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Evolution by means of natural selection without reproduction: revamping Lewontin's account

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Abstract
This paper analyzes recent attempts to reject reproduction with lineage formation as a necessary condition for evolution by means of natural selection (Bouchard in Philos Sci 75(5):560–570, 2008; Stud Hist Philos Sci Part C Stud Hist Philos Biol Biomed Sci 42(1):106–114, 2011; Bourrat in Biol Philos 29(4):517–538, 2014; Br J Philos Sci 66(4):883–903, 2015; Charbonneau in Philos Sci 81(5):727–740, 2014; Doolittle and Inkpen in Proc Natl Acad Sci 115(16):4006–4014, 2018). Building on the strengths of these attempts and avoiding their pitfalls, it is argued that a robust formulation of evolution by natural selection without reproduction can be established. The main contribution of this paper is a reformulation of Lewontin's three principles (Lewontin in Annu Rev Ecol Syst 1:1–18, 1970) stating that minimal evolution by natural selection occurs when two conditions are met in a population: fitness-related variation and memory (population-level inheritance). Paradigmatic evolution by natural selection, which can generate adaptations, takes place when an additional condition is present, namely regeneration.

Keywords Biology · Evolution · Natural selection · Reproduction · Inheritance · Unit of selection

1 Introduction

Lewontin's seminal paper "The Units of Selection" (1970) starts with a three-steps "recipe" (variation, differential fitness and heredity) for evolution by natural selection (henceforth ENS), which has been considered ever since as the benchmark formulation of Darwinian evolution. In the context of Lewontin's paper, this crystallization of the neo-Darwinian understanding of ENS served to establish sound bases for discussing the perennial question of the unit of selection: once we know exactly what it takes

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for ENS to obtain, we can predict its realization, or lack thereof, at various levels of biological organization.

Fifty years later, evolutionary biology has come across unforetold biological entities that stretch to its limits the traditional understanding of Darwinian evolution (Bapteste et al. 2009; Bapteste and Huneman 2018; Doolittle 2000; Koonin and Wolf 2009): integrated communities of microbes (Ereshefsky and Pedroso 2013, 2015; Morgan and Pitts 2008; Xavier and Foster 2007), macrobial–microbial symbiotic systems (Chiu and Gilbert 2015; Douglas and Werren 2016; Margulis 1991; Moran and Sloan 2015; Rosenberg et al. 2009; Zilber-Rosenberg and Rosenberg 2008), the earth system, that is, Gaia (Doolittle 2019; Latour and Lenton 2019; Williams and Lenton 2008), complex networks of genetic materials within and between genomes (Corel et al. 2018; Keller 2014; Halfon 2017; Méheust et al. 2018), etc. A striking feature of these entities is that they do not form vertical and neat lineages as traditional units of selection do (e.g. genes and organisms). While this is sufficient to deny these novel objects the status of unit of selection according to the traditional neo-Darwinian perspective, I argue, in this paper, that there are good reasons to question whether heredity, in a Darwinian context, truly requires lineage formation.

Accordingly, this paper analyzes recent attempts to reject reproduction (with lineage formation) as a necessary condition for evolution by means of natural selection (Bouchard 2008, 2011; Bourrat 2014, 2015; Charbonneau 2014; Doolittle and Inkpen 2018). Building on the strengths of these attempts and avoiding their pitfalls, I argue that a robust formulation of ENS without reproduction can be established. The main contribution of this paper is therefore a reformulation of Lewontin's three principles of ENS (Lewontin 1970) so that three desiderata, extracted from the analysis of the work of Bouchard, Bourrat and Charbonneau, are satisfied: first, the principles are decoupled from reproduction and still provide the basis for explaining adaptations; second, they recognize the heterogeneity of ENS; and third, they are focused on populations rather than individuals. In coherence with these three desiderata, I show that minimal ENS, that is, changes in the distribution of variation due to natural selection, occurs in populations when two conditions are met: fitness-related variation and memory (population-level inheritance). Paradigmatic ENS, which leads to adaptations, takes place when an additional condition is met, namely population regeneration.

Although empirical issues are also clearly at stake and further research should tackle them headlong, this paper prioritizes a conceptual analysis of the theory of ENS, at a high level of abstraction, in order to propose a new take on the philosophical and biological importance of lineage formation within the theory in question. Section 2 provides a short synthesis of the standard view of ENS and the role that reproduction plays in it. Sections 3–5 analyze three recent accounts of ENS without reproduction (Bouchard 2011; Bourrat 2014; Charbonneau 2014). Section 6 details my reformulation of Lewontin's three principles and Sect. 7 then compares it to the "It's the song not the singer" account of ENS (Doolittle and Booth 2017; Doolittle and Inkpen 2018).

2 ENS and reproduction

This section provides a review of standard accounts of ENS, mainly illustrated by Godfrey-Smith's approach (2009), and highlights the central role of reproduction in these accounts. It is important to specify the purpose of such standard accounts. They do not propose an algorithm for predicting change within a population; rather, they are meant to capture the great variety of phenomena that are considered to be cases of ENS, among the even greater variety of evolutionary processes. Therefore, these accounts exhibit a very high level of abstraction and point to key features of entities involved in ENS in order to identify which of those features are necessary to generate ENS. If the aim of a researcher is to predict change in a population then abstract accounts will not do much to help; they would need to specify a great variety of parameters in order to draw any results (Godfrey-Smith 2007, 2009).

ENS is understood, in its most basic form, as evolutionary change within a population where three principles are instantiated: 1—variation; 2—differential fitness (related to variation); 3—heredity (so that the variation governing the differential fitness can be transferred from one generation to the other). This abstract account of ENS, established by Lewontin (1970), has served as a consensual benchmark for evolutionary biology ever since. Most elements of this formulation, if not all, have been generously discussed in the past decades, but the core elements remain to be concretely disputed. While most theoreticians are familiar with such an abstracted account of ENS, it must be noted that the theory is usually supplemented with a normative take on fitness and heredity that specifies how they are to be realized in proper cases of ENS. Building on Lewontin's (1970, 1985) and others' (Endler 1986; Ridley 1996) accounts, Godfrey-Smith (Godfrey-Smith 2007, 2009, 2012, 2015), for example, equates differential fitness with reproductive output.

In *Darwinian Populations and Natural Selection* (2009), Godfrey-Smith details his view. He provides a general summary of ENS using the concept of Darwinian population accompanied by gradient properties that serve to make predictions in regard to the evolutionary potential of Darwinian populations. In short, when a population scores high on most of these properties, ENS can be used to explain the origin of traits and, eventually, of species. When a population has a more nuanced score, ENS will only be able to explain the distribution of traits within the population. Even changes within populations that are Darwinian to a lesser degree can be partly explained by ENS. Hence, the *minimal* definition of the Darwinian population concept gives us a summary of all cases of ENS, while the non-exhaustive list of variables supplies tools with predictive power.

Accordingly, Godfrey-Smith defines the concept of Darwinian population as minimally referring to: "a collection of causally connected individual things in which there is variation in character, which leads to differences in reproductive output (differences in how much or how quickly individuals reproduce), and which is inherited to some extent. Inheritance is understood as similarity between parent and offspring, due to the causal role of the parents." (Godfrey-Smith 2009, p. 39). Differential fitness has been traded for differential reproductive output. Concurrently, heredity, as a general principle, gives way to a specific form of inheritance defined by the causal role of the parent in the generation of offspring that produces likeness among related individuals. In other words, Godfrey-Smith rearticulates two of the three elements of more abstract accounts of ENS in terms of reproduction with lineage formation. Therefore, it is logical for him to define the unit of selection, the fundamental units of evolutionary biology that he calls Darwinian individual, by the minimal capacity to reproduce (at least formally).

