Adaptation, Local Frequency-Dependent and Global Frequency-Independent Selection

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Abstract

There is a tension between, on the one hand, the view that natural selection produces adaptations, and on the other hand, the theoretical results showing that the links between natural selection are weakened in different evolutionary scenarios such as situations of (negative) frequency-dependent selection or more generally in situations where fitnesses are not constant. If these results are taken at face value, in the absence of alternative explanations to natural selection for adaptation, the existence of most complex biological structures will appear as mysterious. In this paper, I provide an analysis of this problem. I show that the theoretical framework establishing only weak links between natural selection and adaptation refers to what I call 'local populations.' In contrast, I argue that assessing such links should be regarded from the perspective of 'global populations', that is populations of local populations which, in some cases, can be constituted of more than one taxonomic group. When natural selection on a trait is looked at from the perspective of a global population, I show that it can be considered as frequency-independent selection, which restores a strong link between natural selection and adaptation. I show the adequacy of characterizing natural selection at that global level of description when one aims at explaining adaptations.

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1 Background

One important project in evolutionary theory is to link natural selection with adaptation, the latter of which refers both to biological structures enabling organisms to be adjusted to their environment, and the process by which this occurs. Although it is often assumed that natural selection leads to adaptation, it has long been recognized that it only does so in a set of very restricted conditions, most notably in the absence of negative frequency-dependent selection.[1] There is thus a tension between two sets of observations, namely, the observation, on the one hand, that adaptations are pervasive around us, and on the other hand, the observation that frequency-dependent selection is common in nature (Ayala and Campbell 1974; Dieckmann and Ferrière 2004; Birch 2016; Svensson and Connallon n.d.). This tension has been well articulated by Birch (2016) and Okasha (2018), who both argue that, in general, natural selection does not lead to adaptation. However, as rightly noted by Grafen, “if the links [between the mechanical processes of inheritance and reproduction, i.e., natural selection and other evolutionary processes, and the appearance of design, i.e. adaptation] are too weak, then I would say that Darwin was wrong, and this has serious implications”(2014b, p. 290). In fact, one main insight from Darwin is that natural selection can explain the

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[1] Note that I use here the term ‘frequency-dependent selection’ in a broader way than it is typically used in population genetics (Cockerham et al. 1972; Hedrick 1973). In fact, in this field ‘frequency-dependent selection’ is typically only used when referring to an *individual* or a *genotype* having a fitness value which is not constant because it depends on the frequency of the genotypes composing the population. I extend its meaning here to cases in which the fitness of an *entity at any level* (whether a gene, genotype, deme, etc.) depends on the frequency of the types composing the population at that level, such as with the cases of dominance, overdominance and underdominance presented above from the perspective of alleles. This is because conceptually these cases are isomorphic to cases of frequency-dependent selection *sensu stricto*, but from the level of the gene rather than the individual. When the fitness of a type decreases as its frequency increases in the population, frequency-dependent selection is called ‘negative frequency-dependent selection’, in contrast to positive frequency-dependent selection. Only situations of negative frequency-dependent selection challenge the view that natural selection can be linked to adaptation.

appearance of design without having to invoke a designer (Dawkins 1986). Thus, the most serious implication is that without appealing to natural selection we are left with no plausible alternative to explain design.

Aiming at tackling this problem, Grafen has, over the last twenty years, developed a framework he calls the 'formal darwinism project' (for an accessible introduction see Grafen 2014a). Within this framework, Grafen links the formalism of the Price equation (Price 1970; Frank 1998; Rice 2004; Okasha 2006) to the notion of adaptation. Grafen establishes that natural selection can be tied to adaptation via four links. When these links hold true, this, according to Grafen, permits us to regard an individual as an agent trying to maximize its fitness. However, on the whole, as argued by Okasha (2018, chap. 3), the extent to which Grafen's formal darwinism project can explain adaptation is limited, since it neither applies to frequency-dependent selection cases, nor does it satisfactorily deal with cases in which genetic constraints lead the fitness of a population to decrease.

In this paper, I start with the same motivation as Grafen and aim at bypassing some of the limitations of the formal darwinism project. I argue that, in general a link between natural selection and adaptation can be forged. The route I take to forge this link is however different from that of Grafen since it relies upon an interpretation of Fisher's fundamental theorem. I argue that although frequency-dependent selection[2] is a widespread phenomenon in nature, it mostly concerns the evolutionary dynamics of what I call 'local populations',[3] which effectively correspond to demes. I define a local pop-

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[2] Note here than in this paper I will focus on negative frequency-dependent, but much of the same analysis could be carried is situations of temporally variable environments, of which frequency-dependent selection is a subset, in which genotypes that perform very well at one point are later disfavored.

[3] 'Local' should not be understood here as synonymous with 'of small size'. A local population might be of infinite size. Note also that focus in this paper on frequency dependent selection, but the conclusion can be extented to any situation in which the fitness of an type depends on local interactions with other types.

ulation as a biological population in which the members interact with one another (e.g., interbreed) in the short term. In contrast, a global population is a population of local populations or a metapopulation where the members of two or more local populations interact over a much longer timescale, that is, the frequency for class of interactions is significantly lower. Although natural selection can be regarded as frequency-dependent within each local population of a global population, once considered from the perspective of a global population, selection can be regarded as frequency-independent (or nearly so), thereby preserving the strong link between natural selection and adaptation. In such a condition, I argue that complex adaptations, insofar as they amount to an increase in mean fitness over time, can evolve. This view of adaptations as referring to structures shared by members of a global population rather than local biological populations is in line with a classical approach to study adaptation, namely, the comparative method.

Key to my analysis is that an increase in mean fitness is a good proxy for adaptation. The concept of adaptation is often associated with the notions of optimization or maximization at the individual level, as in Grafen's formal darwinism project, not at the population level (whether local or global). This might be regarded by some as problematic. In fact, an increase in mean fitness does not account for the fact that there can be vast differences between the individuals of a population. Thus, although the mean fitness of a population might increase, the fitness of a majority of the individuals of the population might be lower than that of their ancestors. Yet, although mean fitness is imperfect at capturing individual-level adaptation (more on this in the conclusion), I will consider that it is sufficiently close to it for my purpose.[4]

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[4] Note that Okasha (2018, pp. 80-82) convincingly argues that mean fitness is a good proxy for individual entities becoming more adapted.

