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ORIGINAL RESEARCH

Reproducees, reproducers, and Darwinian individuals

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Abstract

This paper investigates the concept of reproduction in an evolutionary context. It draws a distinction between objects that are reproduced (reproducees), objects that reproduce thanks to some reproductive autonomy (reproducers), and Darwinian individuals that are reproducers with a high degree of reproductive causal control. This threefold distinction is then applied to different biological objects classically invoked in reproduction processes (e.g., genes, viruses, cells) to explain why they do not have the same status with respect to reproduction. The distinction also provides some fuel for the view proposed by Griesemer: that material overlap during reproduction is a condition for reproduction.

Keywords Reproduction · Inheritance · Reproducer · Darwinian individual

1 Introduction

Reproduction—and the concepts derived from and related to it, particularly those pertaining to transmission—is pervasive in evolutionary thinking. Fitness and heritability, the two main currencies for evolution by natural selection, are often defined as an entity's reproductive output and the extent to which offspring resemble their parent(s) as opposed to other individuals in the parental population, respectively (Lewontin, 1970; Godfrey-Smith, 2007). At the heart of the gene's view of evolution lies the concept of the replicator—an entity able to create copies of itself (Dawkins, 1976, 1982; Hull, 1980; Sterelny, 1996; Godfrey-Smith, 2009, chap. 7). Multilevel selection theorists, including those working on so-called evolutionary transitions in

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individuality, often consider that a type of object constitutes a unit of selection or a new level of individuality when it is a reproductive unit (Griesemer, 2000c; Godfrey-Smith, 2009; Michod, 2005). In cultural evolution, a large body of literature has been dedicated to exploring whether the replicator view of evolution can be extended in the cultural domain under the guise of memes or whether the analogy is misguided (Aunger, 2000; Lewens, 2018).

In light of how fundamental the concept of reproduction is in evolutionary thinking, one would think that the theorizing underlying this and related terms is unified and well accepted. However, nothing could be further from the truth. There exists a menagerie of terms that have been related to reproduction and transmission in some way, without clear conceptual bridges between them. A non-exhaustive list of these terms includes 'reproduction,' 're-production,' 'recurrence,' 'replication,' 'progeneration,' 'multiplication,' 'procreation,' 'copying,' 'inheritance,' 'heredity,' 'transmission,' 'stability,' 'memory,' 'heritability,' and 'reconstitution' (e.g., Griesemer, 2000a, 2005; Charbonneau, 2014; Papale, 2021; Bourrat, 2014; Sperber, 2000; Godfrey-Smith, 2015, 2009; Doolittle and Inkpen, 2018; Veigl et al., 2022).

One obvious reason for the plurality of terms related to reproduction and transmission is that there is a wide variety of contexts, each with its own terminology, in which something like reproduction occurs. Therefore, it is possible that the uses of different terms in varied contexts refer, at least in some cases, to the same phenomena. In other words, some of these terms might be synonymous. Without denying this point, in this paper I argue that the plurality of terms can also refer to different aspects of a process of reproduction. My overarching aim is, therefore, to develop the conceptual resources to be able to relate different situations of reproduction within a single framework and to compare in what ways two situations or explanations involving a process of reproduction are (dis)similar. By refining our understanding of reproduction, I aim to provide new arguments about how to characterize a Darwinian individual—the basic unit of evolution that forms Darwinian populations—as well as clarify some debates over the conditions required for reproduction to occur.

My proposal rests on three types of objects that can be encountered in a process of reproduction. These are reproducees, reproducers, and Darwinian individuals. The two last terms are borrowed from James Griesemer's and Peter Godfrey-Smith's works, respectively. The term 'reproducee' is found once in Godfrey-Smith (2009, p. 88) and is a near synonym of 'scaffolded reproducer.' Although my analysis uses these terms, they should not necessarily be understood in the exact same sense that Griesemer and Godfrey-Smith use them. Nonetheless, my analysis is more aligned with and inspired from Griesemer's account of the reproducer and his reflections surrounding this concept, found in various places (e.g., Griesemer, 2000a, b, c, 2005, 2014), than Godfrey-Smith's (2009) account. Some of the ideas presented here have also been inspired by the developmental system theory view (Oyama et al., 2003; Griffiths and Gray, 1994) where the whole life cycle, as opposed to some part of it, is regarded as the reproductive unit (Doulcier et al., 2023).

I start, in Sect. 2, by making a distinction between an object that is reproduced—a reproducee—and an object that can reproduce—a reproducer. From there, I propose three conditions for an object to be a reproducee; in Sect. 3, I add a fourth condition for such an object to also be able to reproduce or, to use Griesemer's term, to be a reproducer. I argue that what paradigmatically distinguishes a reproducer from a reproducee is that the former has some reproductive autonomy. In Sect. 4, I show how my proposal can shed some light on the debate between Griesemer and Godfrey-Smith over whether reproduction can occur without material overlap between parent and offspring. From there, in Sect. 5, I discuss an additional feature that paradigmatic Darwinian individuals possess when compared to mere reproducers, which I call 'reproductive causal control.' I define reproductive causal control as the extent to which small changes in the nature of an object lead to correspondingly small changes in their offspring. Finally, in Sect. 6, I discuss the evolutionary role of reproducees such as genes, which have a very low degree of reproductive autonomy but a high degree of reproductive causal control.

2 To reproduce or to be reproduced & the minimal condition for being reproduced

In this section, I start by drawing a distinction that will form the core of my framework: namely, that between an object able to *reproduce*, which I call a 'reproducer,' and one *reproduced*, which I call a 'reproducee.' I then propose the minimal conditions for an object to be a reproducee. At first pass, this distinction seems to only emphasize whether an object initiates a process of reproduction (i.e., reproduces) or whether it is the outcome of such a process (i.e., is reproduced). In many explanations involving reproduction, a reproduced object is also an object that will initiate a process of reproduction. However, not all objects that are reproduced can initiate a process of reproduction. Many do not have the capacity to reproduce or, more precisely, have an extremely limited one; they are *mere* reproducees that are either part of a reproducer or composed of them.

This point is crucial because many classical evolutionary explanations involving reproduction refer to trait distributions. In such explanations, one only describes whether some objects are reproduced, not whether the objects that are reproduced are also initiators of reproduction. Instead, it is assumed that the traits discussed are borne by objects with the capacity to reproduce. In the absence of distinguishing between a reproducer and a mere reproducee, one might think that an explanation in which objects are reproduced will also serve for the claim that these objects reproduce; however, this does not follow.

