the predatory bird mistook it for a potential mate and thus had its gaze attracted in the direction of the sparrow. While an event of this sort might rarely recur, I think there is nothing wrong in seeing it as an instantiation of a more coarse-grained circumstantial trait like "being accidentally spotted by a predatory bird," i.e. being spotted for reasons that have nothing to do with one's cryptic coloration, hiding speed etc. Thus, my circumstantial traits may be described at various levels of granularity. Second, Abrams argues that unrepeatable circumstances raise some issues for the propensity interpretation of fitness and the idea that natural selection requires heritable variation in fitness, and that, therefore, some conceptual adjustments to these ideas are needed in order to work around unrepeatable circumstances. He makes a convincing point. However, describing circumstantial traits at a grain that renders them unlikely to be repeated raises no difficulties for the causal view of selection that I adopt here. Let us go back to Futuyma's cow trampling example. In principle, we could define, for our snails, a circumstantial trait like "being stepped on $47652 \cdot 10^{-5}$ of the shell's surface" and another trait with 47651 instead of 47652 and so on for every natural number between 1 and 10^5. It would take a very large population and a whole lot of cow trampling for any of these circumstantial traits to be possessed by more than one individual. But that poses no conceptual problem because, if one individual is stepped on in the exact proportion of one of these circumstantial traits, it will be assigned the value of 1 for that trait; and the rest of the individuals, who are not stepped on or whose shells are stepped on in other proportions, will be assigned the value zero for that circumstantial trait. Individuals of a population may thus vary in reproductive output

because they vary in their values for such minutely defined circumstantial traits. But this does not prevent us from claiming that selection – in the sense of the causal view adopted here – is also operating in the population. Indeed, if the individuals also vary in reproductive output because of differences in a heritable physical trait, then selection is at work. Thus, the fact that circumstantial traits (however minutely defined) cause differences in reproductive output does not seem to pose a problem for the causal view of selection.

Actual drift and the ability to drift. Philosophical discussions about drift have flourished during the past few decades and this calls for other terminological demarcations. Millstein (2002; see also 2021) refines Beatty's (1984) view that drift consists in "indiscriminate sampling" along three important lines. First, she argues that the distinction between discriminate and indiscriminate sampling should be spelled out in causal terms: discriminate sampling (i.e. natural selection) refers to a situation in which differences in heritable physical differences between biological entities are causally relevant to their differences in reproductive success [10]; on the other hand, there is indiscriminate sampling when differences in heritable physical differences between entities are causally irrelevant to differences in their reproductive success. Second, Millstein distinguishes between the *process* of drift (the "sampling" processes themselves in which physical differences are causally irrelevant, e.g. parent sampling, gamete sampling, bottleneck effects etc.) and the *outcome* of drift (i.e. the changes in frequency of genotypes or phenotypes in the focal population[11]). Third, she argues that a distinction between natural selection and drift can undoubtedly be drawn if we characterize them as processes (whereas it may be difficult to distinguish between them if we regard them as outcomes, given that the two types of processes – discriminate versus indiscriminate sampling – might lead to exactly the same type frequencies).

However, a process may not be, at the same time, one of discriminate *and* indiscriminate sampling, and this is why Millstein's view (just like Beatty's) entails that drift is a "separate process" from that of natural selection (Clatterbuck, Sober and Lewontin 2013, 167). An important aim of this paper is to show that – in theory, at least – there is a form of drift that does

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[10] As Gildenhuys (2009) has pointed out, the term "physical difference" had been used by many authors when it came to distinguishing natural selection from drift (e.g. Beatty 1984; Hodge 1987; Brandon 1990). But – and this is a point that Gildenhuys fails to properly acknowledge – Millstein (2002) adds the requirement that these physical differences be heritable.

[11] "The end state, or outcome of this process (again, chosen at an arbitrary point in time), might be that the population is composed of 51% brown squirrels and 49% gray squirrels" (Millstein 2002, 38).

not require a distinct process from that of natural selection. It is therefore impossible for me to use Millstein's process-outcome distinction with respect to drift[12] and I need to replace it with a distinction between "actual drift" and "the ability to drift."

The term "actual drift" refers to whether a population is actually drifting, i.e. whether it actually deviates from the expected frequencies of types or the expected phenotypic value in the population. What I call "actual drift" is, therefore, synonymous with Millstein's "outcome of drift".

The way I conceive it, the "ability to drift" is a property of populations and it simply denotes their *ability* to deviate with respect to the expected frequencies of types or average phenotypic value in the population.[13] This ability may have, I will argue, two different sources and we may distinguish accordingly between the ability to circumstantially-drift and the ability to probabilistically-drift.

A population has the *ability to circumstantially-drift* if its members vary in their value for a circumstantial trait and if this variation causes variation in reproductive output. Take a circumstantial trait for which individual snails may have the values 1 or 0 (like being and, respectively, not being in one of the places where cow hoofs touch the ground). The brown and yellow snails of the population may have the exact same average value for this circumstantial trait: therefore, though the population composed of these two types may have the ability to circumstantially-drift (individuals vary in reproductive output because of the circumstantial trait), this does not lead to a change in type frequencies and, therefore, there is no actual circumstantial-drift.