To make my argument, I start by motivating the problem and present the dynamics of a simple diploid population genetics model with one locus and two alleles. I show that even in this simple model, in the presence of natural selection, the change in mean fitness between two generations is not necessarily positive. I briefly discuss some of the literature arriving at the same conclusion. To approach this problem more abstractly, I then derive a version of the Price equation which contains Fisher's fundamental theorem of natural selection. This version of the Price equation highlights that what is classically understood as the transmission bias term of the Price equation, can be regarded, in part, as the evolutionary change due to indirect effects of natural selection. When this term is negative, it can prevent mean fitness from increasing between two generations. Crucially, I argue that whether this term is nonzero depends ultimately on whether the individual fitnesses of a population are invariant quantities when changes in the population occur. I then argue, following other authors, that if an individual is to be ascribed a fitness value associated with natural selection, it should be invariant to changes in the population context and, more generally, the environment. From there, I argue that in a global population made of an infinite number of local populations, fitness, when computed in this context, approaches the invariance required for it to be associated with natural selection. Finally, I respond to two possible objections to my argument.

2 Motivating the Problem

It is almost common knowledge among evolutionary biologists that in a large population, two alleles at one locus reproducing sexually and panmictically in discrete generations, and where selection acts on viability of genotypes with constant fitness, that the effect of selection on mean population fitness is either to increase it or leave unchanged over time (Wright 1937; Ewens 2004; Gavrilets 2004; Rice 2004; Okasha 2018; Walsh and Lynch 2018).

To see this, suppose that the two alleles are A and a with frequency p and $1-p$ respectively, the genotypes formed are AA, Aa, and aa with frequencies p^2, $2pq$ and $(1-p)^2$ and fitnesses w_{AA}, w_{Aa} and w_{aa} respectively. The frequency of allele A at the next generation is p'. The difference in allele frequency between the two generations Δp tells us the evolutionary effect of natural selection on the population. This difference is equal to

$$\Delta p = p' - p = p^2 \frac{w_{AA}}{\bar{w}} + p(1-p)\frac{w_{Aa}}{\bar{w}} - p, \tag{1}$$

where $\overline{w}$ is the mean fitness of the population and is defined as

$$\overline{w} = p^2 w_{AA} + 2p(1-p)w_{Aa} + (1-p)^2 w_{aa}.$$

We have:

$$\begin{aligned}\frac{d\overline{w}}{dp} &= 2pw_{AA} + 2(1-2p)w_{Aa} - 2(1-p)w_{aa} \\ &= 2(pw_{AA} + (1-2p)w_{Aa} - (1-p)w_{aa})\end{aligned}$$

Using equation (2), we can rewrite equation (1) as

$$\begin{aligned}\Delta p &= \frac{p}{\overline{w}}(pw_{AA} + (1-p)w_{Aa} - \overline{w}) \\ &= \frac{p}{\overline{w}}(pw_{AA} + (1-p)w_{Aa} - p^2 w_{AA} - 2p(1-p)w_{Aa} - (1-p)^2 w_{aa}) \\ &= \frac{p}{\overline{w}}(p(1-p)w_{AA} + (1-p)(1-2p)w_{Aa} - (1-p)^2 w_{aa}) \qquad (2) \\ &= \frac{p(1-p)}{\overline{w}}(pw_{AA} + (1-2p)w_{Aa} - (1-p)w_{aa}) \\ &= \frac{p(1-p)}{2\overline{w}}\frac{d\overline{w}}{dp}.\end{aligned}$$

This result is known as ‘Wright’s formula’ (Walsh and Lynch 2018, p. 119). It can be used to vindicate the view that natural selection is an improving process. Assuming a situation where neither of the two alleles has become fixed in the population, so that $0 < p < 1$, we know that the first term on the right-hand side of Equation (2) is always positive. The second term on the right-hand side determines the direction of change for p. Because Δp and dp have the same sign, it follows that $d\overline{w}$ is necessarily positive. The following *reductio ad absurdum* shows why. Suppose that Δp is positive (negative). Since dp is also positive (negative), having $d\overline{w}$ would mean that $\frac{d\overline{w}}{dp}$ negative (positive), which in turn would mean that Δp is also negative (positive). However, this is not possible since we started from the hypothesis that it is positive (negative).

Although Wright’s formula is an elegant way to marry the idea of natural selection with improvement, unfortunately, the conditions under which $\overline{w}$ necessarily increases over time are very restrictive: selection acts on viability only, mating is random, there are only two alleles at one locus, selection is frequency-independent since the fitness of genotypes is constant. The result has nevertheless has been generalized for more than two alleles at one locus (for a demonstration see Kingman 1961), but when any of the other assumption is relaxed, the relationship between selection and mean fitness increase does not necessarily hold anymore. Population geneticists have shown many ways in which the relationship between natural selection and mean fitness increase can be broken (e.g. Ewens 2004).

One way to show effectively how the relationship between natural selection and mean fitness increase can easily be broken is to use a different framework from population genetics, namely, evolutionary game theory (see Maynard Smith 1982; Hofbauer and Sigmund 1998). Evolutionary game theory studies the evolutionary dynamics of frequency-dependent selection situations. Within this framework, one considers the payoff in terms of fitness of a given strategy S in the particular context of a population in which there are two possible strategies—but the number of strategies can be higher—each with a given frequency. Depending on these frequencies, an individual with S might on average do better than another individual with the other strategy, and vice versa. Contrary to population genetics, the strategies are defined purely phenotypically – even though it is assumed that there is an underlying genetic basis for the phenotype – and that individuals breed true.

One of the most famous evolutionary games is the 'Hawk-Dove game' (Maynard Smith 1982, pp. 11-20). In this game, the two strategies are 'Hawk' H and 'Dove' D. Suppose a population made of two phenotypes H and D. There is some resource in the environment and each patch of resource (V) can only be contested by two individuals at a time. If a patch is contested by an H and a D, the H takes all the resources while the D flies away and gets nothing. If the patch is now contested by two Ds, they share the resources equally so that each gets $\frac{V}{2}$ units of resources. Finally, if the patch is now contested by two Hs, they fight and pay a cost C to each get an equal amount, namely $\frac{V-C}{2}$ units of resources. Assuming resources are directly transformed into offspring, in a population made purely of Hs, if the cost paid by an H is larger than the resources obtained, a D mutant will always have more offspring than an H. Conversely, in a population made only of Ds, an H will systematically reap all the resources without paying any cost, and thus have more offspring than Ds. An equilibrium will be obtained at a certain frequency for H and D (depending on the values given to V and C), known as a 'Nash equilibrium'. At that equilibrium, none of the two strategies does better than the other. It can be shown (see for instance Donovan and Welden 2002, pp. 499-508) that with certain values of V and C, when the equilibrium obtains the mean population fitness is lower than what it was initially, leading to the same conclusion that an increase in mean fitness only obtains in a set of restricted conditions.