One of the clearest examples of this non sequitur concerns the replicator concept, as proposed by Dawkins (1976, 1982). The word 'replicator' elicits the idea of an entity with the capacity to replicate, where replication can be interpreted as a form of reproduction with high fidelity ('copying'). However, the main example of a replicator provided by Dawkins—namely, the gene made of DNA—does not correspond to this definition. A piece of DNA, in and of itself, even in an environment rich in resources, will often not have the capacity to replicate, a point to which I return in Sect. 6. Instead, it will require a whole machinery to be replicated. Thus, following my distinction, applied this time to replication rather than merely reproduction, a gene is replicated but does not replicate. While the distinction between 'being reproduced' (or 'being replicated') and 'reproduce' (or 'replicate') needs to be drawn more

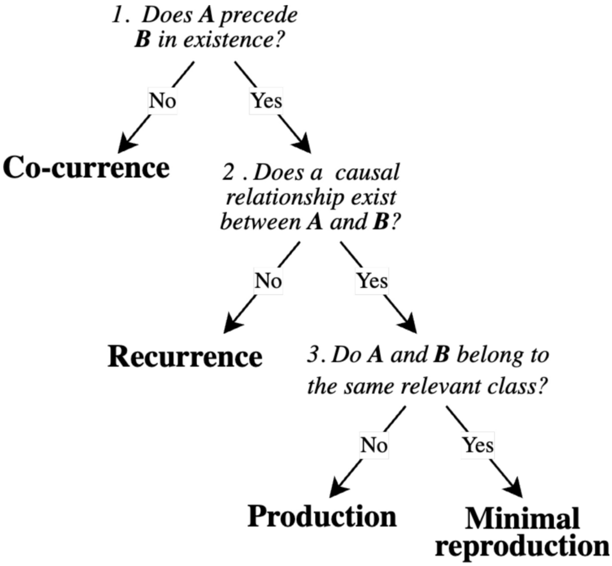

Fig. 1 Decision tree based on three conditions to assess whether an object *B* is a reproducee of another object *A*: that is, the outcome of a process of reproduction

precisely and less categorically, I ask the reader to accept this basic distinction for now. I will return to it in the following section.

With the distinction between a reproducer and a reproducee drawn, I now propose to define the minimal conditions for an object to be a reproducee. In doing so, I distinguish being reproduced from being the outcome of other processes that do not qualify as reproduction. By ‘minimal,’ I more precisely mean both ‘the most abstract’ and ‘the most general’ possible. I follow here the sense of abstraction and generality proposed by Godfrey-Smith (2009; see also Levy, 2021) for whom abstraction has to do with levels of detail (see also Jones, 2005 for a similar interpretation) and generality regarding the number of cases to which it refers. Thus, by ‘the most abstract,’ I here mean the conditions for which eliminating more details when describing an object (i.e., number of properties or precision about a given property) would make it impossible to assess whether this object has been reproduced. By ‘the most general,’ I mean the set of conditions that refers to the largest number of possible cases in which an object can be considered to have been reproduced.

To delineate those conditions, let us suppose a setting in which it is possible to distinguish some objects from their environment. These objects should be conceived of as not only extending in space but also extending in time. Following this setting, I propose, starting from the two first conditions of the extended replicator account proposed by Sterelny et al. (1996, p. 396, conditions (i) and (ii)) and Godfrey-Smith’s (2009, p. 69) conditions for reproduction, that for a focal object *B* to be reproduced from or a reproducee of another object *A*, it should minimally fulfill the following three conditions, which are also summarized in Fig. 1:

1. *B* should come into existence after *A*.

2. A should be a cause of the existence of B.
3. A and B should be of the same (relevant) class of objects set by the description of A.

Let us now examine each condition in turn. The first condition stipulates that for B to be a reproducee of A, its coming into existence should succeed the coming into existence of A. This condition permits us to distinguish a case of spatial co-occurrence (see Fig. 1), where two objects would appear together from a case of recurrence of which reproduction is a subset. As a running example, I will use crystal formation and growth. While this example might, at first glance, seem distant from biological reproduction, one hypothesis proposed by Cairns-Smith (1990) is that life originated from clay crystals that acted as initial replicators. Suppose a setting in which a beaker contains a saturated solution of calcium carbonate ($CaCO_3$) (note that the reason for choosing calcium carbonate will become clearer later). Suppose now that two crystals of calcium carbonate A and B are both produced at the same time in water at two different nucleation sites. We cannot say that B is reproduced from A. Instead, they are co-occurring.

The second condition stipulates that for B to be a reproducee of A, A should be a cause of B. Two calcium carbonate crystals could be produced one after the other at two different nucleation sites, without A being a cause of B. In contrast, crystal B might be reproduced from A by a phenomenon called secondary nucleation (Mullin, 2001, pp. 195–201). As a crystal grows, it might break off at some site and produce an 'offspring' crystal.[1] The second condition permits us to distinguish cases of mere recurrence from cases of production (see Fig. 1), the latter of which is in some sense equivalent here to what Griesemer (2000b) calls 'multiplication.' In the example of the calcium carbonate crystal, a situation of mere recurrence would be one where all the new crystals produced originate from a different nucleation site.

The second condition relates to a recent proposal made by Veigl et al. (2022), who put forward a type of entity they call a 'reconstitutor' and regard as a unit of heredity. They argue that heredity does not require the formation of continuous lines of ancestry (p. 367) and flirt with the idea that there is no requirement for a causal connection between a structure at a given generation and a subsequent one for there to be heredity. They explicitly state (p. 367) that some cases of reconstitution do not require material continuity.[2] I interpret the idea of the reconstitutor as implying minimally a form of recurrence. However, without causal connection, it is difficult to see how something like heritability, even if defined temporally (i.e., without the requirement of clear generations) (see Bourrat, 2015)—what some have called 'memory' (Charbonneau, 2014; Papale, 2021)—could be exhibited by a system. I consider something

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[1] That the crystal might break off would require an explanation as this would not typically occur in natural conditions. I am using this example here primarily for illustrative purposes rather than to describe a natural phenomenon, but see McGinty et al. (2020) for a discussion of situations in which a parental crystal might lead to the formation of independent offspring crystals. Alternatively, one might consider that a secondary crystal forming on a primary crystal, even if it remains attached to the parent crystal, is an offspring crystal.

[2] I note that in all the examples they use, a causal (material) connection exists between two generations. However, it appears it is not required for their account.

like heritability or memory to be required for all instances where there is some scope for evolution by natural selection. Consequently, cases of mere recurrences lacking causal continuity do not correspond to the same type of phenomenon.

Finally, the third condition stipulates that *B* should be of the same relevant class as *A*. This condition permits us to distinguish cases where an object is merely *produced*—'parent' and 'offspring' objects do not belong to the same relevant class—from those where the offspring object is *reproduced*. By 'class,' I mean a collection of entities that share a common property. It should be noted that there are unavoidable pragmatic elements when deciding whether an object belongs to the same class as another. This comes from the fact that any two objects will belong to the same class for some features. For instance, object *A* and object *B* belong to the same class 'object' even though any other property might be different in both. Unless the property 'object' is a relevant property for the particular explanation, it should not be considered in assessing whether they belong to the same class. Related to this point, due to the fact that any description of an object is incomplete, the level of details (abstractness) chosen to compare two objects necessarily involves some choices that will set a reference class. To see this, let us again take our example of calcium carbonate crystals. These crystals can come in three primary forms: namely, calcite (trigonal-rhombohedral), aragonite (orthorhombic), and vaterite (hexagonal)(Ogino et al., 1987). When an offspring crystal *B* is produced, depending on the conditions (e.g., temperature), the parent crystal can act as a template so that both *A* and *B* have the same shape due to the orientation of the lattice formed by crystal units. However, this is not guaranteed since the environmental conditions in which the crystal grows can lead them to be different from the parent; further, calcite is generally more stable than aragonite, which is more stable than vaterite. Let us ignore these complications and suppose instead that each crystal form has the same stability. Now, if the class 'calcium carbonate crystal' is used to assess whether *B* is a reproducee of *A*, any case of secondary nucleation will lead to the conclusion that *B* is a reproducee of *A*. However, if a finer class is used, such as 'form,' there is now no guarantee that *B* is a reproducee of *A* because *A* might, for instance, be vaterite and *B* aragonite or calcite.