On the other hand, a population has the *ability to probabilistically-drift* if its members possess a heritable physical trait that is an intrinsically probabilistic cause of reproductive output. By an intrinsically probabilistic cause I mean a cause whose effect varies – according to a given probability distribution – even if the environment or context within which the causal process

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[12] Stephens (2004) has proposed a version of the process-outcome distinction with respect to drift that is different from Millstein's. But I have a hard time understanding what the "process of drift" actually amounts to for him, given that his view of drift seems to be closer to the camp that sees it as non-separate from natural selection.

[13] A good term for this ability would have been that of "driftability." Unfortunately, this term has already been snapped up by Ramsey (2013) in an insightful article that is, in some respects, complementary to my approach here. But Ramsey sees driftability as being at work at the individual level, while I think of the ability to drift as a population-level property. Another difference is that I distinguish between two such abilities, while Ramsey does not.

occurs is (or is assumed to be) perfectly identical between the trials.[14] A subset of cases of this second type of drift is that in which the population members not only possess, but also *vary* with respect to a heritable physical trait that probabilistically causes them to vary in reproductive output (i.e. cases where indeterministic natural selection is at work, which is a "discriminate sampling" process): in such cases, the population will have the ability to probabilistically-drift even in the absence of any "indiscriminate sampling process." Probabilistic-drift therefore does not require a "distinct process" from that of natural selection or, in more precise terms, a population's ability to probabilistically-drift may depend on the same causal relation (or causal "process") that determines natural selection in the population. Again, let me emphasize that a population may have the ability to probabilistically-drift, and yet exhibit no actual drift: if individuals vary with respect to a probabilistic cause of reproductive output, the reproductive output of some of these individuals will (almost) certainly deviate from its expected value; but if this does not lead to a departure from the expected trait/type frequencies, there will be no actual drift in the population.

The next two sections will present in more detail these two forms of drift.

3. Circumstantial-drift

It is convenient to introduce the first type of drift I will discuss here – circumstantial-drift – as a variation of Millstein's view of drift, but I hope that the apparently minor modification I bring to Millstein's account will at the very least allow us to dispel some of the misunderstandings surrounding this type of drift.

Note that Millstein's account, as presented briefly in the previous section, provides a negative manner of circumscribing drift: it tells us that we have a process of drift when something is *not* the case (i.e. when heritable physical traits are causally *irrelevant* for differences in reproductive output), rather than when something is the case. In my view, this negative manner of circumscribing drift is more of an inconvenience than a virtue. Its main shortcoming consists in suggesting that drift may only occur in populations in which natural

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[14] The term "probabilistic-drift" might not be the most fortunate since all drift is, in fact, probabilistic. But I use it as short-hand for "purely-probabilistic-drift," in the sense that it requires nothing more than an intrinsically probabilistic causal relation between heritable physical traits and reproductive output. The fact that I call this type probabilistic-drift does not mean that circumstantial-drift may not involve inherently probabilistic *circumstantial* causes (I will get back to this below).

selection is not acting. Indeed, if drift may only occur when heritable physical traits are causally *irrelevant* for differences in reproductive output, as Millstein puts it, one might be forgiven for assuming that, for her, drift only takes place when *all* the differences in reproductive output in the given population are caused by something other than differences in heritable physical traits (i.e. when *none* of the differences in reproductive output are caused by differences in heritable physical traits). Millstein's negative manner of presenting drift thus seems to suggest that drift – in her sense – may only occur when all heritable physical traits are selectively neutral or, otherwise put, that drift may only take place in the absence of selection. This is precisely how some authors have understood Millstein's take on drift (e.g. Pfeifer 2005; Ramsey 2013)[15], though, in my opinion this is not what she meant to say.[16]

By modifying Millstein's account so as to obtain a way of defining circumstantial-drift in a positive manner (i.e. by stating what determines it, rather than what does not), I aim to highlight the fact that circumstantial-drift and natural selection may very well coexist in a population. After having brushed upon Futuyma's (2005) cow trampling example, let us take a closer look at an example used to introduce drift in another popular evolutionary biology textbook:

> Imagine a line of 100 pack horses are walking single file along a hazardous mountain path, but only 50 of them make it safely; the other 50 fall off the path and crash down the ravine. It could be that the 50 survivors were on average genetically surer of foot than the rest; the sampling of 50 survivors out of the original 100 would then be non-random. Natural selection would be determining which horses survived and which died. If we looked at the genotypic frequencies among the smashed horses at the bottom of the ravine

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[15] According to Pfeifer (2005, 1136), Millstein "seems to restrict the phrase 'random genetic drift' to cases where the organisms or traits involved are selectively neutral and, therefore, natural selection is precluded." For his part, Ramsey (2013, 3917) states that "driftability can account for evolution in the absence of selection (drift *sensu* Beatty 1984; Millstein 2002) as well as deviation from expectation (drift *sensu* Brandon 2005)." Millstein's (and Beatty's) drift is thus considered by Ramsey to only act in the absence of selection. In the same paper, he had already attributed this reading of Millstein's drift to Brandon (2005): "If Brandon is right, then drift can occur along with (and not exclusively in the absence of) discriminate sampling" (Ramsey 2013, 3912).