In adaptive dynamics (Geritz et al. 1998; Dieckmann and Ferrière 2004; Brännström et al. 2013; Okasha 2018, chap. 4), which is a more recent and sophisticated approach to study frequency-dependent selection than evolutionary game theory, the environment experienced by a mutant variant in a population at any point in time is considered the resident population, which is made of a single resident morph considered at equilibrium and with a phenotype close to that of the mutant. Classical results in adaptive dynamics, like those of evolutionary game theory, show that even though 'fitter' variants might be able to invade a resident population, the overall mean fitness of the population might decrease and be stable.

When these results are taken at face value, they clearly seem to contradict the idea that natural selection can be strongly tied to adaptation when a surrogate for adaptation is taken to be mean population fitness. One might think, however, that although it is easy to break the link between natural selection and adaptation *theoretically*, most natural populations behave in way that conform with Wright's formula. If it was true, counterexamples would show that natural selection does not necessarily lead to adaptation *in principle* without invalidating the claim that it mostly does *empirically*. However, this response will not work. In fact, frequency-dependent selection, as defined here, is an umbrella terms that covers a large number of situations. Under this definition, banal situations of kin selection, where, for instance, an altruist type sees its fitness decreasing as the number of selfish individuals increase in the population, are situations of frequency-dependent situations. Furthermore, as noted by Maynard Smith (1998, p. 69) among others, regarding frequency-dependent selection *sensu stricto*: “There are good ecological reasons for thinking that frequency-dependent selection is a major cause of genetic variability. Many of the most obvious kinds of selection are likely to be frequency-dependent in their effects.” Maynard-Smith proceeds to describe four common non-exhaustive types of ecological situations in which frequency-dependent selection will typically occur, namely, disease, predation, resource utilization, and behavior variability. In light of these two responses, it seems that relegating the situation in which natural selection does not produce a mean fitness increase to rare phenomena will not do to save the link between natural selection and adaptation. In consequence, another strategy must be deployed.

3 Fisher’s Fundamental Theorem

The exact problem discussed in the previous section, namely, that selection is generally not an improving process, has been at the heart of the controversy surrounding the so-called Fisher’s fundamental theorem of natural selection. Fisher wrote a formulation of the theorem as “[t]he rate of increase in fitness of any organism [i.e., the mean fitness of the population] at any time is equal to its genetic variance in fitness at that time” (Fisher 1930, p.35). This formulation puzzled evolutionary theorists for more than 40 years, as it seems to be contradicted by even simple cases of frequency-dependent selection of the type shown in the previous section, until Price (1972b) gave an interpretation of the theorem, itself later clarified by others (Ewens 1989, see Edwards 1994; Plutynski 2006; Okasha 2008).

Following the ‘modern’ interpretation, fitness is here considered in the same frame of reference (Frank and Slatkin 1992), that is, the same environment at all times. By considering the effect of natural selection on mean fitness *while keeping the environment constant*, the theorem shows that natural selection increases mean fitness. However, there is a catch. We saw that in case of frequency-dependent selection, the environment experienced by an individual changes as a result of the change in frequency of individuals in the population. Since this change can be due to natural selection occurring at an earlier point in time, then the 'indirect effect' of natural selection, part of which corresponds to what Fisher (1930, pp. 41-42) called the 'deterioration of the environment', might be opposite to its direct effect. As a result, in spite of a positive direct effect of natural selection on mean fitness, the overall effect might be nil or negative. For that reason, there is no guarantee that when both direct and indirect effects of natural selection are taken into consideration, the overall outcome will result in a mean fitness increase, and consequently that natural selection can be tied to adaptation via mean fitness.

Although the modern interpretation illuminates in what sense the mean fitness of a population increases, it does not permit to vindicate the link between natural selection and adaptation which is classically assumed in modern textbooks. Yet, it is precisely this link that is invoked by evolutionary biologists to explain adaptation. Fisher's fundamental theorem confirms from a very abstract perspective, the conclusions reached in the previous section about the tension between, on the one hand, the view that natural selection leads to adaptation, and on the other hand, the view that this will only be attainable when natural selection is frequency independent. Although the predictive power of abstract descriptions of evolutionary concepts is limited for any given real system, their virtue lies in their explanatory and unificatory power. Such an approach has recently been used in different but related contexts (e.g., Queller 2017; Lehtonen 2018; Lion 2018). In Section 5, I will attempt to alleviate this tension. However, before doing so, I need to formalize the problem posed by the deterioration of the environment so that the solution I will present is not misunderstood.

To start with, recall that Fisher's fundamental theorem, in its modern interpretation, concerns only the *direct* change due to natural selection, while the tension originates from the possible indirect effects of natural selection. Thus, to understand the relationship between these two types of effects, one needs to approach the theorem in the wider context of total evolutionary change. The Price equation (Price 1970; Price 1972a; Frank 1998; Rice 2004; Okasha 2006), permits such an approach. This equation is a mathematical identity (i.e., true by definition) that describes the mean total evolutionary change of a character z between two times. Roughly following Frank (1998), I provide below a version of Fisher's fundamental theorem in a time-discrete setting (synchronous discrete generations).[5]

We start by defining the average value of character z in the population $\overline{z}$ as:

$$\Delta\overline{z} = \overline{z'} - \overline{z}, \tag{3}$$

where $\overline{z}$ and $\overline{z'}$ are the mean values of z at generations θ and $\theta{+}1$ respectively, and $\overline{z} = \sum_{i=1}^{n} z_i$ and $\overline{z'} = \frac{1}{n}\sum_{1=i}^{n} \omega_i(z_i + \Delta z_i)$. z_i is the character of the i-th individual in the population of n entities at the generation t, Δz_i is the average deviation of the offspring character from the value of the character of i, and ω_i is the relative fitness of the i-th individual and is defined as $\omega_i = \frac{w_i}{\overline{w}}$, where w_i is the absolute fitness of i and $\overline{w}$ is the average absolute fitness of the population.

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[5] Fisher's original version of the theorem is proposed in a time-continuous setting.