The liberality with which one can choose the 'relevant' class might appear as a problem. I have four responses to this. First, my account is not the only one facing this problem. Godfrey-Smith (2009, p. 69) says that the parent and offspring should be 'of the same kind (broadly understood).' Similarly, both Maynard Smith and Szathmáry (1995, p. 41) and Griesemer (2000a, 2000b, 2000c) talk about sameness of kind ('relevant kind,' in the case of Griesemer, where 'relevant' refers to acquiring the capacity to reproduce) when discussing replication and reproduction, respectively. I consider 'class' and 'kind' to be roughly synonymous, with the former being less metaphysically loaded. Second, I consider this liberality problem to be one that is necessarily associated with providing abstract conditions. Such conditions might be satisfied at various spatio-temporal scales and there is no mind-independent way to decide whether they should be applied in a particular context. This is one reason why, when discussing his concept of individuality, Griesemer (2018, pp. 158–159) claims that his 'notion of individuality is process-relative: individuality depends on individuation that happens in marking and tracking choices relative to a process of interest.' Third, it is possible to partly get around the liberality (and potentially arbitrariness) problem by assessing whether there is (or could be) some variation in the properties considered and whether such variation could feature in the (biological) explanation of the object produced. Properties that would exhibit variation that features in biological explanations could be used for setting the relevant classes.

Finally, a fourth response is that making the class against which two objects are compared explicit illuminates some of the recent discussions in evolutionary theory. Some of the positions taken by the protagonists in these discussions appear counter-intuitive, I argue, because they make implicit choices about what the relevant class is that do not conform with orthodoxy. For instance, I interpret the ‘it’s the song not the singer’ (ITSNTS) framework to extend the notion of a unit of selection to holobionts (Doolittle and Booth, 2017) and bio-geochemical systems (Doolittle and Inkpen, 2018) as relying on a choice of the relevant class that is very abstract. Following ITSNTS, one can interpret a cycle to be perpetuated because, at a very coarse-grained or abstract level of description, earlier parts of the cycle produce offspring ‘copies’ at a later part. A ‘copy’ here is very abstract, defined purely on the basis of biochemical reaction (not taxonomic group). It is nonetheless a copy if functional activity is the criterion used to define the class. There is *in principle* nothing wrong with making such a choice, but it should be clear that it is very different from the choices made when discussing classical examples of replicators or reproducers. Shifting from a classical reproducer such as an organism to a bio-geochemical cycle without making explicit that different choices of description are made can lead one astray. In the context of cultural evolution, Charbonneau and Bourrat (2021, see also Bourrat 2020; Bourrat and Charbonneau, 2022) have made the case that being implicit about the grain of description when describing events of transmission can lead to a semantic slip where the same word does not refer to the same phenomenon when it is used in different contexts. As a result, stating that cultural transmission is ‘high fidelity transmission’ has little meaning due to the varieties of grains that one can use when assessing this statement.

With these remarks out of the way, in the context of using relevant classes, the third condition permits one to disqualify cases of what I call ‘production’ from ‘reproduction.’ For instance, following this condition, neither a subsequent stage of an organism’s life cycle nor a product secreted or excreted can be considered a reproducee. If the classes chosen are too broad, it will be possible to say that the two stages of a life cycle, or a pheromone and the organism secreting it, belong to the same class ‘made of chemical elements’ and that the object produced is a reproducee. Again, there is, in principle, nothing wrong with this. However, ‘metazoan’ and ‘made of chemical elements,’ because they do not vary in developmental and biological explanations, respectively, might not be relevant classes for the particular explanation sought. Similarly, take the case of moulting in insects. A moult will not be considered a reproducee because the moult and the adult insect do not belong to the same relevant class in the context of a developmental explanation.

3 The reproducer

In the previous section, I proposed three conditions for an object to be considered a reproducee of another object. However, as mentioned there, the relationship between being a reproducee and a reproducer is not symmetrical. In particular, while not all reproducees are reproducers (see Fig. 2), perhaps with the exception of the first reproducer(s), all reproducers are also reproducees: that is, they are objects that came into existence from at least another object of the same (relevant) class as themselves. From there, one might ask what distinguishes a mere reproducee from a reproducer. I propose that the latter can paradigmatically *autonomously* produce a new object with the same capacity (because it belongs to the same class), a property I call 'reproductive autonomy.'

The word 'autonomy' is used in many biological contexts and can mean different things (see Moreno and Mossio, 2015; Rosslenbroich, 2014, for analyses). Because all living systems are open—that is, they input and output physical material to reproduce—they necessarily depend on some external factors. Therefore, in an absolute sense, no biological system is autonomous. However, a biological system can be autonomous for a given (set of) trait(s) and with respect to some features of a particular environmental background. Using this simple definition in the context of reproduction, reproductive autonomy amounts to the capacity to reproduce within a range of (relevant) background conditions. The larger the range (both in terms of features and values for each feature), the more reproductively autonomous the object. Therefore, reproductive autonomy is a property that comes in degree. This yields a notion of autonomy that is *relative* so that if one aims to compare the reproductive autonomy of two or more objects, one must ensure that the environmental backgrounds considered are similar prior to making the comparison. If they are different, it does not make sense to say that one is more or less reproductively autonomous than the other because the autonomies compared are incommensurable. In spirit, this definition of autonomy is close to one of the information-theoretic definitions of relative autonomy proposed by Bertschinger et al. (2008) based on conditional mutual information, a measure of association between two variables. Applied to reproduction, it would involve considering the parental and offspring objects as senders and receivers, respectively, and establishing the extent to which conditioning on the environment decreases the mutual information between parent and offspring. The larger the decrease, the less reproductively autonomous the parental object. Note that autonomy

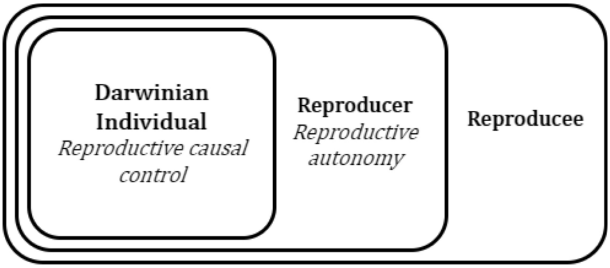

Fig. 2 Relationship between the concepts of reproducee, reproducer, and Darwinian individual

is also related to the notion of causal stability, within the interventionist account of causation (Woodward, 2003; Pocheville et al., 2017), which amounts to whether a causal relationship holds when its background changes. Since a process of reproduction is causal, this notion of stability can also be invoked in the context of reproduction where stability amounts to relative autonomy.

One efficient way to be reproductively autonomous under the proposed definition, and in agreement with Griesemer (2000a, S364–S365), is to have an internal as opposed to external reproductive machinery. However, this should not be regarded as the only way to be a reproducer. In some cases, while an object considered at a particular time might not have an internal reproductive machinery, it nonetheless has the capacity to find itself in an environment that contains this machinery. Objects with this capacity score higher in terms of reproductive autonomy than similar objects with no internal reproductive machinery and without the capacity to find themselves in environments that permit them to be reproduced.