[16] A statement of Millstein's (2005, 172) – quoted by Pfeifer (2005, 1136) – seems to confirm that, in Millstein's view, drift can only occur in the absence of selection. However, I suspect this statement is merely an imprecise formulation, given that, in the paper where Millstein had developed her view of drift, she explicitly analyzed "cases of natural selection together with random drift", i.e. cases "in which both processes are occurring" (Millstein 2002, 44). More specifically, she argued (ibid.) that selection and drift may simultaneously favor the same trait (e.g. brown color) in a given population.

they would differ from those among the survivors. Alternatively, death could be accidental: it could happen whenever a large rock bounced down the mountainside from above, and knocked one horse into the ravine. Suppose that the rocks come at unpredictable times and places and arrive so suddenly that defensive action is impossible; the horses do not vary genetically in their ability to avoid the falling rocks. The loss of genotypes would then be random in the sense defined above. (…) More *AA* horses might have been unlucky with falling rocks; more *aa* might have been lucky. Then there would be some increase in the frequency of the *a* gene in the population. (Mark Ridley 2004, 139)

Ridley presents this case as an example of "indiscriminate parent sampling": unlike others, some horses are hit by falling rocks and thus no longer reproduce; moreover, this difference in survival is in no way dependent on the biological differences between the horses (otherwise put, no differences in heritable physical traits between the individuals in question are causally responsible for their being or not being hit). Ridley presupposes that lethal falling rocks are distributed among the horses of the population in a probabilistic fashion (i.e. an intrinsically stochastic fashion, in the sense I will detail below) and, throughout this paper, I make the same assumption. To put it otherwise, I assume that the complexes of factors that determine the distribution of circumstantial traits (like "being hit by a falling rock") among the individuals in the population act in a probabilistic manner.[17]

We may thus say that, in Ridley's toy case, there is variation between horses in a circumstantial trait, namely "being in the path of a falling rock," and this variation causes variation in reproductive output. Our population of horses thus has the ability to circumstantially-drift, given our stipulation above that a population has the ability to circumstantially-drift if its members exhibit differences in reproductive output that are caused by differences in a circumstantial trait. Many instances of indiscriminate parent sampling that philosophers discuss are precisely of this sort – from Scriven's (1959) classical example of twins that differ with respect to whether they are in the spot where a bomb lands, to Scriven's apocryphal, and even more popular, property of being struck by lightning (the imposing tradition of using this example

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[17] In this paper, I will not defend a particular view on the nature of the probabilities attached to circumstantial-trait "assignments" (more on this on pp. 17-18).

goes back at least to Mills and Beatty 1979), or to happening to be in the path of forest fires (e.g. Beatty 1984; Horan 1994, among many others).[18]

But Ridley's example allows us to be more precise about our claims. Note that the death of a horse hit by a rock is not "drifty," and neither is the sparing of a horse. This is due to the fact that I attribute the ability to drift (as well as actual drift) to populations, not to the individual members of these populations. If we take two horses of the same type from this population (better yet, these two horses may be supposed to be identical with respect to all their traits except the relevant circumstantial trait), then we can unmistakably say that their difference in actual reproductive output is due to their difference in the circumstantial trait "being in the path of a falling rock." We can thus conclude that this population of horses has the ability to circumstantially-drift.[19] (So, if by "drifty" we understand "having the ability to drift", then one could say that the population as a whole – i.e. the entire set of horses moving along the mountain path – is "drifty.") To put it otherwise, a population whose individuals' reproductive output is differentially affected by differences in a circumstantial trait is prone to experience changes in its trait/type frequencies because of this circumstantial trait.

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[18] As already noted, Gildenhuys (2009) has argued that the kind of causes that are conducive to drift are non-interactive, non-pervasive, indiscriminate causes. There are a number of differences between my account and Gildenhuys'. First, I find it more useful to assign these causes to the individuals as their circumstantial traits: an individual has a circumstantial trait in the sense that it is subjected to a particular extrinsic factor of the type I specified above. So, my "circumstantial traits" are non-interactive and indiscriminate, in the sense that the reproductive output of two individuals of different type will be equally affected if they have the same value for a circumstantial trait and an individual's probability of having a particular value for a circumstantial trait is independent of that individual's type. But my circumstantial traits are not necessarily non-pervasive: all the individuals of a population may have a circumstantial trait, but if they vary in their *value* for the trait, then the population may have the ability to circumstantially-drift. Relatedly, unlike Gildenhuys (2009, 540), I do not see circumstantial traits as essentially "killer" traits: circumstantial traits that boost individual reproductive output may just as well lead to drift. Finally, I disagree with Gildenhuys' point that these causes lead to drift by affecting a population's variance effective size. The reasons for my disagreement would take us too far adrift (see Walsh 2022, 70-71 for a relevant argument), but I will merely state here that if we are interested in predicting the potential effects of drift on the population dynamics, then it might be useful to see how Gildenhuys' causes (or my circumstantial traits) affect variance effective population size. But if we are merely interested in determining when a population has the ability to circumstantially-drift and when there is actual circumstantial-drift in the population, we need not go through an assessment of how circumstantial traits affect variance effective population size.