Replacing these terms with their definitions in Equation (3), we get:

$$\Delta\overline{z} = \frac{1}{n}\sum_{i=1}^{n}\omega_i(z_i + \Delta z_i) - \frac{1}{n}\sum_{i=1}^{n} z_i, \tag{4}$$

which once developed leads to:

$$\Delta\overline{z} = \frac{1}{n}\sum_{i=1}^{n}\omega_i z_i - \frac{1}{n}\sum_{i=1}^{n} z_i + \frac{1}{n}\sum_{i=1}^{n}\omega_i\Delta z_i. \tag{5}$$

As I show below, the first and second term of the right-hand side of Equation (5) satisfy the definition of a covariance as $\mathrm{Cov}(X, Y) = \mathrm{E}(XY) - \mathrm{E}(X)\,\mathrm{E}(Y)$, where $\mathrm{E}(X)$, the expectation of X and is defined as $\mathrm{E}(X) = \frac{1}{n}\sum_{1=i}^{n} X_i$. The third term on the right-hand side of Equation (5) is the expectation of the quantity $\omega\Delta z$. Noticing furthermore that $\mathrm{E}(\omega_i) = 1$ and thus that it can added as the product of any term, we can rewrite Equation (5) as:

$$\Delta\overline{z} = \frac{1}{n}\sum_{i=1}^{n}\omega_i z_i - \frac{1}{n}\sum_{i=1}^{n} z_i\frac{1}{n}\sum_{i=1}^{n}\omega_i + \frac{1}{n}\sum_{i=1}^{n}\omega_i\Delta z_i, \tag{6}$$

which is equal to:

$$\Delta\overline{z} = \mathrm{Cov}(\omega_i, z_i) + \mathrm{E}(\omega_i\Delta z_i). \tag{7}$$

Equation (7) is one of the classical forms of the Price equation. The first term on the right-hand side is classically interpreted as the change in z due to natural selection, while the second term is the transmission bias term and corresponds to all other causes of change.

Starting from Equation (7), following Frank (1998, p. 21), one can derive a version of the Price equation that contains Fisher's fundamental theorem in which both the direct and indirect effects of natural selection (i.e., the deterioration of the environment) are present, by considering z to be relative fitness itself, i.e. ω.[6] We replace z by ω in Equation (7), we thus have:

$$\Delta\overline{\omega} = \mathrm{Cov}(\omega_i, \omega_i) + \mathrm{E}(\omega_i \Delta\omega_i). \tag{8}$$

Since a covariance of a variable with itself is the variance of this variable, we have:

$$\Delta\overline{\omega} = \mathrm{Var}(\omega_i) + \mathrm{E}(\omega_i \Delta\omega_i) \tag{9}$$

We define the relative fitness of an individual i as:

$$\omega_i = b_i + \delta_i, \tag{10}$$

where b_i is the breeding value of individual i for relative fitness and δ_i is the residual. The breeding value is defined as:

$$b_i = \sum_{j}^{k} \beta_j x_{ij} \tag{11}$$

which is the multiple linear regression predicting ω, where the independent variable x_{ij} represents the number of alleles of type j in individual i and β_j the partial regression coefficient of ω on x_{ij}. *Mutatis mutandis*, for the $\theta + 1$ generation we define :

$$\begin{aligned} \omega'_i &= b'_i + \delta'_i \\ &= b_i + \Delta b_i + \delta_i + \Delta\delta_i, \end{aligned} \tag{12}$$

where i' is an offsrping of i. Thus, we have:

$$\Delta\omega_i = \Delta b_i + \Delta\delta_i. \tag{13}$$

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[6] Note that Frank derives this equation from a version of the Price equation in which *absolute* rather than *relative* fitness is used. Besides this difference, the equation is similar.

With this in place, we can replace the terms of Equation (9) with the definitions provided in equations (10) and (13). We get:

$$\begin{aligned}\Delta\overline{\omega} = \Delta\bar{b} &= \mathrm{Var}(\omega_i) + \mathrm{E}(\omega_i \Delta\omega_i)\\ &= \mathrm{Var}(b_i + \delta_i) + \mathrm{E}((b_i + \delta_i)(\Delta b_i + \Delta\delta_i))\\ &= \mathrm{Var}(b_i) + Var(\delta_i) + \mathrm{E}((b_i \Delta b_i) + (b_i \Delta\delta_i) + (\delta_i \Delta b_i) + (\delta_i \Delta\delta_i))\\ &= \mathrm{Var}(b_i) + Var(\delta_i) + \mathrm{E}(b_i \Delta b_i) + \mathrm{E}(b_i \Delta\delta_i) + \mathrm{E}(\delta_i \Delta b_i) + \mathrm{E}(\delta_i \Delta\delta_i).\end{aligned} \tag{14}$$

Since for two independent variables we have $\mathrm{E}(XY) = \mathrm{E}(X)\,\mathrm{E}(Y)$, and by definition b and δ are independent, we can rewrite this equation as:

$$\begin{aligned}\Delta\overline{\omega} = &\mathrm{Var}(b_i) + Var(\delta_i) + \mathrm{E}(b_i \Delta b_i) + \mathrm{E}(b_i \Delta\delta_i) + \mathrm{E}(\delta_i)\,\mathrm{E}(\Delta b_i)\\ &+ \mathrm{E}(\delta_i)\,\mathrm{E}(\Delta\delta_i)\end{aligned} \tag{15}$$

Since we also have by definition $\mathrm{E}(\delta_i) = 0$, this equation simplifies:

$$\Delta\overline{\omega} = \mathrm{Var}(b_i) + Var(\delta_i) + \mathrm{E}(b_i \Delta b_i) + \mathrm{E}(b_i \Delta\delta_i) \tag{16}$$

Furthermore, since we have $\mathrm{E}(XY) = \mathrm{Cov}(X, Y) + \mathrm{E}(X)\,\mathrm{E}(Y)$ we can rewrite this equation as:

$$\begin{aligned}\Delta\overline{\omega} = &\mathrm{Var}(b_i) + Var(\delta_i) + \mathrm{Cov}(b_i, \Delta b_i) + \mathrm{E}(b_i)\,\mathrm{E}(\Delta b_i)\\ &+ \mathrm{Cov}(b_i, \Delta\delta_i) + \mathrm{E}(b_i)\,\mathrm{E}(\Delta\delta_i)\end{aligned} \tag{17}$$

Finally, assuming there is no covariance between the parental breeding values and the average deviation of their offspring's breeding values ($\mathrm{Cov}(b_i, \Delta b_i) = 0$), no covariance between the parental breeding values and the average deviation of the offspring residuals from the parental residuals

($\mathrm{Cov}(b_i, \Delta\delta_i) = 0$), and that the expected value of the average deviation of offspring residuals from parental residuals is nil ($\mathrm{E}(\Delta\delta_i) = 0$) (which are all reasonable assumptions since there are no particular biological reasons why any of them would be different from 0), and since by definition $\mathrm{E}(b_i) = \mathrm{E}(\omega_i) = 1$, i.e. expected breeding value of an individual equals expected relative fitness of this individual equals one this equation simplifies into:

$$\Delta\overline{\omega} = \mathrm{Var}(b_i) + \mathrm{Var}(\delta_i) + \mathrm{E}(\Delta b_i). \tag{18}$$