Extremely reproductively non-autonomous objects, once particular features of an object-environment system have been chosen, are objects for which the range of background conditions in which they are reproduced is extremely limited. In the biological domain, this could correspond to a piece of DNA such as a (set of) molecular gene(s) in a cell of a multicellular organism. If one places this piece of DNA in conditions where it will not be degraded but outside the nucleus of the cell, there will be typically no new instances of it produced. Thus, the piece of DNA is highly non-autonomous because the only conditions where it can be reproduced is the nucleus of a cell or some very specific laboratory conditions.

At another extreme, some biological entities exhibit (relatively) a high degree of reproductive autonomy. For example, a bacterium, as long as it can live in an environment, will typically be able to reproduce independently of the specific conditions within this environment. If it is unable to reproduce in a particular environment, it might evolve mechanisms of dormancy so that it will able to reproduce once the conditions are more favorable.

Viruses represent an interesting case that leads me to consider them as *bona fide* reproducers, but perhaps to a lesser extent than bacteria. While they rely on the external machinery of the host cells they infest, contrary to the gene(s) of a multicellular organism, they get into a cell in the first place. This capacity permits them to be reproduced in a larger range of environmental backgrounds or, in other words, to exhibit a greater reproductive autonomy.

The relationship between reproducees and reproducers can now be clarified in light of (relative) reproductive autonomy. The existence of a reproducee necessarily implies the existence of a reproducer. A gene in a multicellular organism that contributes to the production of another copy of itself in an offspring cell (either in the same organism or an offspring organism) is not a reproducer, or only in a very marginal sense, because it has no (or very little) reproductive autonomy. That is, changing its environmental background will generally prevent it from producing a new copy. However, a cell or the multicellular organism that carries this cell, when understood as spatio-temporal objects, are both paradigmatic reproducers because they can reproduce under a much larger range of environmental backgrounds.

So far, I have described the different examples as if reproducers were objects with the autonomous capacity to reproduce 'ready made' when they come into existence. These cases are what Griesemer calls reproducers with 'null development' (Griesemer, 2000a, b, c, 2016, 2018). However, in many cases, a reproducer must undergo a number of transformations before it acquires the capacity to produce another object. Griesemer calls these transformations 'development.' In cases of non-null development, any stage (using a particular level of description), whether it is a developmental stage or a stage where a new object is produced, is necessarily at best a mere reproducee, or a reproducer in a marginal sense. This is so because if a stage of a life cycle were to be considered a reproducer, one would need to assume that all the other stages are part of the environmental background. Altering the environment in various ways would lead to a break in the causal chain from the parental to the offspring stages. Only when all the stages of the cycle are considered together can the environmental background be altered in various ways without this preventing the object from being reproduced. This way to find (relative) reproductive autonomy at a particular scale allows vindicating the view that whole life cycles, not merely stages thereof, are reproducers.

The procedure presented above to establish the spatio-temporal scale at which reproductive autonomy is displayed can be implemented using information-theoretic measures of autonomy following the work of Bertschinger et al. (2008; see also Pfante et al., 2014). To do so, one would compare different ways to create an object/environment spatio-temporal boundary in an object-environment system, assuming a fixed grain of description. One would then assess which boundaries lead to a maximal degree of reproductive autonomy as measured by mutual information between the parental and offspring object conditioned on the state of the environment at the parental generation. One prediction is that the smallest objects for which there is maximal mutual information (maximal reproductive autonomy) refers to what biologists consider an entire life cycle rather than a part of it. This prediction, if correct, could be a vindication of the idea that if being a reproducer comes in degree, a whole life cycle has the maximal degree of it.

4 No reproducers without material overlap

The framework proposed here helps clarify a debate between Griesemer (2014) and Godfrey-Smith (2009, pp. 81–84) that focused on whether reproduction requires material overlap or whether it can also occur in a strict formal sense. Griesemer considers material overlap to be a requirement for reproduction (Griesemer, 2000c, 2005, 2014), while Godfrey-Smith argues that this requirement is overly restrictive since it excludes cases of formal reproduction (2009, p. 83), which are, according to him, bona fide cases of reproduction. The example of formal reproduction taken by Godfrey-Smith is the case of retroviruses. Retroviruses, in their virion stage, are made of RNA that is retrotranscribed and inserted into the DNA of a host cell. At some point in the life cycle of the virus, the DNA is transcribed back into RNA, the latter of which will either be translated into proteins that will become part of offspring virions or become the offspring's genome. If we take a parent and an offspring virion, they do not have any material overlap. Nonetheless, reproduction did occur in this case.

At first pass, Godfrey-Smith's argument seems persuasive. However, one prima facie reason to doubt the conclusion of his analysis is that many cases of reproduction that have classically been thought to involve material overlap could be regarded as cases of formal reproduction, once examined from a different perspective. For instance, in the case of humans, take a mother at the time she gives birth and take her daughter at the time she is about to give birth herself. Now, measure the extent to which the daughter at that time is composed of physical material from the mother. Consider now that human reproduction occurs through a single cell,[3] which contains half of the genetic material of both parents and that an adult contains approximately 30 trillion cells (Sender et al., 2016). A complete sequence of human DNA is about 3 billion base pairs (10,000 times less than an adult's number of cells), which means that even without considering any cell turnover that occurs throughout the life of an organism, we could expect to find only a single base that belongs to the mother in one of 10,000 cells of the daughter on average. For all the other bases, reproduction should be considered formal. A similar conclusion would be reached for developmental resources other than genes. While from this perspective, one would have to conclude that reproduction is formal, one might also argue that the reason it appears to be formal is that it provides an incomplete explanation. To assess whether material overlap is necessary for reproduction, one must track the flow of matter throughout the entire process of reproduction.

The very same response applies to the case of retroviruses. Showing that *some incomplete descriptions* of a process of retrovirus reproduction do not require the existence of material overlap is insufficient to claim that material overlap is unnecessary for this process to occur. For the argument to stand, one should be able to show that no such overlap exists, no matter how the process is described. In the case of retroviruses, if one uses the virion and a few other stages when providing an explanation of how they reproduce, one will miss the point that a retrovirus is a spatio-temporal object that undergoes multiple transformations. Now, that multiple transformations occur does not, in and of itself, demonstrate that material overlap occurs during reproduction. In principle, a parent could be responsible for the production of an offspring without transmitting any of its material. However, this would require an objective way to distinguish a parent from its offspring at all stages of the reproductive process. The problem here is that during any process of reproduction, there will be a point where it is unclear whether the object described is a parental or an offspring object. Instead, there will be parts that will be found in the future offspring object and parts that will remain in the future parental object. Griesemer (2014) calls these objects 'hybrid individuals.' I will call them 'hybrid objects.' To observe a hybrid object might require a fine-grained description, but any explanation that tracks continuously the flow of matter involved in a process of reproduction will involve some hybrid

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[3] As pointed out by one reviewer, this is known not to be the case due to pregnancy-associated microchimerism where cells between mother and fetus are exchanged and mothers' cells have been reported to be found in adult offspring (see, e.g., Maloney et al., 1999). Here, for the sake of the argument, I will assume that there is no microchimerism, even if this might be a biologically significant phenomenon for human reproduction.

objects. Griesemer shows, convincingly, that such objects are found in some life-cycle stages of retroviruses—which, recall, Godfrey-Smith considers clear cases of formal reproduction. However, the point holds more generally. If there always exist some objects during the life cycle of a reproducer that contain both (future) parental and offspring parts, by contraposition, formal reproduction never exists.

