Darwinism without populations: a more inclusive understanding of the "Survival of the Fittest"

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ABSTRACT

Following Wallace's suggestion, Darwin framed his theory using Spencer's expression "survival of the fittest". Since then, fitness occupies a significant place in the conventional understanding of Darwinism, even though the explicit meaning of the term 'fitness' is rarely stated. In this paper I examine some of the different roles that fitness has played in the development of the theory. Whereas the meaning of fitness was originally understood in ecological terms, it took a statistical turn in terms of reproductive success throughout the 20th Century. This has lead to the ever-increasing importance of sexually reproducing organisms and the populations they compose in evolutionary explanations. I will argue that, moving forward, evolutionary theory should look back at its ecological roots in order to be more inclusive in the type of systems it examines. Many biological systems (e.g. clonal species, colonial species, multi-species communities) can only be satisfactorily accounted for by offering a non-reproductive account of fitness. This argument will be made by examining biological systems with very small or transient population structures. I argue this has significant consequences for how we define Darwinism, increasing the significance of survival (or persistence) over that of reproduction.

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1. Introduction

Few concepts in evolutionary theory are as central yet as ill-defined as the concept of fitness. Darwin, following Wallace's suggestion, included Spencer's expression «survival of the fittest» only in the later editions of the *Origin of Species* (starting with the fifth edition). As Paul (1988) points out, Darwin later acknowledged that "Survival of the Fittest" was a better way of expressing the main idea of the theory than the expression "Natural Selection". As Wallace commented to Darwin (see Paul, 1988, p. 416), "natural selection" had teleological or intentional overtones that Spencer's framing eschewed. The disadvantage is that using Spencer's expression seemed to link Darwin's theory to Social Darwinism: after all, many casual readers believed that Darwin (following Spencer) is interested solely in the survival of the fittest *individual organism*. This link was weakened with the rise of population genetics through the development of the Modern Synthesis by shifting the explanatory burden away from individual organisms onto allelic frequencies. While the meaning changed, the term 'fitness' remained at the core of Evolutionary Theory[1]. For better and for worse, Darwinism -defined for our purposes as a broad family of research projects centered on the idea that natural selection is the means by which adaptation is produced in the natural world- is grounded on the idea of the survival of the fittest. In defining Darwinism, I focus on selection and adaptation not because it exhausts Darwin's contribution to biology (it does not), but because these concepts provided one of the first truly compelling alternatives to arguments from (divine) design of the type offered among others by Paley, which, until Darwin, ruled our understanding of the perceived fit of organisms to their environment.

Since the fifth edition of the *Origin of Species*, the concept of fitness has occupied a significant place in the popular understanding of the theory but what does 'survival of the fittest' mean? Aside from the historical transition hinted at earlier (a shift from

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[1] Dobzhansky suggests using "adaptive value" instead of "fitness" in part to shed the Social Darwinist stigma but the shift hasn't been universally adopted (see Dobzansky, 1951, 77–79 and Paul, 1988 for discussion).

individual organisms to alleles), there is a conceptual necessity for providing a satisfactory account of fitness. We need to understand these foundations to truly be able to assess what is the correct domain of application of evolutionary theory: what can evolve and how can we model evolution in nature?

To see why this is a real issue, one needs only look at the most often quoted framing of the process of natural selection, the one offered by Richard Lewontin (my emphasis in bold) (in Levins & Lewontin, 1985, p. 76):

A **sufficient mechanism** for evolution by natural selection is contained in three propositions:

1. There is variation in morphological, physiological, and behavioral traits among members of a species (**the principle of variation**).
2. The variation is in part heritable, so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents (**the principle of heredity**).
3. Different variants leave different numbers of offspring either in immediate or remote generations (**the principle of differential fitness**).

To paraphrase this statement: variants in nature deal with varying success with their environment and if what allowed the 'lucky' variants to thrive is passed on to the succeeding variants, then evolution by natural selection will be obtain. This may seem like a contrived way of reframing Lewontin's statement, but I will argue that there is genuine advantage for such abstraction.

Intuitively the notion of fit between an organism and the problems posed by the environment has always been part of Darwinism. This is not always the case in the explicit scientific models themselves. Whereas the meaning of fitness was originally set out in ecological terms (i.e. the fittest individual organisms survive in their environment), it took a statistical turn in terms of reproductive success of population variants throughout the 20th Century. While this turn doesn't eliminate the ecological characterization of fitness it explicitly pushes it in the background. If there is random variation among the traits of organisms and if some variant traits fortuitously confer advantages on the organisms that bear them then those organisms will live to have more offspring, which in turn will bear the advantageous traits, thereby increasing the frequency of the trait bearers (and their genes) in the population. Fitness is then explicitly described in populational terms: 'good' traits are replicated in a population so the fitter entity is the one with the most descendants. In other words, fitness is usually about differential reproductive success. I will examine various reasons why this account is unsatisfactory (or at least in need of revision). My proposal has three major motivations:

1- *Urgency for our understanding of contemporary evolution*. At least some biological organisms' evolution cannot be adequately understood if we focus exclusively on reproductive success. In this paper, I will focus on one clonal species to show the limitations of a reproductive account of fitness. I will argue that since these clonal organisms are doing something 'right' without reproduction we need to see how our understanding of fitness can be modified.
2- *Urgency for our understanding of past evolution*. The facts that most of life of Earth has not been sexually reproducing and that all sexually reproducing species have evolved from asexual reproducing species behoves us to modify our understanding of evolution so that it can adequately chart out not just the last 500 million years of evolution (about the time sexual reproduction arose) but the 3.5 billion years before that. It's not the case that all clonal species pose a

problem for replication accounts, but rather that many do. We will see that for many clonal species, selection acts on the parts of a growing individual, not a growing population of individuals.
3- *Urgency for our understanding of the origin of life*. Our best current understanding of evolutionary theory is basically making the claim that at some point in the history of life on Earth, entities started reproducing and that that permitted evolution by natural selection to kick in. It might be fruitful to examine how evolutionary theory recast in terms of persistence (my proposal) might be able to explain how life itself arose as the result of the evolution of physical and chemical forms into more persistent biotic forms. Many projects related to inquiry about self-organization or evolution and thermodynamics have been making similar claims, but many lack a unified account of fitness.