If we furthermore assume that $\mathrm{Var}(b_i) \gg \mathrm{Var}(\delta_i)$, so that the variance in residuals can be neglected or that the breeding values predict perfectly the fitness of an individual ($\mathrm{Var}(\delta_i) = 0$), then we get:

$$\Delta\overline{\omega} = \underbrace{\mathrm{Var}(b_i)}_{\substack{\Delta\overline{\omega}_{ns} \\ \text{Direct change due to natural selection}}} + \overbrace{\mathrm{E}(\Delta b_i)}^{\substack{\text{Change due to the environement} \\ \text{(including indirect effects of natural selection)} \\ \Delta\overline{\omega}_e}}. \tag{19}$$

The first term on the right-hand side of Equation (19) represents the partial change in mean fitness due to the direct effect of natural selection and is equal to the variance in breeding value or additive genetic value. It represents the evolutionary change due to natural selection, keeping everything else constant, and is the term referring to Fisher's fundamental theorem in its modern interpretation. Since a variance is always positive, this term is always positive. Thus, it vindicates Fisher's view that natural selection always increases mean fitness. The second term on the right-hand side represents the change in mean fitness due to changes in b over time. For any given individual, whether b changes between two generations will depend on the influence of many factors – the deterioration of the environment following

Fisher – including but not restricted to the indirect effects of natural selection, as well as the effects of the abiotic environment, drift or mutations.

The reformulation of the theorem in the context of total evolutionary change using the Price equation shows that in any population in which the inequality $\mathrm{Var}(b_i)+\mathrm{E}(\Delta b_i) < 0$ is satisfied, the population fitness mean might decrease. Thus whether mean fitness decreases between two generations depends on whether $\mathrm{E}(\Delta b_i)$ is negative and its absolute value superior to that of $\mathrm{Var}(b_i)$. For this to occur, the breeding value b of at least some individuals must be variable. If $\mathrm{E}(b)$ is an invariant quantity, then by definition, so long as there is some variation in breeding values between the individuals of a population, then the mean fitness of the population will increase.

What the formalization of Fisher's fundamental theorem contextualized in the Price equation shows, is that the link between natural selection and increase in mean fitness (and ultimately adaptation) hinges on whether, in the general case, the breeding value, which is used to compute the additive genetic variance, is an invariant quantity. This represents a generalization of the different cases seen in the previous section. If b does not vary, then by definition the second term is nil and the mean fitness of a population will increase over time. If on the other hand, it is not invariant, and more particularly if it decreases over time, for instance, because the environment is deteriorating due to the *indirect* effects of natural selection, then the link between natural selection and adaptation will be compromised.

To derive Equation (19), we have put no restrictions on the variability of b. Similarly, in evolutionary game theory and adaptive dynamics, the fitness of a variant is allowed to vary. In the next section, I argue that allowing fitness to vary can be a problematic assumption with respect to the theorization of natural selection and consequently the links between natural selection and adaptation.

4 Additivity, Fitness and Natural Selection

The idea that the breeding value or fitness of an individual can be a variable quantity will seem quite counterintuitive to many. In fact, the notion of 'additive contribution', upon which the notion of breeding value rests, elicits the idea of a contribution that is independent from the contribution(s) from any other factor. Following this view, the breeding value of an individual is just the contribution to the reproductive output of this individual, independently from any other factor.

Yet, this latter notion of additivity is not the one corresponding to the notion of additivity used in regression analysis, which underlies the conceptual apparatus of quantitative genetics and the determination of b. As aptly noted by Frank (1998, p. 19), the method of least squares used in regression analysis "makes additive the contribution of each factor [...]. But a factor [...] may be created by any functional combination of the individual predictors." Consequently, this means that, in regression analyses, an additive contribution resulting from a particular set of functional interactions between two or more factors in a given context, say the population at the parental generation, measured by the breeding value of an individual, might change or disappear in a different context, say the population at the offspring generation, because the frequencies of the different types, the size of the population and/or the abiotic environment have changed between the two generations. In sum, the notion of independence associated with regression analysis is not a functional one but a statistical one.

The sensitivity to the context of the statistical notion of additivity – that is, additivity in the context of regression analysis – has one important implication I want to highlight, namely, that the same individual in a population of a given size, a given mean and given phenotypic variance might contribute an amount of additive genetic variance which is different from the one it would contribute in a different population of same size, same mean and same phenotypic variance.[7] It follows from this remark that it cannot be concluded that substituting an individual with the same genotype by means of an ideal intervention, following the interventionist account of causation (Woodward 2003; Pearl 2009), by a different individual of a different genotype in two populations of the same size with the the same genetic additive and same phenotypic variance will necessarily lead to the same difference (if any) in additive genetic variance in these two populations – changes in phenotypic variance will however be the same.

This implication is important in the context of the fundamental theorem of natural selection. In fact, as mentioned in the previous section, the additive contribution to fitness of an individual, in the context of regression analysis corresponds to its breeding value. Recall that following the linear regression model of Equation (10), we defined the fitness of an individual as a function of its breeding value, that is, as a function of the additive contribution of its alleles in the population. Yet, if the breeding value of an individual is not an invariant quantity and so can easily change over time and space, this makes fitness itself a variable quantity, which leads to some conceptual difficulties with respect to natural selection.[8]

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[7] It also follows that in two populations of different sizes with the same phenotypic and additive genetic means and variances, the difference made on additive genetic variance by the same intervention on phenotypic variance (increasing or decreasing by the same amount the variance) might be different in the two populations.

[8] As a side note, similar considerations on the notion of additive genetic effect led Fisher to distinguish between what he calls the 'average excess' and 'average effect' of an allele substitution (Fisher 1941), the former of which corresponds to effect of the substitution of an allele in the context of a given population, while the latter corresponds to the effect of the substitution in a larger range of population parameters (e.g., different frequencies of alleles). For more on the distinction between average effect and average excess see

To see that, notice that the idea that fitness is a variable quantity goes against the view that the fitness of an organism can be given independently from the context in which this individual is found. This is, for instance, how Ramsey (2006) conceives of individual fitness, which he defines as an infinite long run measure of the weighted average number of descendants produced by this individual. The weighted average refers to all the possible environments (which include both biotic and abiotic factors) an individual might experience, with consequences on the number of its progeny (see also Abrams 2009).[9] The facts that Ramsey defines fitness as an infinite long run measure, and over all possible environments, are not superfluous aspects of his approach. Rather, they enable him to escape some problems that notions of fitness as a variable quantity all fall into prey, most notably that they do not permit to assess the extent to which a given reproductive output should be associated to drift or other evolutionary processes different from natural selection, rather than to natural selection. As pointed out by Ramsey (2006), making this distinction has been an important motivation to develop the initial propensity interpretation of fitness (Brandon 1978; Mills and Beatty 1979; Rosenberg 1982).