One might think that one way to get around the problem of hybrid objects would be to label all the parts of the future offspring 'offspring' and all the parts that remain in the parent once reproduction is complete 'parental.' For instance, when a cell reproduces, we would have to label each part such that half of its DNA strands are 'offspring DNA' and the other half are 'parental DNA,' so that when a cell is produced, it is not one but two objects: roughly half a parental cell and half an offspring cell. There are problems with this approach. Not only would this way of drawing boundaries go against the biological practice of regarding the cell as an individual, but it would also be purely ad hoc and lead to an infinite regress. Further, it would also lead to the conclusion that the only type of reproduction that occurs is formal, a conclusion Godfrey-Smith does not accept.

One potential counterpoint from Godfrey-Smith could be that if one focuses on what is reproduced (i.e., reproducees), rather than what reproduces (i.e., reproducers), the requirement of material overlap is still too strong. It is indeed the case that the three conditions for an object B to be the reproducee of another object A (see Sect. 2) can be satisfied without any material overlap between A and B. Following this reasoning, the claim by Godfrey-Smith that the Darwinian logic does not require material overlap for reproduction (2009, pp. 83–84) is true. However, it should be clear that when there is no material overlap, the explanation will necessarily be one that does not address the question of the unit having the capacity to reproduce, but instead one that tracks reproducees. In many contexts, this will be acceptable. When an evolutionary explanation involves contrasting objects that have the same degree of reproductive causal control (see next section), such as different possible alleles of a gene in a multicellular organism (assuming they lead to the production of a polypeptide sequence and that they do not cause infertility), or in the context of the infinitesimal model of quantitative genetics where phenotypes are assumed to be the outcome of the effect of an infinite number of genes each having an infinitesimal contribution to it (Fisher, 1918), the reproducer is in the background. However, when the question relies on such contrasts, such as when one asks whether an object has the capacity to reproduce or is a unit of evolution, one cannot neglect this information.

The upshot is that if the debate over material overlap between Godfrey-Smith and Griesemer concerns reproducers as I have defined them, I side with Griesemer in his view that material overlap is necessary for reproduction. However, if in this debate, only Griesemer is concerned with reproducers while Godfrey-Smith considers both reproducers and reproducees, I would argue that they are talking past each other, since they are not always considering the same types of objects. To be fair, it should be noted that Griesemer's proposal, to which Godfrey-Smith responds, was made in the context of defining reproducers in a way I deem to be strongly overlapping with the way I defined them. Answering, as Godfrey-Smith does, that material overlap is not necessary between two objects that, under my analysis, turn out to be reproducees without being reproducers (or very marginally so) is true. Describing that A is a cause of *B* does not imply any material overlap between *A* and *B*, as the case of the reproduction of a retrovirus' virion stage demonstrates. However, this is not faithful to Griesemer's notion of the reproducer and thus does not address his proposal adequately. For that reason, I suspect Griesemer would agree that two reproducees need not have any material overlap (even if in fact they might have some), but that this is not the question with which he is concerned.

5 From reproducers to Darwinian individuals: the importance of reproductive causal control

In Sect. 3, I argued that to be considered a clear reproducer, a reproducee must have some reproductive autonomy, where the degree of (relative) reproductive autonomy of this reproducee amounts to the range of environmental backgrounds in which it can produce another object of the same relevant class. Although a reproducee that is reproductively autonomous, assuming a particular background, characterizes minimally what a reproducer is, this characterization is not sufficient to fully account for cumulative evolution by means of natural selection. This is so because, as I illustrate, two reproducers with the same reproductive output and described using the same grain of description might nevertheless have very different evolutionary fates with respect to their adaptive capacity, a property I associate with Darwinian individuality. I show that differences in what I call 'reproductive causal control' can yield differences in reproductive capacity.

Godfrey-Smith (2009) defines a Darwinian individual as any member of a Darwinian population. According to him, Darwinian populations are paradigmatically 'evolving populations in which significant novelty can emerge, the ones that give rise to complex and adapted structures' (p. 41). This implies that paradigmatic Darwinian individuals are objects with a significant degree of adaptive capacity. Godfrey-Smith proposes several (mostly population-level) features associated with paradigmatic Darwinian populations. These are fidelity of heredity, abundance of variation, competitive interaction with respect to reproduction, smoothness of fitness landscape, and dependence of reproductive differences on differences on intrinsic properties. However, he is clear (p. 63) that there are others or that some of the features he discuss could be fine-grained.

I propose that one such feature described at the individual rather than population level is reproductive causal control, to which Godfrey-Smith briefly alludes—even though he does not label it that way—when he says that 'paradigm cases of evolution by natural selection require not just "variation," but variation of particular kinds. If all available variation involves huge jumps in a space of phenotypic possibilities, cumulative selection again is not possible' (p. 47). To see why Godfrey-Smith's point is important, let us begin by considering the conditions for evolution by natural selection as they are classically proposed. For a population of objects to evolve by natural selection, it should exhibit the following three conditions: variation, differences in fitness (i.e., reproductive output), and heritability (Lewontin, 1970, 1985; Godfrey-Smith, 2007, 2009). There are subtleties relating to these conditions, particularly in relation to populations of objects that are not reproducing (or being reproduced) and to situations in which the population exhibits the conditions but no change occurs. However, I will not tackle these problems here

(but see Bourrat, 2014, 2015; Godfrey-Smith, 2007; Okasha, 2006, chap. 1). Instead, I will assume that the objects composing the population satisfy the conditions for being reproducers, that they vary, that this variation leads to differences in reproductive output, and finally, is transmitted more or less faithfully to offspring.

On first pass, one might think that, once satisfied, these conditions are all that is required for cumulative evolution with the potential for complex adaptations such as an eye. However, this is not so. There are several reasons for this. For instance, if variation is transmitted perfectly to offspring for all the objects of the population, sooner or later, in the absence of mutations, the most successful variant(s) will invade the population and no further evolution will occur. Therefore, for the production of cumulative selection, *new* variation must constantly be produced and transmitted across generations. But even if this further condition is satisfied, this may be insufficient. As was mentioned above in the Godfrey-Smith quotation, and reformulated here, if the variation produced is not fine-grained enough, evolution by natural selection will not be cumulative. Thus, two equally good reproducers might nonetheless depart with respect to their capacities for producing cumulative evolution and should consequently be regarded as having different degrees of Darwinian individuality.

To illustrate this point, consider the following simple example. Suppose two reproducers of different colors, such as ‘red’ and ‘blue,’ respectively. Each might be able to produce offspring objects of the same color as itself. However, when using a finer grain such as ‘crimson’ and ‘azure,’ it might be the case that none of the reproducers are able to transmit their shade to their offspring. Perhaps they can only transmit their property at the level of the color itself so that once the shade of the offspring is measured, it is just one of the multiple possible shades for the color and has no systematic relationship with the parent’s shade. Due to this lack of capacity to produce an object of the same class as themselves when this finer grain is considered, such reproducers do not retain their capacity to be reproducers when the class ‘shade’ is used.

Now, suppose that the red reproducer becomes able to transmit its shade precisely to its offspring. If the environment is such that a particular shade rather than a particular color matters for the persistence of the objects, the red variant will outcompete the blue one. When some of its advantageous ‘mutations’ that occur at the level of the shade will be transmitted to its offspring, those of the blue will not. If we now suppose that finer changes than those at the shade level matter for the relative success of objects in the population, the ability to pass on those features precisely will, in turn, be associated with an even higher degree adaptive capacity and consequently of Darwinian individuality.