A full account of usages of the term fitness will not be offered here (See Rosenberg and Bouchard, 2008). What I will offer here are examples of the difficulty of identifying populations, and difficulties establishing reproductive success for some biological systems and how these should inform our understanding of 'survival of the fittest' and of Darwinism.

I argue that, moving forward, Darwinism should look back at its ecological roots and focus on survival (or persistence) in order to be more inclusive in the type of systems it examines. This move is necessary for the motivations 2 and 3 highlighted above. Reproducing entities have evolved from non-reproducing entities. The question remains as to whether this transition was itself the result of evolution by natural selection or not. How we define fitness is an important component of the answer to this question. I will briefly explore this point at the beginning and end of this paper. The first motivation will occupy a large part of this paper. Many biological systems (e.g. clonal species, colonial species, multi-species communities) can only be satisfactorily accounted for by offering a non-reproductive account of fitness. Such an account will be sketched out in terms of the differential persistence of lineages. I have provided a fuller account of this idea elsewhere (see Bouchard, 2004, 2008) but here I will develop a specific part of this broader argument: extremely small population structures show that that growth and reproduction are not as distinct as we often believe. If this is the case, then it's not so much populations that are needed (contra Lewontin's characterization of the process of evolution) but collections of components. This has deep implications for how we can explain the adaptive change in many biological systems. This will be the core of the argument presented here.

2. Where do replicators come from?

As I stated earlier, one of the main explanatory benefits of Darwin's theory of evolution is the way it provides an explanation for adaptation (i.e. how well organisms seem to fit the demands imposed by their environment). I want to show that one does not need populations per se to get evolution by natural selection (although one needs ensembles or collections of something: and as we shall see the distinction between population and ensembles is not trivial). Further, I will develop some ideas about how to think about fitness in general. Focusing on ensembles instead of populations also changes the role of reproduction. This will be presented not merely as a clever semantic shift, but as a way to understand actual cases of adaptive changes that are not well accounted for by standard accounts of evolution by natural selection.

Under many contemporary interpretations of the theory of evolution by natural selection focused on replicator based explanations, evolution is the accumulation of change in allelic frequencies

in response to environmental pressures. Such interpretations have been very fruitful and underpin the backbone of contemporary evolutionary biology especially in population genetics. There is however a certain malaise with this interpretation when we start thinking about the origin of the genes: how did we obtain these replicating macro-molecules in the first place? In other words, by what process did we go from 'inert' molecules to replicating molecules? The malaise is in part caused by the overly restricted focus on gene frequencies: since the apparition of genes on Earth is contingent, is the claim that evolution by natural selection is an accidental feature of life on Earth? Is the claim that evolution by natural selection may well have never occurred if nucleotides had never been formed? This difficulty is what motivates many to drop the focus of nucleotides in favor of replicators (Dawkins, 1976). Genes are not necessarily the only type of entity that could evolve. They are instances of replicators (i.e. anything that copies itself). Dawkins goes further by arguing that genes are the paradigmatic replicators, but this is a contingent result of how events unfolded on Earth. At the core, the theory should be about replicator dynamics and that's how most biologists and philosophers analyze evolutionary phenomena instead of focusing exclusively on genes. The framework for understanding evolution in terms of change in frequencies of replicators remains compatible with standard population genetics models while allowing for an evolution by natural selection *sans* genes (e.g. in a radical extension of his own framework, this led Dawkins to model cultural evolution in terms of the selection of memes, i.e. cultural replicators such as slogans or trends).

An advantage for biological theory of minimizing, at least temporarily, the definitional role of genes in favor of replicators is that it may help us to better explain the *transition* between pre-biotic and biotic world in evolutionary terms, thereby providing an explanation of the *origin* of genes: the apparition of life and genes would itself be the result of evolution by natural selection. But this explanation requires relaxing our standard view of evolution by natural selection[2]. It is telling that even Dawkins, famed public bulldog of genic selectionism, felt the need to deal with the *transition* and *origin* questions. The first chapters of the *Selfish Gene* (1976) explain how inert pre-biotic molecules may have given rise to replicators (genes in this case) following selection for *stability* (i.e. genes emerged as the most stable copying entities), a sort of primitive evolution by selection. This view entails that evolution by natural selection applies beyond (or before) living kinds. We will not examine this stronger claim in this paper and will instead focus on more pragmatic reasons for biological research to reexamine key concepts of evolutionary theory. I will argue here, that there are other reasons why we should take a second look at this 'primitive' evolution beyond the origin of replicator questions: change in allelic frequencies cannot fully account for certain types of biological evolution, in part because some biological systems adapt while not truly reproducing/replicating. This will be the focus of the rest of the paper.

3. Survival and/or reproduction

3.1. Energy

To see the limitations of reproductive accounts, it is helpful to examine proposed alternatives and the payoff they may provide. As we shall see, others have worried about the three motivations listed in the first section of this paper. A seductive account has been to focus on energy instead of reproduction.

Ariew and Lewontin (2004) point out some of the difficulties in trying to reconcile Darwinian intuitions about the fit of organisms to their environment with explanations provided in contemporary population genetics. Ariew and Lewontin not only argue for the weakness of the dynamical approach to understanding fitness in contemporary evolutionary biology (i.e. a force approach or a vector approach fleshed out by Sober, 1984; see also criticisms of this view in Matthen & Ariew, 2002 and in Walsh, Ariew, & Lewens, 2002), but they also weaken the explicatory adequacy of *any* unified reproductive measure of fitness[3].