[19] Note that speaking of *differences* between individuals (differences in a circumstantial trait causing differences in reproductive output) entails that the ability to circumstantially-drift and actual circumstantial-drift can only be attributed to populations containing at least two individuals. So, if one really wanted to, one could view each individual of a setup as belonging to a population of size 1; however, these would not be the relevant populations for circumstantial-drift. Obviously, how populations should be circumscribed and whether there are criteria allowing us to carve populations at their joints is an issue I cannot tackle here. Some authors have defended such criteria (Millstein 2010, 2014; Matthewson 2015; Baraghith 2020), while others have adopted more skeptical positions (Stegenga 2016).

But this does not mean that there is actual circumstantial-drift in the population. Whether the frequency of types actually changes because of the circumstantial trait – i.e. whether actual circumstantial-drift occurs – depends on a supplementary condition. Suppose that there are two phenotypes in Ridley's horse population (say, X and Y), with one phenotype (say, X) being the better swimmer (for simplicity, let us suppose the difference is genetically based). As Ridley emphasizes, the heritable physical traits of individuals do not make an individual more or less likely to be in the path of a falling rock (otherwise, as noted in the previous section, "being in the path of a falling rock" would not be a circumstantial trait). Therefore, each individual has the same chance of possessing this circumstantial trait. So, the expected frequency of this circumstantial trait for either of the types X and Y will be given by the frequency of that type in the population. However, the *actual* frequencies of the circumstantial trait among the two types may or may not diverge from the expectation. If the actual frequencies precisely match the expectation (the circumstantial trait is distributed between types as per the frequency of types in the population), then, on the whole, being or not being in the path of a falling rock will not lead to changes in type frequencies in the population. We may thus have a population that has the ability to drift, but that exhibits no actual drift for a particular period of time. But if the actual distribution between types of the circumstantial trait values (e.g. 0 and 1 for being and not being in the path of a falling rock) departs from the expectation, then, given that the trait used to identify the types X and Y is heritable, we will have actual circumstantial-drift in the population, i.e. type frequencies of X and Y will change because of our circumstantial trait.[20] So, if the distribution of the relevant circumstantial trait between the types of the population deviates from the expectation, there will be actual circumstantial-drift in the population.[21]

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[20] Obviously, a type frequency change due to another circumstantial trait might exactly offset the change due to "being in the path of a falling rock." We would thus have a zero *net* effect of circumstantial-drift in the population, but this would not mean that actual circumstantial-drift is not occurring therein.

[21] Therefore, explaining the changes in type frequency by appealing to circumstantial-drift remains a statistical explanation in the sense given to the term by Walsh, Lewens and Ariew (2002). That some individuals are hit by falling rocks does not tell us what the probability of a particular change in type frequency is. In order to calculate these probabilities, we need to compute the probability of each deviation from expectation in the distribution of circumstantial traits between types. This is not something we could find out by looking at the complete life history of each individual of the population, but by looking at the statistical properties of the setup. Note that I do not assume that the effect of a circumstantial trait on reproductive output must necessarily be seen as probabilistic (i.e. intrinsically stochastic, in the sense to be detailed below). Indeed, a circumstantial trait that is certainly lethal and that acts before the focal organisms reach the reproductive stage may reasonably be seen as a deterministic cause of reproductive output. However, as already noted, following Ridley, I do assume that the complexes of factors that determine how a circumstantial trait is distributed between the individuals of a population act probabilistically. It is this latter assumption that explains why, in my view, circumstantial-drift is a probabilistic process.

We may now drive home the point that, contrary to how Pfeifer (2005) and Ramsey (2013) have read Millstein, natural selection and circumstantial-drift may well coexist in a population. Suppose that our population of horses also has to swim across a dangerous river and that, because they are better swimmers, individuals of type X have a higher actual reproductive output than individuals of type Y. Given that swimming ability is heritable, there is selection in our population (recall my assumption that we have natural selection when differences in heritable physical traits cause differences in reproductive output). But differences in a circumstantial trait (e.g. being in the path of a falling rock) also cause differences in reproductive output between individuals and, as indicated in the previous paragraph, this may also lead to changes in type frequencies. These are two different causal relations, with differences in reproductive output being causally traced back to differences in heritable physical traits in the first and, respectively, to differences in circumstantial traits in the second. I see no reason why two causal relations of this sort could not coexist in a population.

But this observation also highlights the fact that there is certainly no problem with claiming that natural selection and circumstantial-drift are distinct processes. If selection and circumstantial-drift involve different causal processes, then I do not see how one could argue that natural selection and circumstantial-drift are just different aspects of a single process.[22] So, as long as authors defending the view that selection and drift are distinct confine their claim to circumstantial-drift, their case is convincing.