I argue that the capacity to transmit finer or more determinate properties to offspring is associated with a higher degree of Darwinian individuality. This is so because populations composed of reproducers with this capacity will exhibit a higher degree of cumulative evolution. The same point can be illustrated with the number of features that a reproducer can transmit, rather than the fineness of transmission of one feature. For instance, we could imagine a population of objects of different colors, sizes, and shapes. An object able to transmit solely a change in color—as opposed to its color, size, and shape—will be evolutionarily disadvantaged. If a different size or shape becomes relevant for the relative success of the objects in the population, the types of objects able to transmit solely their color will go extinct.[4]

The above example shows that a cumulative evolutionary process requires reproducers with the capacity to retain their property of being reproducers *as we consider increasingly finer classes*, a property I call 'reproductive causal control' (Fig. 2) and which, when combined with reproductive autonomy, I associate with Darwinian individuality (see Fig. 2). I use the term causal control because we could imagine performing ideal interventions on an object using various 'grains' both in terms of the fineness of a given phenotype (e.g., at the level of the color from 'red' to 'blue' or at the level of shade from 'magenta' to 'scarlet') or the number of features (e.g., 'color' or 'color and shape') and assess whether and how often they can be passed on: that is, under the causal control of the parent.[5] For reproducers with a high degree of reproductive causal control, changing some of their fine characteristics will lead the same characteristics to be found in their offspring, so that they are considered not only reproducers at one grain of description but also reproducers at a finer grain of description.

Using the example of calcium carbonate crystals presented in Sect. 2, we can see the relevance of reproductive causal control for Darwinian individuality. Few of us, if any, would consider these crystals to be Darwinian individuals in a clear or paradigmatic sense. One reason might be that their reproductive autonomy is limited to specific environmental conditions. Another might be because, as mentioned in footnote 1, in many cases, 'offspring' crystals remain attached to their 'parent,' rendering the parent/offspring distinction difficult to apply in this case. However, I will leave these two points aside and instead focus on another problem that I consider to be similarly important. If we were to assess the number of types of interventions one could perform on a crystal that would be transmitted to offspring crystals, we would most likely find that it is very limited. And, indeed, perhaps the finest grain at which these changes will be transmitted is in the corresponding forms discussed earlier and displayed by calcite, aragonite, and valerite, each of which displays a different lattice motif for the arrangement of atoms forming the crystal. Perhaps some other features of calcium carbonate crystals can also be transmitted. Nonetheless, for all these features, it is expected that the fineness of the grain at which the differences will be transmitted is coarse, and the actual number of features that exhibit the capacity to transmit the differences is small.[6] As an outcome, the adaptive capacity of such populations of objects is limited. However, I argue that the capacity to transmit changes to offspring both when the fineness of intervention on a feature or when the number of features on which interventions are performed on a reproducer increases represents an important characteristic of a Darwinian individual because it allows for a greater degree of cumulative selection. This view is compatible with and, to some extent,

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[4] Maynard Smith and Szathmáry (1995, p. 41), in the context of replicators, calls this type of replicator 'simple replicators.' Similarly, we could call the type of reproducers only able to transmit a single property at a grain of description 'simple reproducers.'

[5] The term 'control' should not be understood here in an agential sense.

[6] It should be noted that Cairns-Smith (1990, chap. 12) argues that much finer differences than in the case discussed here might be transmitted from parent to offspring clay crystals, and he considers that they might have been primordial genes.

vindicates the proposal from Maynard Smith and Szathmáry (1995, pp. 41–44) that the interesting form of heredity relevant for Darwinian evolution is *unlimited* heredity, where ‘unlimited’ means here that the number of types potentially produced in a population of replicators is unlimited, as opposed to limited to several types, as in the case of calcium carbonate crystal.[7]

Before moving on, a few remarks are in order. First, note that reproductive causal control and fidelity of transmission are related but distinct concepts. Fidelity of transmission concerns the reliability with which a trait is passed on to the next generation. It is necessarily relative to a particular grain of description. Reproductive causal control concerns the extent to which fidelity of transmission is retained while the grain at which the parent is described becomes finer or the class to which the parent belongs becomes narrower because the number of properties considered for the object is greater. (For instance, the property of being red and having a round shape belongs to a narrower class than the property of being red simply because there are more members in the class ‘red objects’ than the class ‘red and round objects.’)

Fidelity of transmission and reproductive causal control might intuitively be thought of as going hand in hand, but this is not the case. Consider again our example with the colored reproducers. A red reproducer might always produce red offspring objects compared to a blue reproducer that might only produce blue objects half the time. If fidelity of transmission and reproductive causal control always went hand in hand, the conclusion here would be that the red object is a more paradigmatic Darwinian individual than the blue one. However, things might be different when examined at a finer grain. For instance, the red reproducer described more finely might produce a variety of offspring with different shades, in which case it is not a reproducer at this finer grain. In contrast, the blue ‘azure’ object might produce non-blue objects half the time (for which the shade of color does not matter), but when producing blue offspring, the shade is always ‘azure.’ From this finer grain of description, the azure reproducer has a higher degree of fidelity of transmission and has retained its fidelity as the changes in color become finer. Everything else being equal, if finer differences lead to differences in reproductive output, having some fidelity at a finer rather than coarser grain will permit a higher degree of cumulative evolution. On this ground, the blue reproducer scores higher on Darwinian individuality than the red reproducer, despite having a lower fidelity of transmission when considered at some grains of description. The same reasoning can lead to the same conclusion when, instead of using different coarse-grainings for a single feature, different features are used.

Finally, like autonomy, reproductive causal control can be quantified in information-theoretic terms using measures based on mutual information, as proposed by Griffiths et al. (2015) and others (Korb et al., 2011; Pocheville et al., 2017; Bourrat, 2019a, b, 2021a, b). Specifically, one could measure whether increasingly finer ideal interventions on the phenotype of a parental object (e.g., intervening at the grain of the color, then the shade, then the exact RGB value) reduces the uncertainty in the value of the offspring phenotype at that grain (increase in mutual information). This

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[7] They also use the word ‘indefinite’ in lieu of ‘unlimited.’ Note also that, when discussing Penrose’s (1959) essay on ‘mechanical’ crystals, which is analogous here with the example of calcium carbonate crystals, Maynard-Smith and Szathmáry note that they only exhibit limited heredity.

corresponds to the measure *INF*, a type of causal specificity—namely, fine-grained control—proposed by Griffiths et al. (2015) based on Woodward's (2010) analysis. A classical example of a fine-grained cause is the dial of radio for what we hear, whereas the ON/OFF switch has a much smaller degree of causal control. Following Griffiths et al.'s approach and applying it in the context of reproduction, the finer the grain at which causal mutual information is the highest between parent and offspring, the higher the degree of reproductive causal control.

6 Reproducees with low reproductive autonomy but high reproductive causal control

In the previous section, I discussed reproductive causal control in the context of reproducers. However, this feature is also relevant in discussions of reproduction where the entities discussed are mere reproducees. To see this, I start from Godfrey-Smith's argument (2009; 2015) that hearts are not reproducers, but genes are. I then discuss the evolution of reproductive causal control in the context of evolutionary transitions in individuality through ecological scaffolding.