Ariew and Lewontin briefly describe the case of the violet (*Saintpaulia ionantha*) that, like many plants can reproduce both sexually and asexually: for these organisms and many others (other cases will be discussed later in this paper), individuation of the entities involved is both an epistemic and ontological problem. As Ariew and Lewontin point out, this difficulty in individuation translates into difficulties with using any straightforward reproductive success measure of fitness.

> The problem that has plagued evolutionists who deal with organisms that have both sexual and vegetative reproduction is how to count ramets and genets in assigning reproductive fitness. Do all the ramets of a single original stem count as belonging to a single individual or is each to be counted as a separate individual? It might be argued that since the ramets are all connected as a single body, they are collectively one individual. But is the occurrence of a break in the underground stem sufficient to produce a new individual for accounting purposes? Moreover, the problem exists for trees. A tree consists of a large number of flowering stems connected together by branches and a trunk. Why should it matter that these flowering stems are connected above ground rather than below? If a tree is a single individual than so is the collection of all the ramets of a violet. How is fitness to be calculated in such instances? ((Ariew & Lewontin 2004), p.360)

They are not the first to identify the difficulties clonal organisms pose to reproductive accounts of fitness (e.g. Buss, 1983) but they do however entertain an alternative account of fitness that is not often discussed in evolutionary biology: at least for cases such as the violet, they argue that a resource maximisation account of fitness is appropriate.[4]

They argue that the evolution of clonal species warrants a different understanding of fitness focusing on resource maximisation instead of numerosity increase (i.e. increased reproductive

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[2] Gabora (2006) argues that natural selection cannot account for these first molecules and that evolution by natural selection is a process that only occurs once the first replicating nucleotides appear. She suggests that *context-driven actualization of potential* (CAP) can explain the changes between inert and living, between the proto-cells and the genetically driven change that follows. The argument depends in part on the different probability regimes (non-Kolmogorovian vs. Kolmogovarian probability models) at play in the pre-biotic and the biotic world but more generally it retains standard notions of natural selection and adaptation in term of Weismannian change in gene frequencies that by definition cannot accommodate change in pre-biotic molecules. Even though Gabora may well be right in her assessment of the different probability models necessary in pre-biotic change, her conclusion depends on an orthodox understanding of natural selection that will be challenged in various ways throughout this paper.

[3] This is in mild contrast with aforementioned other articles, where Ariew and others had implicitly endorsed the adequacy of population genetics explanation of evolutionary phenomena which rely on differential reproductive success of genotypes within a given population. The distinction will not be explored here but I think the shift is in the explanans. Ariew and Lewontin are concerned with Evolutionary Theory in general (from evolutionary ecology to population genetics), Matthen and Ariew are concerned with evolutionary explanations and how they pan out in population genetics in particular.

[4] "A priori, the most direct connection between evolutionary change and a continuous measure of fitness would be to use proportion of the limiting resources for species reproduction that is pre-empted by a given type. Evolutionary change would then be measured as the change in the total proportion of the limiting resource occupied by the various types. Again, in the case of unproblematic individuation of objects of roughly equal resource occupancy, simple numerosity would be an adequate proxy." ((Ariew & Lewontin 2004(, p. 361).

success). Differential evolutionary success is tied to how much resource is controlled, *not* necessarily how many offspring are created. As they suggest themselves, this intriguing suggestion deserves a more thorough treatment then the one offered in their paper. As they themselves point out components of a resource view of fitness have been suggested in the past (they mention Margalef (1968), and multiple other examples can be found in the ecology literature) but a broader evolutionary account has been provided by Van Valen (1975, 1989, 1991).

Van Valen (1975) explicitly argues for an account of absolute fitness measured energetically. "The momentary or realized fitness of an individual or population as the amount of its ultimately regulatory resources, especially energy, that it controls" (Van Valen, 1975, p. 267).

Part of Van Valen's motivation for proposing an energetic paradigm is his dissatisfaction with the lack of interaction between genetics and ecology (Van Valen, 1989, p. 1). He argues that in many cases examined at an ecological scale, reproductive success loses its primacy despite the central role it plays in population genetics models. As he points out, physical size is important to natural selection and although this fact often translates into population size it cannot always be reduced to it. Physical size in a single organism, whether it be a coral or a plant, sometimes says much more about its evolutionary fate than its reproductive success (often absent for clonal species; more on this later). Van Valen clearly has selection for 'growth' in mind when he writes that "Rather than saying that natural selection is expected differential reproduction, we should say that it is expected differential expansion" (Van Valen, 1989, p. 7). But it is not spatial expansion *per se* that is optimized. Physical expansion is but one efficient means to increase energy control. In clonal species, this increase in energy commandeering is obtained via increased growth in a single individual, while in sexual species, an increase in offspring number (the conventional metric for fitness increase) is the way to increase the energy control at the population/species level.

In trying to link growth cases to normal reproductive cases, Van Valen suggests that the only feature uniting them is increase in energy control. Van Valen argues that energy control is the only thing being maximized in nature by all species and that sometimes this process translates into higher reproductive numbers, whereas sometimes it translates into higher growth of single individual.

I will not assess Van Valen's suggestion in detail here (see Bouchard, 2004 chapter 3 for analysis). I merely wish to point out for now that some of the biologists who have thought the most about evolutionary *theory* in the 20th century (here Van Valen and Lewontin) and how it could apply to a wide array of biological systems have expressed some dissatisfaction with a purely reproductive view of fitness. They have suggested that energy commandeering may be the common denominator. I will suggest that increase persistence offers a better foundation (or better common 'currency') for understanding fitness.