Interestingly, the replicator-interactor framework (Ereshefsky and Pedroso 2013, 2015, 2016; Hull 1980; Lloyd 2018) also acknowledges the importance of reproduction. Proponents of this framework distinguish the role played by a set of entities that replicate (replicators) from the role of another set of entities that sustain ecological interactions with the environment (interactors). Yet entities matter to evolutionary dynamics *qua* interactors if and only if they are associated with proper replicators. Parent–offspring lineages remain a necessity.

This nonetheless generates a notable distinction between Godfrey-Smith's perspective and the replicator-interactor framework: for Godfrey-Smith, non-reproducing yet functionally integrated entities potentially composed of replicators (i.e. interactors) can be conceived as organisms or organisms-like biological systems (organismality, in his view, comes in degrees). While they are undeniably important biological objects, they fail to be directly relevant to evolutionary inquiries when they lack reproductive capacities. The replicator-interactor framework, in contrast, gives a central role to these biological systems in every situation, since they stand as the concrete targets of selective pressures. One could say the levels of biological organization at which we find interactors is the one where Darwinian dynamics truly happen, even if these dynamics are more efficiently tracked at the genetic level.

In the interactor–replicator framework, there is consequently a reproduction-like process involved with Godfrey-Smith's reproduction concept: the high-fidelity replication of components of larger systems (i.e. replicators). Replication involves an intimate causal relationship between parent and offspring. In contrast, the reoccurrence of interactors can be decoupled from lineage formation, but is deemed insufficient (except in cases where an entity is both interactor and replicator) to sustain ENS. While an in-depth discussion on the perennial debate concerning the unit of selection concept is way beyond the scope of this paper, it should be noted that the account of ENS given in Sect. 6 strongly supports a focus on interactors instead of replicators and reproducers, even if they fail to meet the minimal requirements of reproduction or replication.

Godfrey-Smith's take on reproduction[1] can also be distinguished from Griesemer's. According to the latter, material overlap is a central condition for reproduction to be realized in a Darwinianly relevant manner, because it provides offspring with the basic matter required for development (Griesemer 2000a, b, 2005). Development being defined minimally by Griesemer as the process by which biological entities acquire the capacity to reproduce, the two notions translate a recursive pattern in which parents definitely hold a privileged causal (material) input on their offspring that sustains lineage formation.

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[1] I provide only a superficial analysis of Godfrey-Smith's very rich and insightful treatment of the concept of reproduction. This overview should suffice to fulfill the aim of this section, that is, to highlight the consensus according to which reproduction is necessary for ENS to obtain and to identify an abstract definition of reproduction that can apply despite the variety of ways in which it has been defined.

While this account of reproduction stresses an important feature of many biological systems, it has been argued that it fails to account for some relevant entities. Godfrey-Smith, while cataloguing the great diversity of processes that correspond more or less loosely to reproduction, draws the reader's attention to a phenomenon he coins formal reproduction (Godfrey-Smith 2009). Formal reproduction refers to cases where parents are causally connected to offspring, but not through material overlap. Instead, they solely transfer form or structure to their offspring (Booth 2014a; Godfrey-Smith 2009, 2015; Skillings 2016). The reproduction-like processes of retroviruses, prions and "LINE transposons" meet the description according to Godfrey-Smith.

This brief review highlights that despite the diversity of reproduction concepts compatible with a standard view of ENS, there is common ground uniting standard approaches to ENS and reproduction: the ideas that reproduction is necessary for ENS to occur and that it is a defining trait of at least some Darwinian entities are widespread among philosophers and biologists alike (Booth 2014a, b; Dawkins 1976; Doolittle and Booth 2017; Ereshefsky and Pedroso 2016; Godfrey-Smith 2009, 2013; Griesemer 2000a, b; Hull 1978, 1980; O'Malley 2015; Skillings 2016). There is another significant constant among these viewpoints: through reproduction, parents have a privileged causal role in the generation of offspring (and of their specific traits), thus enabling the effect of environmental pressures on the distribution of variation within a generation to be relayed to the next. Since this causal role of parents is believed to be the only way for inheritance to be realized (keeping in mind it can involve material overlap or not, that it can be realized by a germline of replicators or not, etc.), it is held to be a necessary trait of units of selection. In other words, the pervasive rationale is that heredity and differential fitness cannot be satisfied without proper reproduction of individuals. This, Godfrey-Smith claims, is true even if the capacity to reproduce comes in degrees (Godfrey-Smith 2013).

In order to capture the consensual, albeit abstract, dimension of the notion of reproduction, this paper uses the term to refer to any causal process of multiplication by which an individual has a privileged causal input on the structure, function or material constitution of one or many individuals in subsequent generations. The input is privileged in that a parental relationship can be drawn between individuals of successive generations; the parental relationship excludes other individuals in the population. The presence of reproduction thus entails that we can draw elegant vertical parent–offspring lineages out of the chaos of nature; accordingly, it is held as a necessary condition for ENS to shape the fate of a population.

3 Criticizing the standard view: reproduction on the line

This section reviews Bouchard's critique of the standard view of ENS, which targets the necessity of reproduction. It will be shown that his work, although important in various aspects, fails to satisfy an important criterion for a general account of ENS, namely that the theory may conserve its full explanatory power.

Bouchard has been at the forefront of recent attempts to undermine the role played by reproduction in the process of ENS (Bouchard 2004, 2008, 2010, 2011; Bouchard and Rosenberg 2004; Dussault and Bouchard 2017). In a series of papers tackling the notions of biological individuality and fitness, he claims that if units of selection are to sustain ENS, then they should be composed of parts that share a common fate in terms of persistence: they must be integrated in such a way that they will either die as one or persist as one. In a nutshell, his argument relies on the demonstration that some entities sustained ENS without being reproducers. He thus suggests that what was depicted above as the standard view of ENS is too restrictive because it focuses on entities capable of reproduction leading to vertical lineage formation.

Hence, Bouchard's first central claim is that biological individuals, i.e. integrated entities whose parts share a common fate, can sustain ENS simply by persisting differentially. Therefore, one should not be fooled by the fact that reproduction is a mechanism often associated with evolutionary success. Indeed, it remains one of the many "strategies" used by biological entities to foster evolutionary success. Bouchard's articulation of the theory of ENS in terms of persisting *lineages* is thus meant to capture both cases of entities that reproduce and those that do not (the lineage then consists of only one persisting entity).

Another central claim made by Bouchard that is important for the argument of this paper is that ENS is to be understood in terms of ensembles and their parts, rather than populations and individuals. His rejection of the traditional neo-Darwinian terminology is doubly motivated: firstly, Bouchard claims that because populations are conceived as homogeneous groupings, they fail to cover the diversity of evolutionary cases; secondly, the notion of population is intimately related to the notion of reproduction. By promoting the vocabulary of ensembles and parts, he reaches for a more inclusive account of evolution.

These claims are best illustrated by referring to an example used by Bouchard, namely the quaking aspen (*Populus tremuloides*). Bouchard synthesizes the case study as follows:

> As it is the case for many plants, the Quaking aspen (Populus tremuloides) can reproduce both sexually (in the aspen's case by seeds) and asexually (by cell-division, creating runners). When it reproduces sexually one gets fully autonomous trees, and, therefore, populations of trees, but it is the asexual clones that interest us here. Via suckering (each tree sending runners below ground that grow to be what appears to us as genuine trees, but what are in fact branches), many aspen trees grow ever larger instead of reproducing, thereby surviving for thousands of years and reducing competition from other species (the clonal grove takes over the niche much quicker than other species thanks to the nutrient transport provided by the root system) instead of increasing their population size. Some aspen groves grow to be huge integrated clonal groves (the largest is believed to cover over 100 acres). The root system is integrated (i.e. it is functionally integrated passing on nutrients to exploratory stems) and it is relatively genetically homogenous. Another way of putting the issue, is that an integrated clonal grove is exactly like a large unitary tree even though it may appear to us to be a forest of individual trees (Bouchard 2011, p. 112).