Godfrey-Smith argues that, contrary to genes, hearts and other somatic structures of organisms (e.g., enzymes and other organs) are not reproducers but are instead reconstructed. Although some elements of this explanation are on the right track, it is not fully satisfactory. Following the distinction between a reproducer and a reproducee I have drawn thus far, both a gene in a multicellular organism and a heart are mere reproducees because they fulfill the three conditions detailed in Sect. 2 but have a very low degree of reproductive autonomy—therefore, they are not reproducers (or very marginal ones). I do not expect that the case for hearts will appear contentious to the reader. The case of the gene, however, requires more careful handling. Some might argue that genes (or sets of genes) are reproducers of a special kind. This was proposed by Godfrey-Smith (2009), who calls them 'scaffolded reproducers,' but, as noted above, also says that many of them could be called 'reproducees.' I find the category 'scaffolded reproducer' problematic due to its antinomy in light of the condition of reproductive autonomy. If a reproducer is scaffolded, this means it is not autonomous with respect to the background considered. And if a reproducer is not autonomous, it cannot be considered to be a reproducer on par with, for instance, a virus or a transposon. Thus, it appears that the only function of the adjective 'scaffolded' here is to keep genes in the category of reproducers despite their very limited autonomy. As I show below, this comes at the cost of blurring the distinction between, on the one hand, a regular gene of a multicellular organism, and, on the other hand, an autonomous retrotransposon and a virus (or, alternatively, between a mitochondrion and its free living ancestor). Rather than considering them on par, I argue that while the two types of biological objects compared have roughly the same degree of reproductive causal control, the former should be regarded as mere reproducees and the latter as reproducers because they are much more reproductively autonomous in the context considered. Following this reasoning, what separates a gene from a heart is not that the former is a reproducer while the second is a reconstructed object, but rather that both are reproducees, with the former having much more causal control in a process of reproduction than the latter.

To see these different points, let us start with the case of an autonomous retrotransposon (for an overview of the different class of transposons, see Pray, 2008). Retrotransposons are genetic objects found in eukaryotic cells. They are transcribed into RNA and, very much like retroviruses, are then retrotranscribed into DNA and inserted in the genome of the cell. Autonomous retotransposons are a special class of retrotransposons that contain all genetic material—particularly for the production of a retrotranscriptase and an endonuclease—so that they can be reinserted, once retrotranscribed into DNA, into the genome of the cell. Some retrotransposons are non-autonomous and instead rely on other transposons to be retrotranscribed and inserted into the genome of the cell.[8]

There is a clear difference here in reproductive autonomy between a regular gene (or set of genes) and an autonomous retrotransposon. Although we can assume that both have roughly the same degree of reproductive causal control, the former have no capacity to reproduce when considered over a timescale shorter than that required for cell division or, said differently, no reproductive autonomy in the developmental context of the cell. If both a regular set of genes and a transposon are placed in the same (cellular) background, the autonomous retrotransposon has the capacity to replicate itself multiple times before the cell reproduces. The regular set of genes, in contrast, could only be replicated at the same time as all the other genes of the cell: that is, it can only be replicated as part of the cell. Non-autonomous retrotransposons are an interesting middle-ground case since whether they will reproduce before the cell reproduces depends on whether it can be considered that the normal cellular background contains the retrotranscriptase and endonucleanase necessary for them to be replicated. As such, the degree of reproductive autonomy over the timescales shorter than cell division, starting from the highest, begins with autonomous retrotransposons, followed by non-autonomous ones, and finally by regular genes or sets of genes. Consequently, an autonomous retrotransposon can be regarded as a reproducer in this context while a regular gene should be regarded as a mere reproducee. However, following Godfrey-Smith’s distinction, both regular genes and retrotransposons are scaffolded reproducers.

One might complain that I take the degree property ‘reproductive autonomy’ and draw an arbitrary boundary to call one object a reproducer and the other a mere reproducee. However, assuming that the environmental background of the cell is the relevant one, the autonomous retrotransposon has some reproductive autonomy, whereas the regular gene does not. Again, this is a relative notion of reproductive autonomy with respect to both some features of the objects and some features of the background.

So far, I have argued that, assuming a fixed cellular background, regular genes are reproducees rather than reproducers and contrasted them with autonomous retrotransposons, which are reproducers. However, one might still stress that there is an important difference between a heart and a gene or, to make a comparison at the same scale, between an enzyme and a gene when it comes to reproduction. I agree that such

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[8] There are also a number of retrotransposons that are partly autonomous.

a difference exists but argue that this difference is orthogonal to whether these objects are reproducers. The difference can be fully explained in terms of reproductive causal control. This seems to be Godfrey-Smith’s take, too, when he claims that:

> Your parents did have hearts, of course, but their hearts were not causally involved in the appearance of your heart in *the right kind of way* to be parent-hearts. There is no way for newly arising quirks in their hearts to give rise to corresponding modifications in yours, for example. (2009, p. 79, my emphasis)

That causality must be of the ‘right kind of way’ seems only to refer to what I call ‘reproductive causal control.’ One can change a gene’s structure by, for instance, switching one of its nucleotides from A to C (assuming that this does not kill the whole cell or organisms) and observe offspring genes with the same feature. In contrast, changing most features of a heart (again assuming that this does not prevent the organism from reproducing) will not lead to the same changes in the offspring or, if it does, only so by chance. The same roughly applies to other somatic parts.[9]Although what distinguishes a gene from a heart is not that one is (more) a reproducer, while the other is merely reconstructed, this does not mean that such a difference is not important. I agree with Godfrey-Smith that there is an important difference between the two. Evolutionarily, once the first reproducers have emerged, we should expect that if—unlike in the case of $CaCo_3$ crystals—there is some scope for mechanisms of reproduction to become, to a great extent, *separated* from the mechanisms of transmission, there should be intense selection pressure for this. This is so because a reproducer with the same phenotypic difference as another reproducer but with a lower chance of its ability to produce any offspring at all being jeopardized would have a competitive advantage. Of course, a complete separation between phenotype and mode of transmission is not possible. Some phenotypes, such as DNA polymerases, influence the mode of transmission, but we expect them to be separated to a large extent[10] from other phenotypes.[11] This separation between mode of transmission and content of what is transmitted represents a primordial form of modularity, the latter providing some basis for the evolvability of systems (Wagner and Altenberg, 1996). If this reasoning is correct, rather than seeing modern highly evolved genes as reproducers, we should regard them as evolved modules of a reproducer with the function to transmit information (mostly) independently of what other modules do.

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[9] Note importantly, however, that this is not always the case, as studies in epigenetic inheritance have shown (Jablonka and Lamb, 2014, 2020; Bonduriansky and Day, 2009) In addition, some somatic structures might constrain the development of offspring in such a way that a change in the parental phenotype could lead to a corresponding change in offspring. For instance, Gluckman and Hanson (2008, p. 69) claim that girls born with a smaller birth weight have a smaller uterus and that a smaller uterus leads to greater constraint on fetal growth and, consequently, birth weight.

[10] For examples of other functions of DNA polymerases beyond the replication of DNA, see Garcia-Diaz and Bebenek (2007).

[11] My use of the term ‘phenotypic’ includes situations where the sequence of a DNA itself is a phenotype. This use of the term can be found in Rice (2004, pp. 169–170), and it is appropriate here in the context where the notion of the reproducer used is abstract and need not have a genetic basis.