And in fact, one cannot easily do away with a context-dependent notion of fitness, for it would imply that by merely changing the context in which an individual is found, its fitness might instantly change as the environment changes. What is more, different choices of descriptions made by the observer

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Falconer (1985), Plutynski (2006), and Lee and Chow (2013).

[9] For another view that fitness needs to be invariant to be associated with natural selection, see Godfrey-Smith (2009, p. 53) who links fitness and natural selection to intrinsic features of objects forming populations, where he defines intrinsic features as "those that do not depend on the existence and arrangement of other objects." Bourrat (2015a) and Bourrat (2017) develop Godfrey-Smith's view and show, that to be linked to natural selection, the properties of the members of a population should not only be intrinsic but also be invariables. For a formalization of Ramsey's proposal, see Pence and Ramsey (2013).

(i.e., what are the boundaries of a particular population, at which timescales are the fitness measures done, etc.) could equally make an individual change its fitness. Similarly, identical individuals might be considered as having different fitnesses because they belong to different populations. Disposing of the project of providing a general definition of fitness thus comes with a high price, namely, the price of the link between fitness and natural selection being, in the general case, not established. This problem propagates to the link between natural selection and adaptation.[10]

Coming back to the regression analysis used in Equation (19), it seems thus that considering b as the notion of fitness which ought to associated with natural selection *when it can vary between generations* is in tension with the desiderata that this latter notion is an invariant quantity. If fitness is an invariant quantity, then breeding values only correspond to the concept of fitness which ought to be associated with natural selection, and only when they refer to invariant quantities. If such is the case, then we should consider the link between natural selection only when the second term of Equation (19) is nil.

Thus far, we saw that the different approaches to evolutionary dynamics in frequency-dependent selection situations have a variable notion of fitness (which is the equivalent of a variable b such that $\Delta b_i \neq 0$ in Equation (19)). Unless b cannot be defined invariantly (or nearly so), the notion of mean fitness used to vindicate the claim that natural selection does not lead to adaptation presented in Section 2 does not rest upon an adequate conception of fitness. To be in a position to make such a claim, in the next two sections, I argue that there is a perspective permitting us to define fitness as an invariant quantity.

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[10] For in-depth defenses of the view that fitness needs to refer to invariant properties see Ramsey (2006), Bourrat (2015a), and Bourrat (2017).

5 Natural selection and adaptation: local and global populations

In Section 3, we saw that following Equation (19), the mean change in fitness in a population can be expressed as the sum of two terms, namely, one which is the variance in breeding values ($\Delta\overline{\omega}_{ns}$), and the other which is the expected value of the change in breeding values between two generations ($\Delta\overline{\omega}_{e}$). We also established that if the second term is negative and higher in magnitude than the first, then the mean fitness between the two generations will decrease. If the second term is negative and of higher magnitude because of some indirect effect of natural selection (e.g., change in the proportion of different alleles in the population, change in ecological conditions, etc.), then the link between natural selection and fitness (as a proxy for adaptation) cannot be forged.

In Section 2, we saw that frequency-dependent selection is a widespread phenomenon. We also saw that one important motivation underlying evolutionary game theory and adaptive dynamics (two general approaches to study evolutionary dynamics), is to account for frequency-dependent selection. Finally, in Section 4, we saw that the notion of additivity used when referring to breeding values in a regression analysis is a statistical notion that does not necessarily refer to an invariant quantity, so that one and the same individual placed in a population with the same phenotypic mean and variance could have a very different additive genetic contribution because the functional interactions between the different alleles of these two populations are different. I then argued, following others, that if fitness – through breeding values – is not an invariant quantity, then one would have to conclude that fitness cannot be ascribed to entities independently of a particular context.

To solve this problem, breeding values need to refer to invariant quantities – or at least nearly so – so that a fitness value can be ascribed to a given individual independently from its context and its level of adaptation compared with other entities. To be clear, being independent from the environmental context *does not* mean independent from *any environment*. An organism's fitness is always defined in reference to an environment. Yet, to be defined generally, variation of the environment should not affect the fitness of the organism. In this Section, I show that there is one way to define the breeding values as nearly invariant quantities. In doing so, I resolve the tension between the view, on the one hand, that natural selection produces adaptations, and on the other hand, the view that the indirect effect of natural selection could easily counteract its direct effect, with the result that, overall, the entities of a population fail to adapt.

To make my case, consider a situation of a 'global' population made of an infinite number of 'local' populations, each of which is made of an infinite number of individuals. Assume that there is restricted gene flow between local populations,[11] so that each local population can be regarded as a deme. The global population setting is presented in Figure 1. Switching from a local to a global perspective has an important consequence for calculating the breeding value of an individual.[12] Computing the breeding value of an individual in such a setting will typically lead to a different value than when it is computed in a local population if selection in the local populations is frequency-dependent – I assume here that the local environmental (biotic and abiotic) conditions are different in different local populations. This is because

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[11] Potentially the individuals of different populations could belong to different taxonomic groups.

[12] for a review of the standardization of fitness when making comparisons between groups see De Lisle and Svensson (2017).

each allele of a given type will be found in a larger range of environmental conditions than if considered only from a local perspective.

To see why, one needs to note that in a local population the additive genetic effect and consequently the breeding values of individuals are computed when only part of the environment is considered. In fact, each of the alleles of a local population experiences the same allelic environment following our assumptions.[13] Thus, when computing the additive genetic values of the entities by regression analyses, only one allelic environment is taken into consideration in such analyses. Assuming there are interactions between individuals – which is necessarily the case in situations of frequency-dependent selection – this value would have been different had the allelic environment been different. Switching from a local to a global perspective permits us to consider the average difference made by an allele *when its allelic environment varies*. In fact, in a global population of infinite size made of an infinite number of local populations, each allele of a given type will be found in all possible combinations of allelic environments, and the average affect of an allele will be the invariant value. Any deviation from this invariant quantity will be attributable to the particle genetic composition of the local population, that is, interactions occurring between individuals. Another way to see this phenomenon is that local populations are like large individuals composed of a number of alleles which is twice the number of lower-level individuals in a local population, assuming here we are dealing with diploid lower-level individuals. Interactions occur between individuals within a local population and have effects on the fitness of local populations, in the same way that the allele of a diploid organism can have effects on its fitness.