In this description, Bouchard's first claim is explicit: single organisms like quaking aspens fare better, from the perspective of evolution, by persisting instead of reproducing. General accounts of evolution as well as the notion of fitness should take this into account.

The second claim needs to be expounded: when a single organism undergoes vegetative growth, it may play the same role as a population in light of the theory of ENS. In other words, it should be considered a *unit of evolution*, a grouping of entities shaped by ENS, but not a population because its parts do not reproduce in the traditional sense. This means, still according to Bouchard, that the parts that constitute the organism, like the distinct trunks of a single quaking aspen, vary in such a way as to instantiate differential fitness; this differential fitness, if associated to inheritance, has a lasting impact on the distribution of variation within the organism. ENS should thus be conceived as a matter of ensembles and their parts rather than a matter of populations and individuals.

In short, Bouchard's critique of the standard view has two sides to it: first, organisms are not usually conceived as populations, yet some of them feature evolutionary dynamics; second, various accepted units of selection are evolutionarily relevant even if they do not reproduce. The quaking aspen illustrates both.

Given this interpretation of Bouchard's argument, there is a major flaw that needs to be addressed. Without reproduction, his account cannot sustain the most powerful explanations that the theory of ENS is expected to provide, namely *origin explanations*. Theorized by Godfrey-Smith (2009),[2] the distinction between distribution and origin explanations refers to distinct uses of the theory. In certain cases, which are associated to distribution explanations, the theory is used to account for changes or for stability in the distribution of variation in a population. In other cases, which are associated to origin explanations, ENS accounts for the creation of novelties (adaptations) within a population (this happens more readily in paradigmatic Darwinian populations). The latter explanations mobilize the former, since the more generalized a trait is within a population, the more chances it has of giving rise to novelty through the accumulation of further mutations.

Bouchard's account allows the treatment of populations[3] of individuals that do not reproduce. Yet in such cases, no matter how well individuals persist, we can only expect the population to eventually go extinct. The theory of ENS would explain how the distribution of variation changes over time, why some individuals disappear faster than others and, to a certain extent, how the population goes extinct. But by relying solely on persistence, one has a hard time explaining how new traits can arise through ENS because the population will most likely go extinct before individuals can accumulate beneficial mutations.

Indeed, in the traditional view, reproduction and heredity mute this issue before it arises: reproduction allows for the population not to go extinct. In contrast, Bouchard's view can only solve the problem by suggesting that cumulative change *within* individ-

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[2] While the expression "origin explanation" has indeed been coined by Godfrey-Smith, it should be noted that Neander (1995a, b) similarly highlighted the creative power of natural selection, in cases of cumulative (rather than single-step) selection. Her claim sparked a debate with Sober (1995), who famously emphasized the negative power of selection (Sober 1984).

[3] As it is shown shortly, I reject Bouchard's claim that the notion of population needs to be replaced by the concept of ensemble. I keep using the concept of population even when discussing his work in order to simplify the analysis.

uals (ensembles of parts) leads to adaptations by processes such as vegetative growth that, he claims, are not reproductive. But this claim unearths a well-recognized conceptual puzzle that can be summarized as follows: in certain cases, reproduction and growth seem to fade into one another because some growing organisms can be sectioned, thereby producing many physiologically independent units. As Godfrey-Smith puts it: "[the] question becomes whether the clonal production of a new physiological individual is ever a case of reproduction, or whether organism-level reproduction in the context of evolutionary theory is always the production of new genetic individuals" (Godfrey-Smith 2009, pp. 71–72). Bouchard limits the use of the term "reproduction" to cases in which new genetic individuals are created.

However, this occults a change in scale, which is at the heart of Bouchard's own use of the quaking aspen example. Indeed, a single quaking aspen can be said to feature evolutionary dynamics and adaptations because it is something like a population of cells, trunks, etc. which is being regenerated over time. This regeneration involves the production of new cells or new trunks, which can vary both genetically and phenotypically even if this variation is less significant than the one that results from sexual reproduction. The asexual variation involved can lead to differential growth of the parts of the organism, such that some sections of it prosper while others wither away; ipso facto, the fittest trees (or cells) and their copies can ultimately spread throughout the population (organism). In the context of Darwinian explanations, this is a case of reproduction where trunks (or cells) have privileged causal input on the creation of entities of the same relevant kind. If there is no reproduction at all or if the capacity of the parts to reproduce tends to degenerate (as is often the case), then senescence arises and weakens the evolutionary potential of the population of cells or trunks (the organism).

Godfrey-Smith's treatment of vegetative growth supports this view. For example, he discusses the "growth" of strawberries, as a process by which a single genet (genetically defined biological individual) may produce many physiologically independent ramets, usually construed as tokens of a given genet or genetic type: "if a strawberry produces ramets that vary, that differ in their further ramet production and that pass along their quirks to new ramets, then we do have the ingredients for Darwinian change: if ramet production is only a reproduction-like process, then reproduction-like processes are enough." (Godfrey-Smith 2009, p. 85.) Hence, the growth of an organism, in such cases, comes down to the reproduction of its parts (see Godfrey-Smith 2011 and Reydon and Scholz 2015 for related discussions). In the context of Darwinian explanations, this issue is more than a semantic quibble. If growth is a reproduction-like process, then it cannot be mobilized as an example of ENS *without* reproduction.

To sum up, I do agree with Bouchard in that ENS can explain change and novelty within a single quaking aspen, but this is best explained when construing reproduction inclusively, to cover cases like the cloning of tree trunks (or cells) that sustains the population and fosters evolutionary change. In this sense, lineage formation is still involved. Consequently, it must be noted that Bouchard's account cannot provide a basis for origin explanations *without* reproduction. A major contribution of this paper is to alleviate this flaw and show that origin explanations can be provided by the theory of ENS even in actual cases of populations without reproduction.

Because Bouchard's second claim, the suggested replacement of populations and individuals by the notions of ensembles and their parts, is justified by examples like the quaking aspen supposedly being unanswered for by the notion of reproduction, I retain the traditional vocabulary. Moreover, the fact that the writings of Bourrat and Charbonneau accommodate the concepts of population and individual to a reproduction-free framework strengthens the case for keeping these terms.

In this section, I showed how Bouchard laid foundations for developing accounts of ENS that are inclusive enough to explain the great diversity of evolutionary processes they are meant to tackle. Namely, his work shows that both fitness and ENS in general cannot rely solely on reproductive output. However, his account of ENS should be supplemented in order to understand how Darwinism might retain its full explanatory power without reproduction. In the next sections, I analyze two recent attempts to do just that (Bourrat 2014, 2015; Charbonneau 2014).

4 Populations of survivors, temporal heredity and origin explanations

In Sect. 3, it was shown that Bouchard failed to illustrate how the theory of ENS without reproduction can nevertheless explain adaptation. Satisfying this requisite is the first and most important desideratum of this paper. This section shows how Bourrat's work (2014, 2015) provides an in-depth understanding of the issues at stake. In Sect. 6, I merge his insights with Charbonneau's (2014), whose approach is reviewed in Sect. 5, to produce a robust account of ENS without reproduction.

In Bourrat's view (explicitly inspired by Bouchard's work), selectability is the basic trait of evolutionary individuals because it is sufficient to sustain evolutionary dynamics. The requirement of selectability is fulfilled minimally by what Bourrat calls survivors, that is, individuals that do not reproduce (Bourrat 2014). According to him, ENS is the population-level process that results from variation and differential fitness, but in which heredity, as traditionally construed, is not necessary. In other words, selectable survivors, as soon as their survivability differs from one another, satisfy the basic requirement for ENS. This is in line with Bouchard's view.