A couple of points need to be made before we end our discussion of circumstantial-drift. First, let me provide a brief indication of the relationship between population size and circumstantial-drift. I do not intend to offer a full-fledged model illustrating this relationship (this would take us too far adrift), but merely to discuss a restricted case for the sake of motivating intuitions. Note that in Ridley's example, the falling rocks kill exactly half of the population. Let us suppose that the population contains equal proportions of the two phenotypes (X and Y), and, as a consequence, the circumstantial trait "being hit by a rock" is equally likely to be bestowed upon an X or a Y individual (i.e. a rock that hits a horse has a ½ probability of hitting a horse of

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[22] Of course, one could *analyze* a case involving both selection and circumstantial-drift by building the potential effects on reproductive output of heritable physical traits and circumstantial traits into a single probability distribution of the evolutionary change (I will expand on this point in Section 5). But the fact that we can analyze the case in this manner does not invalidate the distinction between the two processes involved (i.e. the causal process involving heritable physical traits and the one involving circumstantial traits).

type X and a ½ probability of hitting a horse of type Y). It is easy to see that the probability that all the killed individuals be of the same type (say, X) gets smaller and smaller as the population size increases. In a population with N = 4, it will be 1/4, then it decreases to 1/16 when N = 8, to 1/256 when N = 16 and so on.[23] The point I want to make with this is that the larger the population, the smaller the probability that circumstantial-drift will lead to large changes in type frequencies per time slice. Conversely, the smaller the population, the more likely it is that circumstantial-drift will lead to significant changes in frequencies of types per time slice. The fact that the rate of type frequency change brought about by drift depends on population size is, of course, a commonplace of most – if not all – conceptions of drift. Here, I just wanted to signal that things are no different for circumstantial-drift.

Finally, Ridley's horse example that I have extensively used above is a case of indiscriminate parent sampling. It must be emphasized that the other traditionally accepted types of indiscriminate sampling (see e.g. Beatty's 1992 list) might also be interpreted as circumstantial-drift. Indiscriminate gamete sampling can be reduced to differences in (admittedly fine-grained) circumstantial traits for gametes.[24] In cases of bottleneck effect, many individuals die because of dramatic changes in the environment, but some happen, by the mere play of circumstances, to survive (otherwise we would be dealing with an extinction, not a bottleneck). In cases of founder effect (see, e.g. Dobzhansky and Pavlovsky 1957, discussed at length by Reisman and Forber 2005 and Bourrat 2018), it is usually the geographical location of some individuals at the moment when an artificial or natural barrier severs them from the initial population that determines which individuals remain in the mother-population and which go on to found a new population. The cases usually subsumed under one of these kinds of indiscriminate sampling can thus be described as involving differences in reproductive output

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[23] These probabilities are calculated with the binomial distribution formula. The number of trials (i.e. the number of individuals affected by the circumstantial trait) is N/2. A successful trial is one in which an individual of type X is affected by the circumstantial trait. And, as already noted, the probability of success of an independent trial is ½. What we are after is determining the probability of having N/2 successful trials out of the N/2 trials (this is what we are looking for when we are trying to determine the probability that all the individuals affected by the circumstantial trait be of type X). Note that I assume here that the proportion of individuals affected by the circumstantial trait remains the same (namely N/2) when the population size increases (which implies that the number of individuals affected by the circumstantial trait increases as we increase the population size). I make this assumption in order to avoid making a trivial point. Indeed, if we assume that the number of individuals affected by the circumstantial trait remains constant as the population size increases, it is obvious that the total effect of the circumstantial trait on the trait frequencies in the population will get smaller and smaller as the population gets larger.

[24] But note that the description grain of these circumstantial traits is not necessarily finer than it would be for indiscriminate parental sampling in many unicellular organisms.

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between individuals that are caused by differences in their values for one (or more) circumstantial traits, i.e. they can be described as forms of circumstantial-drift.

4. Probabilistic-drift

It is at least theoretically possible that there be cases involving an inherently stochastic causal relation between heritable physical traits and reproductive output. In such cases, we are dealing with a cause (e.g. a heritable physical trait) whose effect (e.g. reproductive output value) varies according to a probability distribution even if all the conditions within which this causal relation occurs are or are assumed to be absolutely identical for all trials. Examples involving causal relations of this sort have been used by Ramsey (2013, 3925) and Strevens (2016, 153) as arguments against Gildenhuys' and, respectively, Millstein's views of drift. Would such causal relations change anything to our analysis of drift? Yes, they would.

As emphasized above, circumstantial-drift implies a separate process or causal relation to the one on which natural selection might rely, the former causally linking differences in reproductive output to differences in circumstantial traits, while the latter links them to differences in heritable physical traits. These are two parallel, separate causal processes, just like Millstein's notion of drift requires. On the other hand, in cases in which individuals possess a heritable physical trait that is an intrinsically probabilistic cause of differences in reproductive output (for example, in cases in which indeterministic natural selection is at work), the population may deviate from the expected frequency of types/traits even in the absence of any circumstantial trait (or, in Millstein's terms, of any indiscriminate sampling process) that could contribute to this deviation. In cases of this sort, it is the same process – the probabilistic causation of differences in reproductive output by differences in heritable physical traits – that undergirds both the ability to drift of the population and its possibility of being subjected to natural selection.