Furthermore, because there are restricted gene flows between local pop-

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[13] Minus the effect of the focal allele, but in an infinitely large population this becomes negligible.

ulations, this implies that the interactions between individuals of two local populations occur at a different rate than they do between individuals within a population. One can suppose that the timescale (T) over which fitness interactions of a given magnitude occur between members of two local populations is much larger than the timescale (t) (with $T \gg t$) over which interactions of the same magnitude occur between two individuals of a local population. This assumption can be justified on the basis, for instance, that two individuals are less likely to interact – directly or indirectly – with one another if they live far apart from each other. As a result, when studying the evolutionary dynamics of the global population over a timescale close to t, the fitness interaction between members of two local populations can be considered as negligible, and consequently selection regarded as frequency independent at the global level.

Thus, by switching from a local to a global perspective, the problem posed by frequency-dependent selection, which leads b to vary between generations, is largely eliminated. In fact, for any individual i, we can now define its fitness as

$$\Omega_i = B_i + \Delta_i, \tag{20}$$

where the capital letters denote that the values are defined in a global rather than local population. We can then plug Equation (20) into Equation (9), which, following the same assumption as in the previous section with the local population, becomes:

$$\Delta\overline{\Omega} = \mathrm{Var}(B_i) + \mathrm{E}(\Delta B_i). \tag{21}$$

Assuming that the main reason why $\mathrm{E}(\Delta B_i)$ changes between generations is that the frequency of different alleles of the population changes due to

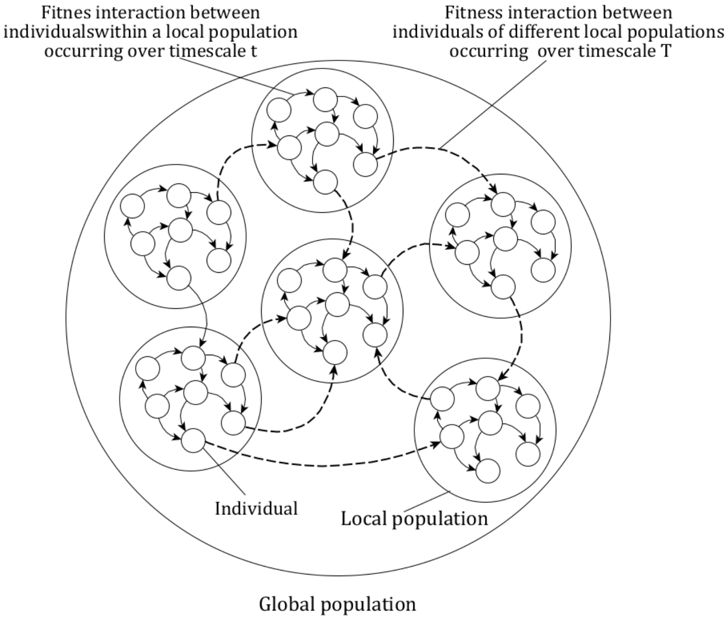

Figure 1: Schematic representation of a global population composed of local populations made of individuals. Fitness interactions (solid arrows) occur between individuals of a local population at a timescale t. Fitness interactions of the same magnitude occur between local populations (more particularly members of two local populations) at a timescale T much larger than t. Because of this difference in timescales, over which interactions of a given magnitude occur, frequency-dependent selection processes within local populations will result in a global nearly frequency-independent selection process, since b, when computed globally as opposed to locally, is nearly invariant over periods of time in the vicinity of t.

the indirect effect of natural selection, this term becomes nil or nearly so, leading to:

$$\Delta\overline{\Omega} = \mathrm{Var}(B_i), \tag{22}$$

which can be interpreted, following our assumption that an increase in mean fitness is equivalent to a process of adaptation occurring as vindicating the link between natural selection and adaptation.

Having presented a theoretical solution to the problem of forging the link between natural selection and adaptation, this does not mean, however, that this solution is supported empirically. In the next section, I respond to two possible objections one might have in response to the move from a local to a global perspective, that I made in this section, which deals with the problem of empirical adequacy. However, before proceeding, I should note that Svensson and Connallon (n.d.) have recently discussed the implication of frequency-dependent selection in relation to some biological problems such as maladaptation, biological conservation, and evolutionary rescue. Worthy of note is that Svensson and Connallon (n.d.) shows, using a quantitative genetic model, that mean fitness can generally increase when, together with negative frequency-dependent selection, there is also a process of directional frequency-independent selection due to abiotic factors (see also Svensson 2017). This conclusion might be recast in terms of invariant (or less variant) fitness values in the population in spite of variation in reproductive output due to frequency-dependent effects.

6 Response to Objections

6.1 A global population is not the type of population in which adaptation occurs

Perhaps the strongest objection one might have against switching from a local to a global population perspective, as a solution to the problem of forging a link between natural selection and adaptation, is to say that evolution occurs in local populations rather than in a global one. My response to this objection is that forging the link between natural selection and adaptation is a project that concerns, in many cases, the evolutionary dynamics of a global population, not the evolutionary fate of local populations. In fact, taking any of the classical structures referred to as ‘adaptation’ being the result of the process of natural selection, they typically refer to structures found across taxonomic groups, which furthermore often do not interbreed.

One very clear example of this might be the lens eye, which is considered an adaptation in many taxonomic groups. One might imagine a situation in which some local population being able to better see, thanks to some rudimentary eye, has some detrimental effects on the mean population fitness over time. Yet, when considered over whole taxonomic groups, individuals able to see in a large range of conditions will generally have an evolutionary advantage. Thus, the global perspective is the one relevant to forge the link between natural selection and adaptation in this situation.

However, perhaps the case of butterfly Batesian mimicry will make a better case in point, since it might be argued that in the case of the eye, selection will most typically be frequency-independent in local populations. Batesian mimicry is classically regarded as a good example of negative frequency-dependent selection. It is initially advantageous for some palatable species (mimics) to resemble species that are unpalatable or poisonous (the models). In fact, a predator preying once on an unpalatable individual will quickly learn not to prey anymore on individuals with the same phenotype. Yet, as the frequency of mimics increases, the advantage conferred by their phenotype decreases, since naive predators preying by chance on the phenotype exhibited by both the mimic and the model are less likely to receive the deleterious effect since a larger frequency of prey are palatable mimics. Examples of Batesian mimicry can be found in Futuyma (2005, pp. 445–446) and Ruxton et al. (2019, chap. 10, which provides a synthesis of what is known about batesian mimicry to date).