Bourrat's work, and especially his 2014 piece "From Survivors to Replicators: Evolution by Natural Selection Revisited", is of great importance for my analysis as he directly addresses the importance of reproduction in relation to ENS's explanatory power. Referring to Okasha's use of the expression *weak selection* (Okasha 2006), Bourrat coins the expression *weak ENS* to talk about the evolution of populations of survivors. The main idea is that such populations hardly ever evolve adaptations because they go extinct before their constitutive individuals get the chance to accumulate fitness-increasing mutations. *Contra* Okasha, however, Bourrat argues that this does not make weak ENS a fundamentally distinct process from paradigmatic ENS (that is, ENS that is likely to generate adaptations). His argument relies first on the idea that the distribution of variation in populations of survivors is shaped by the effect of natural selection and, second, that reproduction and heredity, hallmarks of paradigmatic ENS, can actually be conceived as adaptations that stem from populations of survivors. This second point is the main thesis of his paper. Hence, weak ENS, although it will most likely lead to the extinction of the population, sometimes leads to adaptation, given a large population and adequate mutation rates (Bourrat 2014).

It is thus extremely important, in Bourrat's view, to provide an account of ENS that includes populations of survivors. This entails recognizing the heterogeneity of ENS captured by the distinction between weak and paradigmatic ENS. Those two aspects of Bourrat's work (recognition of survivors as proper units of selection and of the heterogeneity of ENS) are fundamental for producing an accurate account of ENS.

His argument, however, fails to offer a solution to the problem expounded in Bouchard's work. Bourrat recognizes that populations of survivors can evolve adaptations, given specific conditions. In order to have adaptation-producing evolutionary dynamics, reproduction or at least *procreation* (reproduction without any input of the parent on the traits the offspring presents) has to be introduced within the population. This becomes obvious in his suggested four-steps scenario in which reproduction and heredity spread, as adaptations, in a population of survivors. The first step (*a*), is the introduction of a new mutation in the population, and more precisely a mutation that confers an individual the capacity to procreate. At this point, procreation is not being inherited from parent to offspring; consequently, it cannot spread among the population, which will eventually go extinct as if it were a population of survivors alone.

The second step (*b*) is reached if the new mutation introduces minimal reproduction (reproduction that transfers the capacity to reproduce minimally to the offspring) instead of procreation. This allows for significant spread of the capacity to reproduce and, concurrently, for the population to maintain its size or increase it. This, according to Bourrat, is an important step that allows populations to develop adaptations: "Thus, a population in which procreation has emerged is unable to maintain its size and the type of ENS observed in this population is very similar to weak ENS. I call it quasi-weak ENS. This result is good evidence that heredity must be part of the reason why a population is able to display paradigmatic ENS and more proximally to satisfy *b*, simply because without heredity of the ability to procreate, a population will become extinct." (Bourrat 2014, p. 526). The problem with this argument is that it neglects the possibility for the population size to be maintained without individuals reproducing. At first sight, it also fails to assess whether a population could sustain heredity processes when individuals do not reproduce. The first concern will be addressed shortly as Charbonneau's work is mobilized to provide a solution. The second concern can be answered by looking at another paper by Bourrat.

In another piece, Bourrat (2015) shows that there is an additional reason for developing a conception of ENS that takes survivability into account. The text is meant to answer a paper by Earnshaw-Whyte (2012) who argues that cases where generations overlap within a population, which are far from being marginal, provide an argument for abandoning "recipe approaches" to ENS. Earnshaw-Whyte's argument is that the notion of heredity, which is traditionally linked to vertical lineage formation and concurrently to reproduction, is not necessary for ENS and that it does not capture the impact on the distribution of variation generated by individuals that persist across generations.

Bourrat's answer is that this does not require a rejection of recipe approaches, but the revision of heritability (the measure of heredity for specific traits).[4] According to him, the heritability of a trait should measure its persistence in a population that is due to both the survival of its bearers and their reproduction with fidelity. This inclusive notion of heritability is called temporal heritability. By embedding temporal heritability into recipe accounts of ENS, Bourrat adapts them to cases of overlapping generations.

The debate between Earnshaw-Whyte and Bourrat shows that what is necessary for ENS is for some sort of stability to be maintained across time in order to ensure that the effects of selection are not randomly lost after it operates. It must be recognized that the formation of vertical lineages by reproduction is but one way to achieve this stability.

In summary, a few elements from Bourrat's work are important for the elaboration of an account of ENS without reproduction: first, he reiterates and reinforces the idea that reproduction is a facultative condition of ENS; second, he shows that even when there is reproduction, a general account of ENS that relies solely on reproduction is still not accurate (thus the need for temporal heritability); and finally, ENS is a heterogeneous process and accounts of ENS should recognize this fact (second desideratum). However, by claiming explicitly that origin explanations require some form of reproduction so that the population can maintain or increase its size, his view does not offer a solution to the problem found in Bouchard's work.

5 The distinction between a local-level process and its population-level effects

The attempts to provide a general account of ENS without reproduction considered so far failed upholding the full explanatory power of ENS. Both Bourrat's (explicitly) and Bouchard's (implicitly) accounts suggest that reproduction is a requirement for explaining how ENS may efficiently create new traits. As Bourrat shows, what is lacking in populations of survivors is a way to maintain population size without the introduction of reproduction. In this section, I review how Charbonneau (2014) accounts for such a possibility by clearly distinguishing the local-level process of reproduction and its population-level effects.

The thesis of his paper "Populations without Reproduction" (Charbonneau 2014) is that, contrary to what is normally assumed, reproduction is not a necessary condition for ENS. The objective of the argument is to answer Godfrey-Smith's claim that cultural change is a process distinct from ENS, a claim based on the necessity of reproduction with lineage formation (Godfrey-Smith 2009, 2012). In order to achieve this, Charbonneau shows that what is necessary is not reproduction itself (a local-level process involving individuals), but rather its population-level effects, namely generation and memory: "I will divide reproduction into its two component processes [that is, multiplication and inheritance,] producing parent–offspring lineages and examine the

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[4] In a recent paper (Bourrat 2019), Bourrat further theorizes heritability by developing a causation (interventionist) account of it. While the paper is extremely interesting and has great practical value, the issue tackled therein is orthogonal to the more abstract and conceptual debate broached in this paper.

role of each in allowing a population to evolve in a Darwinian manner. I will argue that it is their population-level effects that are really necessary for a population system to undergo Darwinian evolution and that a multitude of local-level processes can ensure these roles, not all of which involve parent–offspring lineages." (Charbonneau 2014, p. 728).

In short, Charbonneau shows that reproduction can be broken down into two relevant components, multiplication and inheritance, which are fundamental for understanding the role it plays in a Darwinian context.[5] While insisting on the populational nature of ENS, he shows that multiplication and inheritance have important effects at the level of the population, because they set up two conditions that are necessary for ENS: *generation* and *memory*. The alleged necessity of reproduction in the standard view of ENS results from confusing reproduction with these two population-level conditions: "the mistake is to assume that only reproduction, that is, multiplication and/or inheritance with local-level lineages, can effect these population-level conditions." (Charbonneau 2014, p. 738). I now explore both components of reproduction and their associated population-level effects in order to assess the reach of Charbonneau's argument.

Charbonneau defines multiplication as any "process where one or many entities or processes produce or participate in the production of a new entity of the relevant kind" (Charbonneau 2014, p. 729). This includes processes like translations, by which the molecular apparatus of a cell produces proteins (the proteins are being multiplied). Hence, the producer and the produced do not need to be of the same kind. Reproduction is one specific mechanism of multiplication that entails lineage formation in which the producer and the produced *actually are* of the same kind (and where parents have a privileged causal role).

Not all kinds of multiplication can sustain ENS, as it is necessary for individuals of the relevant kind to be produced. Once this constraint is taken care of (by *memory*), multiplication plays its role in a Darwinian process because it "produces, at the level of the population, both a renewal of population parts and a time frame to differentiate developmental changes from evolutionary changes. This dual population-level role assumed by multiplication I will term here 'generation'." (Charbonneau 2014, p. 730). The renewal of the population is believed to be necessary by the author because it sustains the population size, echoing Bourrat's claim about paradigmatic ENS. Charbonneau further specifies that it is important to delimitate developmental change from evolutionary dynamics, since the two are usually considered as distinct processes.