About populations of this sort I will say that they have the ability to probabilistically-drift, where the adverb "probabilistically" is meant to emphasize that such populations deviate from the expectation because of *nothing else* than the probabilistic causal relation from which the expectation itself derived (i.e. because of no separate, different cause than the cause whose potential effects are distributed according to the probability distribution that the expectation itself summarizes). Of course, during a given time slice, a population of this sort may or may not

actually deviate from the expected trajectory – i.e. it may or may not exhibit actual drift; but this does nothing to deny the fact that it has the ability to probabilistically-drift because of the simple fact that within it there is a probabilistic causal relation between a heritable physical trait and reproductive output. Therefore, one cannot dismiss probabilistic-drift simply by considering it an outcome-based view of drift: even if a population exhibits no actual deviation from its expected trajectory (i.e. there is no "outcome" of drift), the population still has the ability to probabilistically-drift, and it does so because of the inherent stochasticity in the causal relation between physical traits and reproductive output of its members.

Let me add that I will not insist here on the ways in which this inherent stochasticity may be instantiated. One way would probably be that of assuming probabilistically-defined propensities/dispositions to have certain reproductive levels that mediate the relation between heritable physical traits and reproductive output in a given environment, as per the classical approach of the propensity interpretation of fitness (Brandon 1978; Mills and Beatty 1979), especially if one argues that these propensities are irreducibly probabilistic (Brandon and Carson 1996; Brandon 2005). (However, as already alluded to above and as I will suggest in the next section, if embraced, such propensities should preferably be construed as specific to particular traits, rather than to the whole complex of traits borne by a biological individual.) In a different line of reasoning, Sober (2020) suggests that there may be some brute probabilistic properties and that mixed strategies in evolutionary game theory might be of this sort. But, as Abrams (2007a) has pointed out, there are other conceivable manners in which the intrinsically probabilistic relation between physical differences and reproductive output may be instantiated. Therefore, I will not delve here into the ontology of these intrinsically probabilistic relations, but I will defend and detail the notion of drift that derives from them.

An objection against the idea of probabilistic-drift immediately comes to mind and presenting it requires a hypothetical example. Think of a population composed of two types, A and B, that vary with respect to their values (C_A and C_B) for a heritable physical trait C that is an intrinsically probabilistic cause of reproductive output. Because they have C_A, the A-individuals may have a reproductive output between 0 and 5, with a 0.75 probability of having 5 offspring and a 0.05 probability of having each of the other reproductive levels between 0 and 4. In turn, the B-individuals have the same range of possible reproductive levels, but the probability associated with them differs: a 0.75 probability of having 2 offspring and a 0.05 probability of

having each of the other potential numbers of offspring (0, 1, 3, 4 and 5). You can think of this case as one involving two dice with 6 faces numbered from 0 to 5, each die being loaded to favor a particular outcome (5 for the first, 2 for the second). The expected reproductive outputs are 4.25 for A and 2.15 for B. So the A-type is expected to have nearly twice as many offspring as the B-type. And yet, it is possible that, for a few reproductive rounds, the Bs reproduce more than the As. Moreover, it is improbable, yet possible, that all the As produce 0 offspring, while the Bs reproduce as expected or nearly so. It is thus possible that, in a single generation, the type that should be favored be in fact eliminated from the population entirely (just as it is improbable, yet possible, that rolling for a number of times the two dice with different loads lead to a sum of 0 for the first die and a non-zero sum for the second).

One could consider the unlikely result of my case above as a result of natural selection, not drift. The reasoning behind this conclusion could be the following: the probability that the A-type be eliminated from the population in a single generation is an immediate consequence of the probabilistic effects of C_A and C_B on reproductive output. Any reproductive output value that may obtain as a result of C – no matter how low its associated probability – should count as an effect of C. So, even though the fact that the normally disadvantaged B is fixed in the population may seem counterintuitive and improbable, this is among the potential effects of C and therefore this outcome should be attributed to natural selection. Another way to formulate this line of reasoning is to say that it is differences in *actual* reproductive output that are relevant for natural selection *even* in cases in which heritable physical traits are probabilistic causes of reproductive output: any difference in *actual* reproductive output – no matter how improbable – that results from this probabilistic causal relationship would thus be attributed to natural selection.

For my part, I think this type of reasoning is best avoided if explanations appealing to natural selection are to hold on to their relevance. The problem is that, with respect to probabilistic causes of reproductive output (with probabilistic distributions that overlap), if we embraced such a reasoning we would be forced to say that: a) the types with the higher expected reproductive output will probably spread because of natural selection; b) and when they do not spread, it is because of… natural selection.

And this problem might affect more cases than we think. Millstein (2002, 2000) argued that we should remain agnostic about whether the process of natural selection is fundamentally deterministic or indeterministic. This leaves open the possibility that natural selection is, for the

most part, intrinsically probabilistic, i.e. that most cases of natural selection involve heritable physical traits that are inherently stochastic causes of reproductive outcomes. If this were so, considering unlikely outcomes as results of selection in such probabilistic cases would entail accepting that the theory of natural selection lose much of its explanatory power, because explanations by natural selection would cover *all outcomes*: those in which the favored type spreads, as well as those in which it perishes. Any outcome would be a result of natural selection and, as a result, explanations by natural selection would become superfluous.