3.2. Survival

Biologists and philosophers have tried to tease out the relative importance of reproductive success in our accounts of evolution. Although obviously fecundity and fertility are keystones of evolutionary explanations, survival and the means by which organisms survive are a necessary aspect of the story. I have so far highlighted the reproductive aspect of fitness but in fact, most accounts of fitness (whether in population genetics or evolutionary ecology) have two components (see Sober, 2001): survival AND reproduction. This is not surprising since one needs to survive to be present at and take advantage of opportunities to reproduce, and many adaptations are correlated to the survival of organisms not their reproduction. Even though most would accept both components of fitness, the survival aspect is often downplayed (e.g. Dobzhansky, 1951, p. 78). But this is not always the case in the biology literature. While the survival component of fitness is often analyzed as merely instrumental to the reproduction component of fitness, some go further in focusing on survival.

In his exhaustive survey of natural selection experiments, Endler (1986) points out that many studies in evolutionary biology focus exclusively on intra-generational success and phenotypic selection (i.e. focusing on the survival component of fitness). In some experiments, phenotypic selection, more than selection of offspring, is the proper handle to understand the adaptation of biological entities (Endler, 1986, pp. 12–13). Sober makes a related point (Sober, 2001) showing that the mathematical representation of fitness found in population genetics downplays the ecological factors that are in fact a significant aspect of fitness in other studies. Bouchard and Rosenberg (2004) go further, by arguing that ecological fitness *simpliciter* is the best way to understand fitness and that other means of understanding it are merely measures or proxies to evaluate an organism's fit to its environment.

Following this insight, we may wish to re-examine the evolution of some biological systems that *prima facie* appear to be evolving as a result of selection even though the full explanation is sometimes difficult to articulate in reproductive terms (e.g. quaking aspen groves, certain colonial organisms and symbiotic communities); many biological systems display adaptive change as a response to the selective environments and these changes accumulate and are fined tuned over time in order to increase the system's capacity to survive. However these systems' evolution is not adequately captured by a concept of evolutionary fitness that is defined solely in terms of differential reproductive success.

As Ariew and Lewontin noted earlier, asexual species have always been a problem of sorts for evolutionary biology[5]. Asexual species also often put stress on our concepts of heredity and heritability. Clonal species' phenotypes are often affected by somatic mutations that can be passed on. Weismannism describes how only changes in the germ line can be passed on to the next generations and this is the type of heritable variation that is the focus of standard evolutionary biology. But as Leo Buss (1983) points out convincingly, the evolution of protists, fungi and many plants which are in large part the result of selection on somatic changes cannot be accommodated by Weismannism. Buss uses this idea to justify a hierarchical view of selection. Many of the examples given by Buss literally do not reproduce. Buss is correct in explaining how, in the cases he presents, evolution can happen via selection on sub-organismal variation where the 'good' variations in the parts within an organism are passed on to the organism itself. As we will see for some plants, the notion of component or part is more relevant than the notion of offspring. If this story is accurate then at least for some cases of evolution by natural selection, there are no actual populations, which should worry advocates of purely 'populational' accounts of natural selection and fitness or more generally anyone wanting to define fitness exclusively in terms of differential reproduction.

Is the problem with replication itself or with specific accounts of the role of replication? Evolutionary fitness has usually been defined in terms of offspring contribution: the more offspring one can have, the fitter that organism is. In contemporary

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[5] In the preface of a book on evolution and clonal organisms Jeremy Jackson, Leo Buss and Robert Cook correctly point out that: "Ever since Darwin, the development of theory in ecology and evolution has been implicitly constructed for fruit flies, birds, and people, unitary organisms whose populations comprise readily distinguishable, sexually derived individuals of approximately determinate adult body size and life span. Grasses, vines, sponges, corals, and other clonal organisms, which commonly dominate much of the land and sea and do not commonly display such characteristics, have been largely ignored by theorists" (Jackson, Buss, & Cook, 1985, p. ix).

philosophy of biology this is often translated as the propensity view of fitness (See Beatty & Mills, 1979; Brandon, 1978). If an organism can survive and has the potential to reproduce in greater numbers than its competitor, it means that it is better adapted to the environment in which it lives.

The propensity view has specific problems (see Beatty & Finsen, 1989). But, I would argue that any account of fitness focused on replication creates certain problems for Darwinism[6]. It cannot account for all adaptations: certain systems seem to respond to pressures from their environment via selection on some variation in a way that increases their potential to survive, but they do so without reproducing. I will argue that in fact Darwinism is flexible enough to encompass these systems' evolution[7]. In my account, reproductive success is still a powerful mechanism for evolution to occur, but it is recast, not as the fitness itself, but as one of many strategies by which a system can better respond to pressures from its environment. Reproduction shifts from being the exclusive engine of adaptation to being just another adaptive strategy—a very good one- to get complex adaptations.

As we shall see, I argue that for clonal systems and many others, adaptive change is obtained through slow accumulation of changes among the parts of the system not through inter-generational change within populations. This will have to be so since the systems examined here do not have offspring per se. I am not the first to make this observation (e.g. Gill & Halverson, 1984) but the generalization that I will draw from it is, I believe, novel.

As part of a larger research project (Bouchard, 2004, 2008) I argue that at least for organisms such as many clonal species, *Persistence Through Time* of a lineage (hereafter PTT) is the property maximized by evolution by natural selection: maximization of relative reproductive success is only one strategy for persistence of a lineage but for many asexual species (but not all) reproductive success is actually minimized if not eliminated. This view is in contrast of course to reproductive success views of fitness but also in contrast with resource maximisation accounts defended by Van Valen, Ariew and Lewontin and others (increase in energy control may well be a good strategy to increase the potential for persistence, but resource minimization could also be a good strategy in other selective contexts). To show this, I will blur the distinction between growth and reproduction by an examination of how small populations deal with natural selection. Many standard evolutionary explanations focus on competition between members of a population. But, as Darwin remarked himself, the idea of competition underlying the struggle of existence should not be overplayed. Differential success is necessary to have evolution, and often this differential success is the result of competition, but two isolated plants of the same species can be said to respond to natural selection without being in actual competition for resources. The examples examined in this paper tend to downplay the role competition plays in evolution by natural selection. Clonal examples (we will examine a specific case in a moment) shows us that selection can act on the parts or components of a biological system. One way to model this is via energy commandeering. I argue that a more inclusive account lies with a persistence account. Before fleshing out this proposal we need to see how the difficulties in accounting for systems such as the quaking aspen stem from how to think about what constitutes populations and competition between what types of entities.