Charbonneau argues that reproduction is not the only kind of multiplication that enables *generation* at the population-level. He takes the example of prions whose multiplication relies on the collaborative labor of DNA sequences producing proteins, which are then (re)folded by agglomerations of prions into copies of themselves. The multiplication of prions, according to Charbonneau, is not lineage-dependent. Such a process however, can be associated to Godfrey-Smith's notion of formal reproduction (Godfrey-Smith 2009). Indeed, reproduction, in such cases, does not involve mate-

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[5] Charbonneau explicitly acknowledges that the resulting analysis is not a comprehensive in regard to the complexity of reproduction and the role it plays in the biological world. However, he claims that focusing on those two aspects allows for sufficient precision relative to its role as a necessary condition for ENS. This nuance is completely endorsed and reiterated in the context of this paper.

rial overlap between parent and offspring, but it does imply the transfer of form or traits. This ambivalence regarding prion lineage-formation suggests that the argument for ENS without reproduction would gain by adding a more straightforward example of how generation can be decoupled from reproduction. While the capacity of holobionts, defined as functional entities composed of a macrobial host and all its symbiotic microbes, to sustain ENS is a currently hotly debated topic (Douglas and Werren 2016; Lloyd 2018; Margulis 1991; Moran and Sloan 2015; Skillings 2016; Zilber-Rosenberg and Rosenberg 2008), holobionts nonetheless provide examples of multiplication without reproduction.

In a recent paper, Roughgarden and colleagues (Roughgarden et al. 2018) introduced a model for holobiont evolution, which has been afterwards improved by Roughgarden (2019). Importantly, the most recent paper introduces a version of the model that allows for non-vertical transmission of symbionts, that is, multiplication without lineage formation. To model the evolutionary dynamics of holobionts, Roughgarden focuses on the hologenotype, which is given by the representation of each taxa in a holobiont as well as that of alleles for loci of interest. Holobiont evolution is accordingly defined as changes in the distribution of hologenotyes in a population.

The model works through successive stages (I only review the version of the model that targets horizontal transfer): after colonization of the host by the microbes, they proliferate according to density-dependent ecological models. Then, holobiont selection occurs: the holobionts with more beneficial microbes multiply more than the others do. However, the new generation of microbes and hosts are decoupled from one another and sent to respective source pools, one for hosts and one for microbes; individual holobionts in the new generation are composed of a host and microbes *randomly* sampled from the source pools. According to Roughgarden, the results of her simulations sustain the hypothesis according to which holobiont selection can drive evolution: across time, the population of holobiont will feature an increase in the frequency of holophenotypes with many beneficial symbionts in them. While it is important to note that this scenario is evolutionarily relevant, another aspect of the model is more crucial to the argument herein.

In the model, holobiont selection involves reproduction (Roughgarden uses that term), but not as the word is used in this paper. *Indeed, holobiont-level transmission is too diffuse for it to be reduced to vertical transmission*. While a parent holobiont is causally connected to holobionts in the next generation, for example by transmitting the host organism, it is just as well connected to many other offspring by transmission of symbiotic microbes. Each holobiont ends up being connected to a wide array of holobionts from other generations. The phenomenon at play surely is a form of multiplication that leads to the population of holobionts being regenerated (i.e. Charbonneau's generation), yet the random recomposition of holobionts, highly composite entities, disqualifies the notion of reproduction (with lineage formation) as a proper label for the phenomenon described in the model. Parent–offspring lineages irrelevant. Again, further empirical inquiries will have to be conducted based on the argument made in this paper, but the description of holobionts in these terms establishes the prima facie potential of observing multiplication without reproduction for evolutionarily relevant entities in the biological world.

Turning back to Charbonneau's view of multiplication and generation, three points need to be stressed. First, I reject his claim that generation is *necessary* for ENS to occur, but this rejection must be nuanced. Indeed, it is worth reiterating the claim according to which the regeneration of a population is not strictly necessary to sustain Darwinian change (Bouchard 2008, 2010, 2011; Bourrat 2014, 2015). The differential persistence rate of non-multiplying individuals explains the modalities of the extinction that a population without multiplication will eventually undergo; the theory of ENS still provides explanations for the distribution of traits within this population. However, as already highlighted, such populations can hardly undergo adaptive change. For populations to present individuals with adaptations explained by ENS, it is most helpful for them to sustain or increase their size. The model of holobiont evolution just presented suggest that Charbonneau is right to stress that this crucial feature can be satisfied without individuals in a generation playing a privileged (or any) role in the production of offspring, that is, without vertical lineages. Hence, half of the causal role that usually justifies why reproduction is seen as a mandatory feature of units of selection is being dismissed since regeneration is realized without it and ENS can happen without regeneration.

Second, there are concerns to be noted about the suggested importance of the establishment of a gap between generations. This is an artifact resulting from the belief that the population-level effect of multiplication is necessary for ENS. In contrast, if it is claimed, as Bourrat and Bouchard do, that populations of survivors sustain ENS, then there is no reason to believe that evolutionary processes guided by natural selection must involve discrete generations because a population of survivors present no such delimitations. Furthermore, as the debate between Bourrat and Earnshaw-Whyte suggests, even populations with reproduction lack discrete generations, as there is constant overlapping of lifespans. All these elements suggest that accounts of ENS would be more accurate if they covered cases of overlapping generations and non-overlapping ones alike; in other words, the requirement of discreteness should be jettisoned when it comes to setting the conditions for ENS. Even in cases of origin explanations, the important population-level effect of multiplication is the regeneration of population, not the tracing of boundaries between generations. I therefore use the term *regeneration*, rather than the term *generation* favored by Charbonneau.

The third specification regarding multiplication and regeneration is that the possibility of having population regeneration without reproduction is a point of departure between Charbonneau's account and Bourrat's. The latter postulates that strong ENS usually requires reproduction because he neglects the possibility for regeneration to happen within populations without reproduction. Given recent advances in microbiology related to the possibility of conceiving phylogenetic composites, e.g. holobionts, as units of selection (Bouchard 2010; Dupré and O'Malley 2009; O'Malley 2014, 2015; O'Malley and Dupré 2007; Papale et al. 2019; Roughgarden 2019; Roughgarden et al. 2018; Zilber-Rosenberg and Rosenberg 2008), it seems that Charbonneau's insight, echoed by Doolittle and collaborators (Doolittle and Booth 2017; Doolittle and Inkpen 2018), concerning the possibility to have units of selection *being produced* rather than *reproducing* should be taken seriously in any account of ENS.

According to Charbonneau's work (2014), the second phenomenon sustained by reproduction and necessary for ENS is inheritance. The same rationale he used with regeneration can be applied to this second issue. ENS obtains if and only if the distribution of variation in a generation is correlated with the previous generation's ecological interactions. Charbonneau calls this population-level phenomenon *memory*. Memory allows for evolution to be guided in a steady direction and for variations to build on previously selected traits. In an idealized situation, memory could ensure that the distribution of variation at a given time is only the result of selective pressures, meaning that the distribution of variation (frequency of individual-types in the population) would be left unchanged by factors other than natural selection. In most cases, other factors such as random mutations do step in. Specific cases of evolution must be studied in order to establish whether past selective pressures are part of the explanans of the current state of the population or not; if they are, then memory is realized and ENS might also be. A general account of ENS, contrarily to such specific explorations, must acknowledge the importance of memory, but cannot specify its modalities, given the varieties of ways in which inheritance can be realized in the biological world (e.g. niche construction, LGT, epigenetic mechanisms, sexual reproduction, asexual reproduction, etc.).