Therefore, if we want to hold on to the explanatory relevance of the theory of natural selection, we should admit that in populations involving inherently probabilistic causes of reproductive output i) the differences in reproductive output that are relevant for selection are the differences in the *expected* reproductive output brought about by the relevant probabilistic heritable physical trait[25] and ii) such populations should be recognized as having the ability to probabilistically-drift given that individuals having the probabilistic trait may exhibit different deviations from the expected reproductive output brought about by that trait even when subjected to absolutely identical conditions. Over a specified time interval, this ability may or may not lead to actual probabilistic-drift. In my toy example above, it may happen that the average deviation from the expected reproductive output brought about by their values for C be negative for the A-type and positive or zero for the B-type. If this happens, we will have actual probabilistic-drift in the population. More generally, there will be actual probabilistic-drift when the deviations from expectation of the effect of a heritable trait on reproductive output are unevenly distributed between individuals of different types; or more precisely – and somewhat convolutedly –, there is actual probabilistic-drift when there are deviations from expectation in the distribution between types of the inevitable departures from the expected effect of a heritable trait on reproductive output. In such cases, we therefore have a departure from the expected type

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[25] How this expected reproductive output should be defined is not something I will discuss here. In my toy example, because they have C_A and C_B, the types exhibit similar variation in offspring number, so the arithmetic mean would suffice for determining the differences in expected reproductive output brought about by the difference in C. In cases with significant variation in offspring number, the geometric mean might be a more appropriate measure (see Gillespie 1977), while in cases involving delayed selection or differences in timing of reproduction, even more complicated measures might be necessary (see Pence and Ramsey 2013). Ariew and Lewontin (2004) argue that we need not necessarily have a single measure of fitness for all types of cases. Like Ariew and Lewontin, I do not think it necessary to measure the expected reproductive output brought about by a trait in a single manner for all types of cases involving intrinsically probabilistic causes of reproductive output. For a discussion of the difference between my notion of expected reproductive output due to a probabilistic heritable physical trait and the mainstream notion of individual or type/trait fitness, see Section 5 below.

frequencies that derives from the probabilistic nature of this cause of reproductive output and from no other, extraneous reason. Accepting this type of drift would allow us to distinguish unlikely outcomes from the more likely ones in populations involving probabilistic heritable traits and the theory of natural selection would thus keep its explanatory relevance.[26]

Probabilistic-drift should thus be admitted at least as a theoretical possibility. But this type of drift does not require a distinct process from that of natural selection. Therefore, if the authors claiming that drift and selection are just two aspects of a single process were to confine their claim to probabilistic-drift, they would make a strong case.

Let me add that, while I do not aim to provide a full-fledged model of the relationship between population size and probabilistic-drift, in closing this section, I will briefly discuss a restricted case in order to suggest that population size does matter for probabilistic-drift. Going back to my example above, let us suppose that our population is formed only of two individuals (population size N = 2), one A and one B. Even though the A individual has an expected reproductive output almost double to that of B, it still has a 1/20 chance of leaving 0 offspring if this individual's actual deviation from its expected reproductive output happens to be at its maximal negative value (-4.25). If this happens, the A type is eliminated from the population after just one generation. With N = 4 (two As and two Bs), the chance that both As get the same maximal negative deviation (-4.25) decreases to 1/400; with N = 6 (3 As, 3 Bs), this chance goes down to 1/8000 and so on. The higher the population size, the lower the chances that probabilistic-drift will lead to high values of per-generation change in type frequencies. And vice versa, the lower the population size, the more likely it is that probabilistic-drift will lead to significant per-generation changes in type frequencies.[27]

5. Fitness and the two kinds of drift

I distinguished here between two kinds of drift without using the notion of "fitness," which, according to many authors, is the fundamental notion for making sense of natural

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[26] Authors defending the statisticalist view of natural selection (Matthen and Ariew 2002; Walsh, Lewens and Ariew 2002; Walsh, Ariew and Matthen 2017) might object to this conclusion, as well as to some of the assumptions I made in reaching it. A separate paper would be required in order to defend the view proposed here from potential statisticalist objections.

[27] It might seem out of place to speak of the effects of drift after a single generation, given that population geneticists usually measure the magnitude of drift in terms, for example, of the number of generations until fixation of a type. But biologists do sometimes speak of effects of drift after a single generation (see, e.g., Rice 2004, 181-187).

selection and, correlatively, of drift. Fitness (or adaptedness, as it is sometimes called) is usually defined as the ability of an individual or of a type/trait to survive and reproduce in a given environment and this ability is often probabilistically defined as a propensity to leave particular numbers of offspring (Brandon 1978, 1990; Mills & Beatty 1979). Some authors hold that the central notion for understanding natural selection is individual fitness (e.g. Ramsey 2006; Pence and Ramsey 2013), others hold that it is type/trait fitness (e.g. Walsh, Lewens & Ariew 2002; Abrams 2014; Sober 2020), while some authors pit these two notions against each other arguing that their meanings might diverge more than we would suspect (e.g. Matthen and Ariew 2002; Walsh, Ariew & Matthen 2017).