4. Populations

Thinking about populations has taken many forms in contemporary philosophy of biology, from evolutionary populations defined explicitly by ecological factors (e.g. Brandon, 1990; Millstein, 2006; Sober, 1984) to populations conceived as abstract statistical entities (e.g. Walsh, Lewens, & Ariew, 2002; Matthen & Ariew, 2002; Walsh, 2007). In this latter view, evolutionary phenomena become strictly population-level phenomena that are completely described by some of the mathematical models provided by population genetics. In this statistical interpretation view, knowing the particular ecological circumstances would not add anything to natural selection explanations because the statistical patterns are captured by the mathematics alone (in an analogy to how entropy is described by statistical mechanics). Most notions of populations are too limited to apply to microbial evolution, clonal evolution and symbiotic evolution. For these cases of evolution, I argue, we will be looking for *ecologically* defined collections of entities that cannot always be tracked by following changes in gene frequencies or even reproductive success (see Bouchard, 2010).

This is intended as a novel way of understanding what can act as a Darwinian population (one can find related arguments in Godfrey-Smith, 2009): between the mathematical excesses of the statistical interpretation of evolutionary theory where the ecological properties of populations are completely abstracted away, and the organism centric view of populations that restricts too much what type of entity can count as a member of a population, lies a view of natural selection that relies on variation among the parts (or components) of a biological system and in which differential success is defined in terms of differential persistence instead of differential reproductive success.

Given the centrality of the concept of population it is surprising how rarely it is explicitly defined by biologists. This will not correspond to all uses of the word (obviously) but one gets roughly two notions of populations in many biology texts (for a detailed review of the concept of population see for example Waples & Gaggiotti, 2006 and Godfrey-Smith, 2009).

  A- An *organismal* notion: A population is a collection of organisms of one species in a given context (be it spatial, interbreeding etc.)
  B- A *genetic* notion: A population is the collection of alleles in a given context (be it spatial, interbreeding etc.).

These two widely used notions of populations will sound familiar to most philosophers of biology and have been redefined in more inclusive terms by Dakwins, Hull and others.

  A- An organismal population (roughly) corresponds to a population of *interactors*.
  B- A genetic population (roughly) corresponds to a population of *replicators*.

In these definitions (and in most others that could have been presented here), it is assumed that we have collections of relatively similar, related, reproducing individuals with clear physiological boundaries. But nature is often messier than this. First, it should be pointed out that one should not confuse individual and organism. This article is not intended as a review of the literature on biological individuality (good places to start are Leo Buss, 1987, R.A. Wilson, 2004, 2007) but to anyone who was wondered about the individuality of coral reefs, Portuguese Man-o-war, and many other examples, it seems obvious that the organismal notion of individuality is doomed to fail often.

The genetic/replicator notion of population is more inclusive (because to it isn't tied a specific notion of biological organization), but as Buss (1987) among others argued, the view of evolutionary

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[6] Griesemer, 2005 extensively charts the issues related to the role of replication in our understanding of Darwinism.
[7] Godfrey-Smith, 2009 identifies similar difficulties but comes to a different conclusion by relaxing notions of what constitutes populations.

change it relies on is based exclusively on Weismanian processes which often do not obtain in nature. In the contemporary literature (Doolittle, 1999; Bapteste et al., 2005 and see special issue in Biology and Philosophy, *forthcoming 2010*), the prevalence of Lateral Gene Transfer transforms our understanding of how alleles are 'vehicled' in organisms and how this affects our understanding of the structure of the tree of life. Populations of microbes are notoriously difficult to identify because some genes are transferred during the microbe's ontogeny, and the distinction between an organism and colony is both fluid and ephemeral (see O'Malley & Dupré, 2007 for some of the philosophical implications of this problem). Not surprisingly, similar issues arise for populations of these entities.

I argue that it's useful to restrain the use of the term 'population' only to ensembles of related interactors or replicators (i.e. a population is a special kind of ensemble/group/collection). But restricting the concept of population as such, forces us to broaden our understanding of evolutionary processes. I wish to show that while *ensembles of parts* are necessary for evolution by natural selection one does not need *populations of genuine individuals (be they genes, organisms, or something else related to replicators)*.

To put in a different way, populations are ensembles of similar units at the same level of organization and usually of the same species. This similarity could be morphological, but in most cases the similarity that biology is interested in is shared history: common ancestry or common inter-reproductive history is the similarity uniting populations in most usages of the term.

Ensembles of parts (such as a collection of symbionts) or organs do not fit this view of population well. One could have ensembles of vastly heterogeneous units (different populations, different species etc) which would not count as populations in the conventional sense[8]. We will see that to have evolution by natural selection, one needs variation within parts of ensembles, but one does not need populations of independent related entities. To see this, it is helpful to focus on extremely small populations

Is a population of 1 individual a population? Let's start with a very simple thought experiment: imagine a clonal organism, last (or first) of its kind. At each generation it is able to produce two offspring and the parent dies immediately after its offspring's birth.