Indeed, there are no reasons to assume that there is unity in regard to this phenomenon. Of course, if parents have causal input on the phenotype of their offspring, as is the case with reproduction, then memory surely is realized. What Charbonneau highlights, *contra* standard accounts of ENS, is that lineage-formation is not the only inheritance mechanism that can sustain memory at the level of the populations. Therefore, in the context of an abstract account of ENS comparable to that of Lewontin, memory is best defined, minimally, as the trait of a population translating the correlation between past and the current states of a population relatively to the frequency of individual-types within the population. Note that reference to generations are avoided to ensure the concept's coherence with population of persisting entities (echoing's Bourrat's work on temporal heredity and marking a distinction with Charbonneau's memory). In actual cases of ENS, memory enables the lasting influence of past ecological pressures. Given this formulation, the higher the rates of random mutations or migration are, for example, the weaker memory is. Implicit to this formulation is also the idea that memory can be decoupled from ENS (e.g. in cases of drift).

To illustrate the suggested pluralism concerning memory, Charbonneau (2014) uses a thought experiment in which an algorithm-guided machine synthesizes bacteria, mimics environmental pressure on them, takes notes of the differential evolutionary success and then synthesizes a second (then third, then fourth, etc.) generation by taking those evolutionary successes into account.[6] The end result is a population of bacteria evolving by natural selection: variation, differential fitness and memory are all in place so that cumulative changes enable origin explanations. This feat is accomplished without any privileged causal input on the offspring by parent(s). In

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[6] Given the aim of the paper, one might think I am suggesting that the evolutionary success of an entity should only be calculated in regard to its persisting capacities. It is *not* the case. Calculating fitness in regard to reproduction and survivability is an extremely powerful way to make evolutionary predictions. This is true even if reproduction is but one evolutionary strategy among others that generate success. In the thought experiment now being discussed, reproduction could be taken into account in the evolutionary success as calculated by the machine before a new event of creation. Hence, there will sometimes be causal input by parent on the offspring, and sometimes not. This is coherent with the claim that reproduction is neither a defining trait of units of selection nor necessary for ENS to occur.

other words, reproduction, defined as a causal process of multiplication by which an entity has a privileged causal input on the structure, function or material constitution of one or many individuals in subsequent generations, is not involved in this sort of evolutionary process.

Both memory (Charbonneau 2014) and temporal heredity (Bourrat 2015) allow one to decouple heredity from reproduction. While there are fine-grain distinctions between the two notions, the aim of this paper is to provide a general account of ENS in which such specific information is abstracted away. Consequently, an in-depth analysis of the contrasts between both notions is beside the point and will be left out for further work on the issue. In what follows, I privilege the use of the term memory, which perfectly suits the needs of a population-level reproduction-independent reformulation of Lewontin's conditions for ENS.

In summary, Charbonneau's analysis shows that reproduction is not necessary for a population to be regenerated. Hence, it rebuts Bourrat's claim that reproduction is what turns weak ENS into strong ENS by mobilizing the notions of memory and regeneration. While Charbonneau only argued that reproduction is not necessary for memory and regeneration to be realized, I use his analytical tools to provide a full-fledged account of ENS without reproduction that answers issues identified in the work of the authors reviewed so far.

6 A reformulation of Lewontin's three principles

The analysis presented of Bouchard's, Bourrat's and Charbonneau's work allows for the formulation of a novel account of ENS without reproduction that addresses problems found in each. Three desiderata that must be met by a proper account of ENS were extracted from their work: first, the formulation must sustain origin explanations; second, it must account for the heterogeneity of evolutionary dynamics; third, it must be focused on populations rather than individuals. Table 1 summarizes how this view contrasts and aligns with the various accounts of ENS reviewed in this paper. It should also be noted that, in opposition to a recent proposal by Doolittle and Inkpen (2018), the reformulation of the theory of ENS required by the rejection of reproduction is, I argue, very much Lewontinian in spirit.

I suggest that natural selection, defined as the overall influence of selective pressures from the ecological context, can be expected to be a major factor orienting evolutionary dynamics (i.e. changes in the distribution of traits over time) of populations:

- that **minimally** feature:
  - variation among constitutive individuals that leads to **differential fitness**;
  - **memory**;
- that **paradigmatically** feature:
  - the two preceding conditions;
  - **regeneration**.

Table 1 Summary of the main concepts used in the accounts of evolution by natural selection (ENS) featured in this paper

	How is ENS depicted, as a heterogeneous or homogeneous process?	Fitness: measure of the expected evolutionary success of individuals	Differential fitness	Heredity: transfer of (genetic, morphological, etc.) characteristics from one generation to the next	Various processes leading to the multiplication of biological entities
Papale (2020) (Sect. 6 of this paper)	Heterogeneous account of ENS (marginal ENS and paradigmatic ENS)	Measure of the capacity of individuals to sustain or increase the ratio of their individual-type in the population, as expected based on their intrinsic characters and ecological context	A trait of populations that feature individuals with different fitness values	Memory: the correlation between successive states of a population relatively to the distribution of variation	Regeneration: the capacity of a population to sustain or increase its size through any process of multiplication of its components
Traditional perspective, as represented by Godfrey-Smith's work (e.g. Godfrey-Smith (2009); Sect. 2 of this paper)	Godfrey-Smith uses a gradual description of Darwinian populations explicitly meant to tackle the heterogeneity of evolutionary processes	Reduced to reproductive output of individuals	Differential reproductive output within a population	Necessarily realized through individual reproduction	Multiplication is necessarily realized by individuals, *qua* reproducers (or replicators)
Bourrat (2014) and (2015)(Sect. 4 of this paper)	The weak and strong ENS distinction takes into account the heterogeneity of ENS	Same[a] as Papale: importantly includes differential persistence and survivability	Same as Papale	Temporal heredity: describes the transmission of character states and importantly includes the stability of persisting entities	Procreation, minimal reproduction and reproduction (reproduction-like processes tied to individuals rather than populations)

Table 1 continued

	How is ENS depicted, as a heterogeneous or homogeneous process?	Fitness: measure of the expected evolutionary success of individuals	Differential fitness	Heredity: transfer of (genetic, morphological, etc.) characteristics from one generation to the next	Various processes leading to the multiplication of biological entities
Charbonneau (2014) (Sect. 5 of this paper)	ENS is theorized as a homogeneous process	Not explicitly defined by the author	Not explicitly defined by the author	Same as Papale (although discussed only in relation to generation, neglecting populations of persisting entities)	Generation: considered as a necessary condition for ENS to be realized; stresses the importance of having a demarcation between subsequent generations within a population
It's the song not the singers (Sect. 7 of this paper; Doolittle and Booth 2017; Doolittle and Inkpen 2018)	ENS is theorized as a homogeneous process	Same as Papale: importantly, it applies to songs (i.e. processes whose stability is independent of that of their constitutive lineages)	Same as Papale (again, differential fitness of songs is allowed)	Heredity is realized by individuals (songs or singers) forming persisting (stable) lineages	Re-production and reproduction with 'too many parents'; not discussed as traits of populations

[a] In order to simplify the table, I use the expression "Same as Papale" when the definition of a concept in my account matches the one provided in another account. However, it should be kept in mind that my use of these concepts stems from the work of the authors concerned, especially that of Bourrat and Charbonneau

Fitness[7] is a measure of the capacity of individuals to sustain or increase the ratio of their individual-type in the population, as expected based on their intrinsic characters and ecological context; **differential fitness** is a trait of populations that feature individuals with different fitness values. **Memory** refers to the correlation between successive states of a population relatively to the distribution of variation (the more similar states are, the stronger memory is); the function linking successive states is determined by various factors: other traits of the population, such as population structure, its connectivity to other populations or its size, traits of its constitutive individuals, such as the presence of inheritance mechanisms, and its ecological context, namely the effect of natural selection. **Regeneration** is understood as the capacity of a population to sustain or increase its size through any process of multiplication of its components. ENS is explicitly represented as a two-speed process. When the **minimal** conditions are being realized, the theory can account only for changes in the distribution of variation. When ENS is **paradigmatically** realized, it can account for evolutionary dynamics leading to adaptations.