I have deliberately avoided all these positions and the main reason for this was that making use of the notion of fitness defined in propensionist terms would have rendered my theoretical enterprise impossible. My aim here was to distinguish between two sources of drift, and this is simply not possible when one assumes the mainstream notion(s) of fitness.[28] Let us start with individual fitness. This ability to survive and reproduce of an individual in its environment refers to the number of offspring that that individual is likely to produce in that environment. This ability is computed over all of its heritable physical traits and over all the values for the relevant environmental features it is likely to come across. Therefore, two individuals having the same expected fitness may vary in actual reproductive output, but based on the difference in fitness alone it is impossible to tell whether the difference in reproductive output is due to differences in the environmental features they actually encountered or due to the fact that one or more of their heritable physical traits (including the one we use to define the types) are intrinsically probabilistic causes of reproductive output. To put it otherwise, the probability distributions we take to be essential for the notion of individual fitness do not discriminate between situations in which the effects of an intrinsically probabilistic cause of reproductive output exhibit different departures from expectation for two individuals and situations in which the variation in reproductive output derives from deviations from expectation of one or more environmental features. Because fitness is computed globally over all the traits of the individual and all the environmental features it is likely to encounter, a finer description of the sources of deviations from expectation of actual reproductive output values is impossible to provide.

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[28] Unless, of course, one operates significant modifications to these widely shared notions of fitness.

The same holds for type/trait fitness. Whether one claims that this notion should be defined statistically as the average value of the fitnesses of the individuals of that type or possessing that trait (Mills and Beatty 1979; Walsh, Lewens & Ariew 2002; Sober 2020) or as an underlying property of the type/trait that may be only estimated by averaging over individuals (see e.g. Abrams 2014), the problem remains. The fitness of a type remains the total expected number of offspring an individual of that type is likely to have. But why is trait/type fitness probabilistically defined in the first place? Is it because i) the trait that defines the types is an intrinsically probabilistic cause of reproductive output and the individuals of the same type might, as a result, vary in their reproductive output? Or is it because ii) the individuals of the same type may encounter different environmental conditions than expected and their actual reproductive values might vary because of this? Without additional theoretical work, the notion of type fitness simply cannot discriminate between cases i) and ii). This is why, in this paper, I have avoided the notion of fitness as it is usually understood.[29]

My approach here allows us to discriminate between cases such as i) and ii). As emphasized in Section 4, actual probabilistic-drift occurs when there are deviations from the expected frequencies of types that ultimately occur because the types of the population vary in their values for a heritable physical trait that is an inherently stochastic cause of reproductive output. On the other hand, if, in a population, there are changes in frequencies of types that take place because differences in circumstantial traits cause differences in reproductive output between individuals, then we are dealing with circumstantial-drift.[30]. The distinction between these two kinds of drift is therefore based on the two potential sources of change in the frequency of types, namely circumstantial traits and heritable physical traits that are inherently probabilistic

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[29] One could reply that, in the previous section, I made use of the notion of expected reproductive output that is due to a heritable trait (an intrinsically probabilistic one), and that this is nothing more than another name for trait/type fitness. But this is not the case. The expected reproductive output due to a heritable trait that I used in the previous section is simply a component of the reproductive output of an individual, that component of the reproductive output that the relevant heritable physical trait is likely to bring about. It does not refer to the *global* reproductive output that an individual having that trait is expected to have. And it is this expected global reproductive output that the notion of type/trait fitness refers to. This significant distinction between the two notions is worth keeping in mind.

[30] As noted above, circumstantial traits may be either deterministic or probabilistic causes of reproductive output (though I do see the factors responsible for the way these traits are distributed between individuals as probabilistic ones). Regardless of whether the relevant circumstantial trait is a probabilistic cause of reproductive output or not, if, because of this trait, there are changes in the frequency of types in the population, we have actual circumstantial-drift. Therefore, the distinction between circumstantial- and probabilistic-drift is not reducible to a distinction between deterministic and indeterministic drift. (The latter distinction has been recently brushed upon by Bourrat 2017, 2018, but it was already implicit in the discussions about the deterministic/indeterministic nature of evolutionary processes by Horan 1994 and Millstein 2000.)

causes of reproductive output. Let me also point out that, because circumstantial-drift and probabilistic-drift involve separate causal processes – linking differences in reproductive output to differences in circumstantial and, respectively, probabilistic heritable physical traits –, I see no reason why these two forms of drift could not coexist in a population.

6. Conclusion

I argued that, when we categorize them according to their sources, two forms of drift are theoretically possible, one of which involves a process of its own (circumstantial-drift), while the other (probabilistic-drift) requires no other process than a probabilistic causal relation between a heritable physical trait and reproductive output, i.e. requires only a causal relation on which the work of natural selection could also depend. This indicates that debating about whether or not drift is a distinct process from that of natural selection is a partly misguided endeavor. Indeed, I hope to have shown that the answer to the question undergirding this debate depends on the type of drift one has in mind. This also suggests that the debate should be more interestingly geared towards more empirical issues concerning the sources of drift.

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