Now imagine that the environment can only support one organism of that kind at any given time (carrying capacity of 1). One of the two offspring dies immediately after birth. You have a lineage where the population is effectively 1 at all times except for brief intervals where the population is 2. There is selection on variants, there can be response to selection (after all only the fitter of each generation survives), and therefore there can be evolution by natural selection. But do we have populations when we have merely succession or replacement of individuals? In a formal mathematical sense we can still use the word 'population' even when its N is 1 but in a conceptual context, the word is less useful. The idea here is that to have adaptation, one can have effective populations with sizes of 1 (most of the time) with brief intervals of populations of 2. But to speak of a population of 1 is somewhat perverse. Here we have a succession of individuals. There is selection on individuals if you will, but the example shows that populations here are not as fundamental as one would think to have adaptation. Population thinking (see Sober, 1980) as it emerged in contemporary evolutionary thinking was intended as a way of abstracting away from individual circumstances in order to track only the mathematical properties of populations. In the thought experiment

described above, the individual circumstances and population properties are one and the same thing, and differential reproductive success, while still there, becomes much less interesting than the differential survival of the entities involved.

But is this merely an artifact of the thought experiment or a broader lesson concerning how we conceive the process involved in natural selection? First, it should be pointed out that many clonal species on the verge of extinction will have a pattern resembling the one in this thought experiment. But to show the full breadth of application of this thought experiment, let us change it a bit. Assume the phenotype of our clone corresponds to spatial position. I would argue that spatial position is part of the phenotype since you can select on position in the same way that you can select on height (height is unequivocally an aspect of an organism's phenotype in many selective contexts; what we must not forget is that height is ultimately about vertical position). Now imagine that offspring can come to the world either on the left or the right of the parent. If the carrying capacity remains 1 and the parent dies, if there is selection to be (let's say) on the left (e.g. nutrients could be on the western slope of hill), the lineage will slowly 'move' towards the left. By selection on the variant's position, the lineage will evolve towards a more left-leaning position.

Now imagine the clones remain physically connected, one iteration to the next. This is actually how the shape of many plants is determined. A branch grows in a given direction because the other directions are less hospitable. This is usually described *merely* as growth and therefore is not usually described in terms of evolution by natural selection, but consider the similarities. What we have is selection on various positions. This is a single individual and there can be selection on some of its components. And the response to selection can increase the capacity of the whole system to survive (instead of increasing the numerosity of the individual). With an individual organism it may seem a bit strange to talk about evolution by natural selection, but I think this is more an epistemic point than an ontological one. (see Gil & Halverson, 1984 for more on how this point has broad implication for how we understand the evolution of plants). The location of the variation of parts on which selection can act upon will not always be the same. Among sexual species the variation may be between members of the population, while as I have argued the variation in some asexual organisms will be between the parts of single organisms.

Janzen (1977) makes this point explicitly when describing what he calls Evolutionary Individuals.

Janzen uses dandelions as counter-intuitive case of biological individuality:

> "Instead of viewing the set of short-lived dandelion plants in a habitat as a many-membered population with a very high growth rate, I suggest a quite different view. I suggest that the dandelion population contains a small number of highly divided [Evolutionary Individuals] with very long lives and very low population growth rates. (...) the [Evolutionary Individual] dandelion is easily viewed as a very long-lived perennial organism. At any time, it is composed of parts that are moving around ("seeds" produced by apomixes), growing (juvenile plants), dividing into new parts (flowering plants), and dying (all ages and morphs). Natural selection could just as well have produced an organism with all these parts in physiological contact, but in view of the type of resource on which the EI dandelion

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[8] As Godfrey-Smith correctly points out in describing my view: "Note that when Bouchard claims that some of his phenomena do not involve "populations", this is because he is assuming that all populations include reproduction. So his "population" concept is narrower than mine.)" (Godfrey-Smith, 2007) He's right, and I think cases such as clonal species show the necessity for this distinction. I think populations should be restricted to reproducing entities. We don't want to equate population to any and all ensembles because it would become trivial: Populations are implicitly about interactors, and interactors are explicitly defined relative to replicators. Since I wish to show that replicators are not always the relevant causal nexus, I prefer to drop the use of populations to mark the distinction between ensembles that are populations and those that are not.

specializes, this alternative arrangement of parts is clearly optimal" (Janzen, 1977, p. 586).

Elsewhere I develop this point for a specific species, namely the Quaking aspen (see Bouchard, 2004, 2008). Let us quickly reprise a few details from this specific case. 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[9]. The meaningful fact is that a functionally integrated clonal grove often beats out the sexually reproducing aspens. I.e. The Quaking aspen does better (i.e. persists longer) by growing instead of reproducing[10]. A population of 1 clone often beats out a population of 1000 individual trees. The shape of the integrated grove changes in response to pressures from its environment, i.e. it adapts, and this change explains why it succeeds over its competition. But can we really think about this change in selectionists terms? After all, according to most standard accounts of evolution by natural selection, one needs variation among members of a group to have an eventual response to selection. I argue that there is variation in the case of the clone, but not variation among individuals in a population. The variation is amongst the parts of the individual and there is selection amongst the parts of the individual (there is competition between ramets for soil nutrients, i.e. intra-individual competition, but there is also competition between groves, i.e. inter-individual competition). The continuing growth depends on prior growth and how it was affected from pressures of the environment. The groves that survive the longest are those whose growth has better responded to the pressures from the external environment. There is selection on variation (but not necessarily variation between individuals) and response to selection (the best response overtakes the competition).