This formulation of ENS displays at least four points of departure from Lewontin's account. First, heredity and differential fitness are decoupled from reproduction. Given the understanding of memory and population regeneration exposed in the previous section, this account of ENS retains the full explanatory power of the theory and fulfills the first desideratum.

Second, variation and differential fitness merge into a single principle, while regeneration is added. This change is meant to lighten the formulation.

Third, there is an explicit recognition of the heterogeneity of processes of ENS, translated by the dichotomy between minimal and paradigmatic ENS. This satisfies the second desideratum. Ideally, this dichotomy would have to be traded for a continuum in order to provide finer information about the diversity of cases. This is especially important for the criterion of regeneration since the Darwinian potential of populations with lesser regeneration could be enough to sustain origin explanations, given certain conditions are met. This echoes Godfrey-Smith's general descriptive methodology (Godfrey-Smith 2009, 2013). The criteria of variation and memory should also be considered as continuous, but establishing a gradient for any of them and, potentially, a threshold is beyond the scope of this paper.

Fourth, the reformulation refers only to traits of populations, satisfying the third desideratum. This is coherent with the widespread view according to which ENS is a populational process (Ariew 2008; Keller 1987; Millstein 2006; Godfrey-Smith 2009) and the recognition that it can be sustained by individuals in a plurality of ways (Charbonneau 2014).

Figure 1 contrasts the traditional understanding of ENS with the one defended herein. Each panel of the figure is meant to illustrate a scenario of ENS (changes in the frequency of individual-types are guided by natural selection). These scenarios are as abstract as the traditional account (1a) and ENS without reproduction (1b) allow.

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[7] As this paper is focused on the notion of reproduction and hence on those of memory and regeneration, it leaves the notion of fitness somewhat unspecified. Nonetheless, building on the work of Bouchard and Bourrat, the abstract definition provided here fulfills the needs of a general account of ENS. Further specifications of parameters can be added to fulfill the needs of specific empirical inquiries, when required (e.g. Roughgarden et al. 2018).

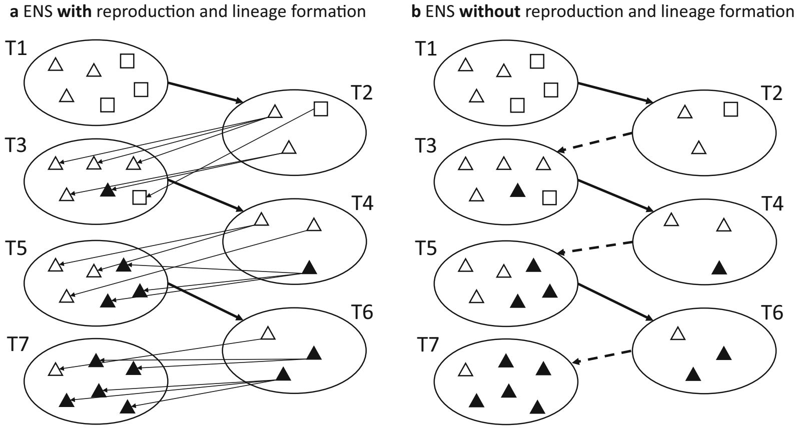

Fig. 1 Evolution by natural selection with (**a**) and without (**b**) lineage formation. Figure 1 represents two similar and idealized scenarios of evolution by means of natural selection, one with (**a**) and one without (**b**) reproduction with lineage formation. Triangles and squares represent units of selection of three different types. Ovals represent populations; there is one population in each panel, which undergoes change across time (7 phases, T1 to T7). Thick arrows represent selection events that lead to changes in the distribution of variation within the population. Thin arrows (**a**) represent events of multiplication with lineage formation (i.e. reproduction), while thick discontinuous arrows (**b**) represent events of multiplication without lineage formation (the mechanisms at work are not specified); multiplication events contribute to the realization of differential fitness and regeneration and they allow mutation (black triangles). In both cases, memory is also fulfilled as the distribution of variation across time is modulated only by differential fitness (realized by persistence and re-production) and mutations. In both cases, minimal ENS is realized and can lead to adaptations if selective pressures remain stable

That is, both scenarios are idealized so that only mutation, selection and differential multiplication rates act on the distribution of variation; drift is excluded a priori, just like migration.

On the left-hand side, continuity across time regarding the distribution of variation (memory) and sustainment of population size (regeneration) are realized by traditional reproduction with lineage formation, as explicitly illustrated. In contrast, panel 1b represents a similar phenomenon with the same evolutionary outcome (black triangles spread in the population). In this second scenario, there is no explicit connection between individuals in successive states of the population, yet the population features memory as the frequency of individual-types is tributary of past selective pressures and differential multiplication rates (both assumed to be dictated by the fitness of individual-types, as this is an idealized scenario). This means that there is an underlying process of multiplication that sustains memory, but no assumption regarding what it is or should be. As mentioned in Sect. 2, general accounts are meant to capture the great variety of cases of ENS, not to identify empirical characteristics of specific cases. Hence, the suggested reformulation of Lewontin's "recipe" is actually a generalization of ENS, insisting that it applies to other populations than those composed of *bona fide* reproducers.

This move is warranted by the fact that the necessary conditions of ENS can be realized by a great variety of mechanisms. For example, Panel 1b could turn out to be a case of holobiont re-production, as modeled by Roughgarden and colleagues

(Roughgarden 2019; Roughgarden et al. 2018). The population of holobionts is being regenerated (holobionts are being re-produced) by the random association of holobiont parts coming from source pools created by the aggregated effect of individuals present in past states of the population. In this scenario, holophenotypes with high fitness contribute more generously to source pools of parts, thereby assuring memory is realized at the level of the population through mechanisms that are too diffuse to invoke lineage formation. *Ipso facto,* mutations can accumulate and give rise to adaptations.

The generalization of ENS here proposed, by rejecting lineage formation, entails that a greater variety of biological systems than it is usually accepted might have the necessary characteristics to evolve by natural selection. As the holobiont model illustrates, this generalization is empirically both useful and relevant. While such questions as “Can multispecies symbiotic consortia form populations that evolve by means of natural selection?” are ultimately to be answered by biologists, the proposed reformulation of Lewontin’s three conditions has shifted the burden of proof on those claiming a priori that populations of non-reproducers cannot sustain ENS, as this claim runs in contradiction to an abstract but accurate account of the said theory.

Before concluding, it is important to draw the parallels and distinctions between this view and another account of ENS without traditional reproduction that has recently been proposed.

7 Comparing this reformulation with “It’s the song not the singer”

In a couple of recent papers, Doolittle and collaborators (Doolittle and Booth 2017; Doolittle and Inkpen 2018) developed the ITSNTS theory in which they outline a major conclusion that aligns with the main idea of this paper, namely that reproduction is not necessary for ENS. Their argument, however, is quite distinct from the one I present here.

In their 2018 article, Doolittle and Inkpen ground their argument in a familiar statement: holobionts, biological entities composed of a macrobial host and its associated microbes, cannot form vertical lineages. As they clearly illustrate, holobionts, even if they are functionally integrated wholes, cannot be conceived as *hereditary* units. Indeed, their parts all have distinct lineages so that a single holobiont can have “too many” parents, meaning that the resulting parent–offspring relationships involved are hereditarily irrelevant. In other words, the many-to-many relationship between parents and offspring entails that related individuals do not resemble each other any more than they resemble random ones in the population (or only do so trivially because they are related to most individuals in the population). Given this lack of continuity between generations, the traditional view tends to deny holobionts the unit of selection status.