Another reason why one might consider genes and hearts to be different, while retaining the idea that genes are reproducers, is to start from the history of life. Modern organisms are the result of a number of evolutionary transitions in individuality (Buss, 1987; Maynard Smith and Szathmáry, 1995; Okasha, 2006; Michod, 1999; Bourke, 2011; Bourrat, 2022; Takacs et al., 2023; Bourrat, 2021c) in which reproducers at one level have become reproducees and part of larger reproducers at a new level of organization. One reason one might want to consider genes as reproducers but not hearts is that modern genes might be the descendants of primordial self-replicating molecules, such as hypothesized by the RNA world hypothesis for the origin(s) of life (Neveu et al., 2013). If true, genes were reproducers that became reproducees as part of larger reproducers. Conversely, hearts do not exhibit this lineage relationship. Perhaps an appropriate term for reproducees like genes would be 'historical reproducers.' One concern, however, with this denomination is that the material structures of modern genes are probably very different from those of their ancestors; consequently, this might lead to the false idea that naked pieces of DNA were once floating in a soup and replicating. Nonetheless, discussing genes—understood here more abstractly than molecularly—as historical reproducers might be one way to salvage the idea that genes are reproducers.

Before concluding, I move to a model of evolutionary transitions in individuality, of which the evolution of multicellularity from unicellularity is a prime example, to illustrate from a different angle i) why an object having a high degree of reproductive causal control without reproductive autonomy is not sufficient for it to be considered a reproducer, but ii) might nevertheless represent an important step for the evolution of a new level of reproduction. A possible way to explain the evolution of multicellularity is to assume that some internal component(s) of ancestral unicells changed and drove the formation of collective-level entities that subsequently complexified and became, over time, full-blown multicellular organisms. An illustration of this path to multicellularity is exemplified with the work on snow-flake yeast, where a single mutation prevents a full separation of yeast cells during division and leads to the production of snow-flakes, which can be regarded as proto-multicellular organisms (Ratcliff et al., 2012).

Black et al. (2020), inspired by experimental work involving *Pseudomonas fluorescens* (Hammerschmidt et al., 2014; Rose et al., 2020), proposed instead a different type of explanation where the properties of collectives (multicellular groups) made of particles (cells)—predominantly boundaries and timing of reproduction—are exogenously imposed by environmental conditions. These conditions create a population structure in bounded patches filled with resources on which independent cells can live. When resources are exhausted, the cells on the patch die, allowing this patch to be colonized again. Periodically, some cells from a patch are taken and seed vacant patches with a single cell. The number of cells taken from a patch to seed new patches depends on the number of cells on this patch at that time.

In this setting, while the cells on a patch are independent, they nonetheless behave like a collective with its own traits, including a survival rate and fertility rate measured in number of propagules produced. However, a collective is unable to reproduce autonomously; expressed differently, whether it reproduces is highly sensitive to its environmental background. It depends almost entirely on the exogenously imposed population structure at all stages of its ‘life cycle.’ Changing the characteristics of the population structure would nearly fully determine whether a collective reproduces, very much like changing the environment of a piece of DNA in a cell. As a result, a collective has no (or very little) reproductive autonomy. However, in such a setting, cells do have fine-grained reproductive causal control. The specific values for the traits of a collective depend almost entirely on the trait values of the propagule. Black et al., as well as others (Doulcier et al., 2024; Bourrat, 2022, 2024; Bourrat et al., 2024; Neto and Meynell, 2023; Neto et al., 2023; Griesemer and Shavit, 2023; Veit, 2021), have argued that while this ecological scaffolding scenario can be regarded as an initial step in an evolutionary transition in individuality, a second step—the endogenization of the scaffold—is required for these multicellular collectives to be regarded as Darwinian individuals in their own right. Endogenization involves the capacity to gain some reproductive autonomy: that is, to become less sensitive to environmental variations. Recast within the reproducer/reproducee framework, ecologically scaffolded collectives can be regarded as reproducees with a high degree of reproductive causal control without being reproducers because they lack reproductive autonomy. The fact that they already have a high degree of reproductive causal control ‘for free’—that is, as a byproduct of properties of lower-level Darwinian individuals (the cells)—means that evolving reproductive autonomy at the collective level is much easier than if the collectives were not exhibiting it.

Notably, one might think that switching the boundary between the object and the environment to include the scaffold (i.e., the patches) as part of the collective rather than considering it as part of the environment could yield a collective reproducer. However, this is not so because the patches in Black et al.’s model are not reproducees; they are *recurring structures* that depend on some exogenous variables. Endogenization, or the evolution of reproductive autonomy, requires that either some of the properties of the patch becomes reproducees—perhaps through the actions of the cells on the patch—and coupled with the cells, so that the system patch/collective can be regarded as a reproducer, or the collective acquires the capacity to reproduce as a unit independently of the patch.

7 Conclusion

In this paper, I clarified the concept of reproduction by distinguishing between several objects that do not have the same status within reproduction processes. These are summarized in Fig. 3 using a two-dimensional space inspired from the Darwinian space of Godfrey-Smith (2009). I first argued that objects that are reproduced—reproducees—are not always the same as the objects that reproduce—reproducers—where being a reproducer amounts to having some reproductive autonomy (lower right corner in Fig. 3). When an object scores low on reproductive autonomy, it is a mere reproducee (lower left corner in Fig. 3). I then made a distinction between mere reproducers and paradigmatic Darwinian individuals, with the latter having a much higher degree of reproductive causal control than the former (higher right corner in Fig. 3). Based on these distinctions, I argued that, often, (sets of) genes (higher left corner in Fig. 3), in contrast to autonomous retrotransposons and viruses, cannot be

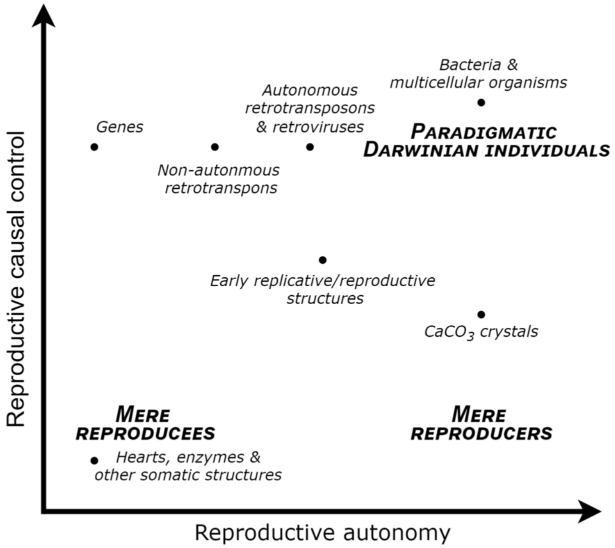

Fig. 3 Two-dimensional space for reproduction processes with corresponding regions for mere reproducees, mere reproducers, and paradigmatic Darwinian individuals

regarded as reproducers let alone Darwinian individuals. Rather, like hearts, they are key parts of reproducers with a special function, namely permitting efficient adaptive evolution of larger reproducers. Finally, I showed how the debate regarding whether reproduction can be formal is clarified by the distinction between reproducees and reproducers. On this view, I concur that reproduction involving reproducers necessarily involves some material overlap. However, if the objects discussed are reproducees as part of larger reproducers, their reproduction does not need to involve material overlap between a parental and an offspring object.

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