One way to dismiss this case would be to argue that the clonal phase is but a phase between sexual episodes. Growth would remain 'merely' growth and evolution would occur only during the genuine reproductive events. Two points: 1- many plants do not have access to the dual reproductive apparatus that the aspen possesses, i.e. many plants are only clonal integrators and do not produce autonomous entities. Our accounts of fitness should be able to accommodate these species. 2- In the case of the aspen, sexual reproduction doesn't not merely 'wait' for the right environmental heterogeneity (evolution is not on hold), it is actively suppressed by the asexual growth. The aspen is not waiting for its day to evolve; it is evolving via different strategies in different environmental circumstances. If

a single organism beats out its offspring via its growth for thousands of years (which is the case for the aspen), and if the capacity to persist fluctuates in response to selective pressures on the variations of its parts, it seems perverse to reject the possibility that we are faced with evolution by natural selection. This cursory description of the Quaking aspen (see Bouchard, 2008 for a detailed account) hints that it may be more helpful to put the notion of offspring/copies aside, in favor of the idea of 'parts' of a single individual, and when examining the question of parts (a population of sexual reproducing organisms could then be recast as a single system with multiple parts, i.e. multiple individual organisms), the question of how they contribute to the overall persistence of the whole system will be crucial. This erases some of the conventional chasm between growth and reproduction, but more importantly it focuses on collections of parts instead of on populations of individuals. The issue will play out differently in different biological systems. One can have selection on parts on many clonal species without endangering the survival of the whole individual; this will not be the case for mammals for example. The variation for most sexual organisms will be inter-individual and not intra-individual. But the fact remains that one can observe response to selection in many asexual organisms in part because the boundaries of biological individuals are not as fixed as for many of the sexual organisms that we are used to dealing with. Notions of individuals, reproductive success and therefore populations are murky in the cases of many clonal species (as Ariew and Lewontin reminded us with the case of the violet) but the problem is compounded in cases of microbial evolution and symbiosis evolution.

Elsewhere I argue (Bouchard, 2009) that many symbiotic associations display emergent adaptations. The symbiotic association between squid and bacteria (*Euprymna scolopes* and *Vibrio fischeri*) leads to a complex bioluminescent trait. The squid provides nutrients to the bacteria, while the bacteria provide bioluminescence in the squid's mantle. It is believed that this bioluminescence (which does not usually occur in the bacteria outside of the squid) allows the squid to avoid its predators (the squid's predator hunts by identifying its preys' shadow; a glowing squid doesn't have a shadow). In this case, part of the phenotype 'belongs' to the interaction between two species and not to one species alone (i.e. it is an emergent community trait). Since the adaptation depends *not* on the number of bacteria within the squid but on their density (via a quorum sensing mechanism), what is useful is the functional structure of the community interaction more than the numerosity of the organisms involved. The symbionts are parts of this community, and it is the selection on these parts and the response to this selection that determines whether the community (i.e. the association between squid and bacteria) thrives or not.

What is the individual or the unit evolving at any given time? As I pointed out earlier, individuality is a central problem of most biological projects—most scientific projects for that matter. The problem is often left unsolved, scientists preferring to adopt intuitive accounts of individuality often based on functional individuation as it appears in organisms. Not surprisingly, the problem is thornier that this simple approach allows.

The first problem is that, as Janzen highlighted, there is potentially an asymmetry between biological individuality and evolutionary individuality. The reason is obvious for anyone who admits a multi-level or pluralistic conception of evolution by natural selection. *If* selective pressures operate at various

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[9] Sometimes the clonal groves do split (thereby splintering into autonomous individuals), but the point remains, that in some ecological contexts, growth overtakes reproduction as a means by which response to selective pressures arises. One reason to distinguish the ontology of a fragmented clone (a 'splitter' clone) from a cohesive integrated one (permanent integrator) is that they seem to have different evolutionary fates –even though they might occupy the same surface area, have the same number of ramets and have somewhat similar selective environments. An integrated clone, by its capacity to share nutrients amongst its parts may take advantage of a less hospitable patch by virtue of its capacity to shoot out more exploratory runners and have some of them grow to maturity faster than its competitors.

[10] Again, here we follow Van Valen's insight: "It is just as good, and maybe better, for a massive coral or a tree to stay alive, occupying the same good site, as it is for it to reproduce into an uncertain world. ... Persistence is an important component of fitness" (1989, 5).

levels of organizations (genic, organismal, group, species, etc.), then the same biological individual will be part of many selection regimes acting on various levels, where the individual animal for example is not always the central unit of selection. Since groups sometimes favor group-traits that don't directly benefit any given individual member of the group, we have to assume that the units of selection do not always correspond to biological individuality[11].

I will bracket the individuation problem and use 'lineage' as my unit as common definitions of lineages are flexible enough to accommodate all the biological examples given so far. A lineage is generally understood as a descent group with a common ancestry back to a single parent. Hull defines lineage as "an entity that changes indefinitely through time as a result of replication and interaction" (Hull, 1980, p. 327). Hull's definition is given in the context of his seminal paper on levels of selection, in which he stresses that lineages can evolve: "they are the most inclusive entities that are 'actively evolving entities' to use Wiley's phrase" (Hull, 1980, p. 328). If Hull is correct, then reproduction cannot be the core of fitness increases, for lineages do not all 'really' reproduce. They may split and as such have parts (species, sub-species, populations, individual organisms, etc.) but a lineage that evolves does not necessarily 'do better' if it generates more lineages than another lineage.

Lineages are inherently genealogical (or historical) entities. They include individuals or groups across many generations. The notion of lineage is inclusive enough for our purposes since we want to be able to say that an entity may belong to various lineages depending on the time-scale one is interested in, something that is allowed by the definition of lineage. Lineages are carved up temporally, which, as we will soon see, permits us in theory to make evolutionary comparisons at any temporal scale of interest.

Another advantage of thinking temporally is that it does not put much importance on actual physiological integration (the issue raised by Janzen). Lineages are not defined in terms of spatial continuity but in terms of temporal continuity. There might not actually be evolution by natural selection on lineages on a given temporal scale (i.e. evolution at the clade level might not actually occur), but that is an empirical question not something that should be ruled by definition.