Contrary to the traditional view, I propose that heredity, one of Lewontin’s principles, is misleadingly conceived as a requirement to be realized by individuals, *id est* by their capacity to have a privileged causal input on individuals in the next generation. On the contrary, heredity, or Charbonneau’s memory (2014), is more accurately conceived as a trait of populations, at least in a Darwinian context. It is undeniably fulfilled when individuals form vertical lineages but can also be realized by other inheritance mechanisms. Whenever selective pressures on the population at time *t* also impact the distribution of variation at time $t+1$, whether this continuity in time is the result of features of individuals or not, then memory is at least minimally fulfilled.

The answer that Doolittle and Inkpen give is quite different. They start by acknowledging the lack of material continuity between successive multispecies consortia such as holobionts, which can be problematic in the light of the standard view. They then stress the continuity of functions or *processes*, such as metabolization, over time. Their whole argument thus relies on a significant shift in the ontology of the explanandum of the theory of ENS. Contrary to approaches that set the origin of organisms and species as their main target, they turn to explaining the origin of stabilized processes (Dupré 2017) such as those realized by holobionts, conceived as incongruent taxonomic assemblages: “it seems reasonable to regard the redundancy [of genes and taxa] as real and irreducible, and the stability and change over time of the more broadly defined processes implemented by redundant taxa as that which a complete theory of ENS needs to encompass and explain.” (Doolittle and Inkpen 2018, p. 4008).

Once this shift is established, the authors tackle the complex task of explaining how processes can fulfill the requirements of ENS by generating the continuity lacking in material dimension of multispecies consortia. This involves interplay between material taxa and stabilized processes, or the new units of selection. In a nutshell, stabilized processes (the song in the metaphorical name of the theory) are evolutionary products whose very existence involves a variety of interchangeable biological taxa (the singers). Those taxa can “make a living” by performing steps of the processes, so that guilds (groups of species capable of fulfilling comparable tasks in the realization of the process) evolve to “take advantage of these opportunities”. The last step in ensuring stability is met when the resulting guilds reassemble in the environment in order to re-produce the process. This stability of processes leads to their capacity to gain adaptations over time (e.g. lateral gene transfer). The fact that they are being re-produced but are not reproducing entails the rejection of reproduction as a necessary condition to ENS. The authors favor a Bouchardian stance towards persistence: “We must allow that ENS can address differential persistence as well as differential reproduction, and that re-production can be how the former is underwritten.” (Doolittle and Inkpen, p. 4011). In summary, ITSNTS has three key features: its processual ontology, the shift towards persistence (the rejection of reproduction as a necessary condition) and the possibility to think of re-production as sustaining the persistence of lineages of processes.

These conclusions echo, for the most part, the work being done in this paper (or vice versa). Accordingly, these views could be taken as two distinct but complementary ways of reaching similar conclusions. There are nonetheless two major differences between them. The first difference translates an important objection to ITSNTS and the second one illustrates the reach of the argument presented in this paper.

On the first hand, I avoid the move towards a processual ontology because it fails to solve the problem of the evolutionary potential of symbiotic consortia. While Doolittle and Inkpen argue that it is not the consortia themselves that are units of selection but the processes they realize, this line of argument only transfers the problem onto another ontological plane. The argument made by many authors who disregard the evolutionary status of certain consortia, such as holobionts without vertical inheritance, is that the evolution of their traits is better explained in terms of the evolution of their parts, which are *bona fide* reproducers. Hence, holobiont and multispecies biofilms appear only as epiphenomena in a Darwinian context.

The fact that one focuses on processes does not solve this issue. Why are "higher-level" processes, such as metabolic capacities of organisms, not better explained in terms of the evolution of "lower-level" processes, which are themselves tied to more tractable material structures such as single cells? In fact, it could be argued that there is a discontinuity between higher-level processes while cellular or molecular related processes feature the continuity required for ENS, as mitosis perfectly exemplifies.

For this very reason, arguing for the evolutionary potential of holobionts is better served by rejecting the requirement of reproduction straightforwardly, thusly challenging the normative power of the arguments relying on it. The issue at stake remains an empirical one (whether multispecies consortia can form evolutionary populations or not), but the conceptual work done here enables one to reject conceptual arguments against the evolutionary potential of such consortia based on their lack of reproductive capacities.

On the second hand, Doolittle and Inkpen aim to solve the evolutionary puzzle emerging from the stabilized functional integration of various taxa by analyzing individual processes and their dynamics of persistence (or re-production). They mobilize a methodology that this paper argues against, namely the focus on individuals in order to assess population-level dynamics. This kind of approach is pervasive in the literature. By showing that it misleads one to impose unnecessary conditions to ENS, like reproduction, my aim is to refocus conceptual analysis of the evolutionary potential of biological entities where it belongs: at the level of populations.

8 Conclusion

In this paper it was shown that by reworking Lewontin's three principles (see Sect. 6) it is possible to provide an account of ENS without reproduction (understood as implying vertical lineage formation) that maintains the theory's capacity to explain cumulative change. This was achieved by reviewing and building on the work of Bouchard (2011), Bourrat (2014, 2015) and Charbonneau (2014). By merging the strengths of their arguments and avoiding their weaknesses (see Table 1 for a summary of the similarities and distinctions between the revised accounts and the one presented here), I suggest that ENS is a heterogeneous process realized minimally in populations featuring variation related to differential fitness as well as memory. ENS is paradigmatically realized when population regeneration joins the first two conditions. Given that this formulation avoids positing *reproduction with lineage formation* as a necessary condition, arguments relying on that biological function to deny certain biological entities the status of unit of selection are left wanting.

Given the generalization of ENS that results from the reformulation here provided, it follows that a great variety of already-observed phenomena, aside from reproduction, can and should be considered as potential processes that fulfill memory and regeneration. For example, niche construction (Odling-Smee et al. 2003; Pigliucci and Müller 2010) could be modelled not only as a process that sustains inheritance, but also as one that leads to the regeneration of a population when niche constructing behaviors increase the odds of certain individual-types being re-produced across time (holobiont re-production from source pools of holobiont parts could be interpreted in this light; see Roughgarden 2019). Another empirical issue that would gain from being reassessed in light of ENS without reproduction is the evolution of early life. Hypothetical ancestral progenotes, for example, are held to have formed non-Darwinian communities because of their incapacity to form meaningful organismal lineage (Woese 1998), a claim that might need to be revised. In other words, the conceptual generalization of ENS resulting from the rejection of the constraint of lineage formation could translate into a proportional expansion of the empirical reach of ENS.

The work done in this paper also invites the reassessment of various core concepts of the theory of ENS related to reproduction. Among others, the concepts unit of selection and population, which have been widely defined in terms of reproduction, must be the targets of renewed philosophical analysis. As for the unit of selection, its decoupling from reproduction, partial or otherwise, has already been suggested by various authors (Bouchard 2010; Dupré and O'Malley 2009; Ereshefsky and Pedroso 2015; Lloyd 2018; Wilson and Sober 1989). These propositions should be reviewed and supplemented in light of the conclusions presented in this paper. This will allow tackling the evolutionary status of the various entities that have only been recently uncovered by evolutionary biology and that stretch our understanding of Darwinian evolution (Doolittle and Inkpen 2018; Papale, Saget and Bapteste 2019).

Regarding populations, a more substantial ontological enterprise is required as the concept has been irremediably associated to reproduction (Dobzhansky 1970; Gannett 2003; Godfrey-Smith 2009; Okasha 2006; see Millstein 2009, 2010 for a potential starting point). Given that the population is the main evolving unit of Darwinian dynamics and that those dynamics can do without reproduction, a new conception of evolutionary populations needs to be fleshed out. The challenge will be to propose an ontologically adequate description of evolutionary populations, but also to provide criteria for setting and justifying the boundaries of populations in coherence with the account of ENS without reproduction that has been argued for in this paper.

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