How far back in the past, how far ahead in the future, or to what degree of relatedness, branches should count as part of the same lineage *is* to a large degree interest-relative. The relevant lineages are identified on the basis of the relevant comparison of interest. The objects may well be real, but their boundaries are function in part of our research interests, or rather, as the hierarchical view pointed out with force, the same entity may be selected on directly or be selected on indirectly as a part of a larger entity that is selected on.

Intrinsic to the idea of lineage is the idea of succession. Succession need not be strictly generational, since, as I have argued, reproduction is not always necessary. Modifying Hull's definition of lineages to include cases where single clonal systems change by change within their parts, we could define lineages as *biological entities that change indefinitely through time as a result of differential persistence of their components*. When those components are offspring, we get a definition of lineage in line with Hull's definition. In non-reproducing lineages (such as a persisting Quaking aspen grove), persistence becomes a more salient aspect of fitness.

To put it briefly (see Bouchard, 2004, 2008 for details), fitness comparisons in a more inclusive account of evolution would look like this:

(Lineage) X is fitter than (lineage) Y if X has a higher propensity to persist for Z amount of time than Y.

The comparison is time relative, and allows for interspecific comparisons. The latter doesn't appear in current scientific understanding of fitness comparisons (which are solely intraspecific) but it often appears in laymen's understanding of Darwinism (many non-experts intuitively wish to compare the adaptadness of, let's say, wolves and cougars even though this type of comparison is ruled out by definition in standard accounts of evolution by natural selection). Focusing on persistence instead of reproduction allows for these comparisons.

5. Conclusion

If we can't agree on the boundaries and number of individuals for many biological systems, we cannot obtain meaningful notions of populations defined in terms of membership or otherwise. Thinking solely in genetic terms (genes of Quaking aspen, or genes of bacteria and genes of bobtail squids) may seem more helpful but the genes alone don't always track the trait we wish to account for in the first place. As is the case in many symbioses, only the ecological context can tell us whether the genotype leads to parasitic phenotypes or mutualistic phenotypes. As it has been known for a long time, carving out the number of biological individuals is very complicated in cases of symbioses. The problem will affect how we think of populations of these individuals as well.

One could have looked at many other examples (clonal evolution, microbial evolution and symbiotic research is rife with similar cases). The point is, if how to identify biological individuals remains controversial, then it's difficult to identify reproductive success and defining populations will be even more difficult to achieve. This difficulty percolates up to any attempt to describe the evolutionary trajectories of these biological systems. I suggest that bracketing the question in favor of lineages and how they persist is more fruitful.

Ariew and Lewontin conclude their examination of the 'confusion of fitness' by entertaining the possibility that resource maximisation may be the best way to understand clonal species' evolution. Such an account has been entertained by others as well, namely Van Valen, and it does seem to capture some features of evolution that cannot be captured by traditional accounts of fitness described in terms of differential reproductive success. However, I argued here that differential persistence is a more inclusive and more useful understanding of fitness. One needs collections of components (the variation on which selection can "act upon"), but not necessarily populations of autonomous units. The account provided here is woefully incomplete (see Bouchard, 2004, 2008 for the fuller explanation). My hope is that the sketch offered here shows that, in light of the diversity and complexity of the biological systems that respond to selection, there is a real necessity for a broader and more abstract understanding of Darwinism. Understanding fitness in terms of the capacity of a system to persist via the differential persistence of its components may seem to some too abstract, but, as I pointed out at the onset, there is a real biological urgency in adopting differential persistence as a definition of fitness and as a way of redefining Darwinism:

1- *Urgency for our understanding of contemporary evolution*. At least some biological organisms' evolution cannot be adequately understood if we focus exclusively on reproductive success.

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[11] For a thorough group-selection argument to explain the existence of altruism see Sober & D.S. Wilson (1998) and Okasha (2006). For good opinionated primer concerning the unit of selection debate see Sober & D.S. Wilson (1994).

2- *Urgency for our understanding of past evolution.* The fact that most of life of Earth has not been sexually reproducing and that all sexually reproducing species have evolved from asexual reproducing species behoves us to provide an exhaustive account of clonal evolution. It's not the case that all clonal species pose a problem for replication accounts, but rather that many do. There is something strange in the lack of worry about the fact that our standard accounts of evolutionary processes cannot adequately describe the evolution of most life on Earth, not just now but for most of the history of life on Earth.

3- *Urgency for our understanding of the origin of life.* It might be fruitful to examine how evolutionary theory recast in terms of persistence might be able to explain how life itself arose as the result of the evolution of physical and chemical forms into more persistent biotic forms. Many projects related to inquiry about self-organization or evolution and thermodynamics have been making similar claims, but many lack a unified account of fitness. Aside from these explanatory urgencies, there are other possible explanatory benefits in adopting a PTT framework.

4- *Urgency for our understanding of evolutionary mechanisms in general.* A related benefit might be the extension of evolutionary explanations. Evolutionary theory is primarily a theory about change in biological entities. But by focusing on persistence, previously merely analogous cases of evolution such as cultural evolution might find real traction in evolutionary theory. We might come to the conclusion that evolutionary theory can explain much more than biological processes not just in a metaphorical sense but because they are genuine evolutionary processes. It could then be said that one reason that biological systems have been the focus (so far) is merely a consequence of us focusing on reproducing entities instead of studying changing but persisting entities.

Populations are implicitly about interactors, and interactors are explicitly defined relative to how they are involved with the 'goals' of replicators, but the examples presented here do not easily fit into a replicator-based view of evolution. I have argued that reproductive success or to put it more broadly, replicative success is not a condition for evolution by natural selection and so it shouldn't be the best and only way to define fitness. But persistence (viability, survival, etc.) is always in the picture. To put this a different way, differential persistence seems to be necessary to have evolution by natural selection while differential reproductive success seems to be a contingent strategy for a lineage to survive. The irony is that this account was always in our face: Darwinism is usually understood, not as "reproduction of the fittest" but as "survival of the fittest".

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