Although Batesian mimicry is a classical case of frequency-dependent selection, there is, from the perspective of a global population comprising of multiple species in the right ecological conditions, an advantage of being a species producing some morphs which are able to mimic models. And in fact, all other things being equal, individuals of a given species being (better) able to mimic rather than not (or able to mimic less well) will have a higher fitness. Even though the deterioration of the environment in many local populations when looked at independently (with Equation (19)) might seem as if there is no constant increase in mean fitness, when looking at things from a global perspective (with Equation (22)), there certainly is. The claim that mimicry is an adaptation—an antipredator adaptation—which one can easily find in the literature (Ruxton et al. 2019, pp. 152-153), does not refer to any particular local population, but is rather a claim that, everything being equal, it is better to be able to mimic rather than not. Moving from local to global populations and performing a global regression analysis, can be seen as performing—although imperfectly—an intervention on an independent variable While holding everything else constant within the interventionist account (Woodward 2003; Pearl 2009; Woodward 2010). This is because at least some of the correlated variables within a local population will appear as uncorrelated in a global population.

This remark leads to the last point I want to make. Harvey and Pagel (1991) write: “If we compare snowy owls with tawny owls and polar bears with brown bears, we note that the different species often match the colour of their habitats. This leads to the reasonable conjecture that natural selection against being conspicuous has produced the colour differences”. Harvey and Purvis present here a classical way of reasoning about adaptations known as the ‘comparative method’. The comparative method ultimately relies on comparing a single phenotype among different taxonomic groups.[14] Because

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[14] This example, presented by Harvey and Purvis, is oversimplified. In fact, recent methods relying on phylogenies and hypotheses about the rate of evolution permit to estimate whether a phenotype observed in different taxonomic groups is due to natural selection, or, for instance, a recent shared ancestry (Harvey and Pagel 1991; Harvey and

this approach relies on comparing phenotypes between different taxonomic groups, the distinction between local and global populations I made is in tune with this classical approach to the study of adaptation.

One further advantage of the comparative method is that it permits us to evaluate whether some structures lacking variation in a local population (because they have been fixed in the populations or variation is so rare that it cannot be detected) are nevertheless adaptations. The recognition that structures shared between different taxonomic groups can be clear cases of adaptation gives more weight to the claim that if natural selection can be linked to adaptation, fitness should be regarded as an invariant property.

Before going further, it should be noted that the term 'adaptation' needs not refer solely to global adaptation. In fact, local adaptations, which depend on the particular environmental conditions of a population have been studied in many taxonomic groups (for a review see Kawecki and Ebert 2004). Yet, local adaptations only refer to units for which there is frequency-independent selection at the level of the local population. Kawecki and Ebert (2004, p. 1136) write that "[i]n general, frequency dependent selection will tend to obscure local adaptation (if it favors rare genotypes), or to create an appearance of one (if it discriminates against rare genotypes)". This means that local adaptations will occur when the breeding values of individuals in the local population are invariant between generations at the local level or variables over timescales that are much larger than the timescale at which the environment changes. Said more precisely, appeal to local adaptation will only occur when the deterioration of the local environment is much lower than the direct effects of selection or going in the same direction. In all other situations, there will not be any scope to invoke adaptation.[15]

Purvis 1991; Martins 2000).

[15] One important point to note is that what is regarded as a local adaptation, might

6.2 The deterioration of the environment occurs whether one refers to local or global population

The second objection against my proposal is that changing the scale of application of Equation (19) does not ultimately solve the problem of the environment deteriorating. Whether considered locally or globally, the environment being finite, it always deteriorates.

My response to this objection is that it does not take into consideration the importance of evolutionary novelty that has occurred since life emerged on Earth. The amount of energy available on Earth at any point in time is finite and roughly constant. This certainly means that *ultimately* even the mean fitness of a global population comprising all of life on Earth always oscillates around zero. This is actually one reason that led Fisher to claim that the environment must always deteriorate, otherwise the mean population fitness would increase indefinitely. This is also the main argument that led Van Valen to propose the red queen hypothesis (see Van Valen 1976). Yet, although the logic of this argument makes sense, it does not take into consideration that the energy received on Earth can be transformed into biomass with different levels of efficiencies. Assuming that, on the whole, organisms over evolutionary time become better at converting energy into biomass (think, for instance, about the invention of photosynthesis), and that the maximal possible efficiency is still nowadays far from having been reached, then some scope for adaptation exists. Evolutionary innovations such as photosynthesis or respiration, permitted the use of energy in a way

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globally be regarded as a global maladaptation if adaptation is measured over a larger timescale. This remark leads us to species selection territory (see, Jablonski 2008), in which the fitness of a phenotype when looked at at the individual level or short term, such as asexual reproduction, can provide a (spatiotemporal) local advantage that one might consider as a local adaptation, while from a (spatiotemporal) global or clade perspective, there clearly is a long-term advantage for a different phenotype, such as sexual reproduction (Bourrat 2015b).

that was not possible before they occurred. All that is required for adaptation to occur on a global scale is that new ways to utilize energy or more efficient ways to convert it into biomass emerge at a rate that outpaces the deterioration of the environment. Felsenstein (1978) provides a simple macroevolution model vindicating this point. As summarized by Pennell and O'Connor (2017, p. ii): "[m]ost remarkable is that [Felsentein's] model suggests the possibility that the total energy content of an ecosystem may be generally predicted by adaptive evolution of energetic efficiencies."

7 Conclusion

There has been a long-standing view that the link between natural selection and adaptation does not come out of standard evolutionary theory. In this paper, I have shown, focusing on frequency-dependence as a specific case, but this analysis applies to other cases, that if one takes a global perspective on evolutionary dynamics, this worry does not have as much as a grip as it seems. There is no reason to consider adaptation solely from the perspective of a local context. If the process of natural selection is ubiquitous, and the structures we regard as in need of evolutionary explanation are displayed in taxonomic groups above the level of the biological population, then it is at that level of description that they should be assessed. Using a model that refers to the wrong target system (i.e., the local population instead of the global population) will simply not yield an appropriate answer to the question being asked.

Having said that, using a notion of fitness that refers to the global population (i.e., extremely invariant) comes at the cost of being unable to predict the evolutionary dynamics of a local population since this invariant quantity is generally unknown. The trade-off between generality and precision is a well-known one in the philosophy of modeling (Levins 1966; Matthewson and Weisberg 2009). Studying evolutionary dynamics over the short term is very valuable, and the advances of evolutionary game theory and adaptive dynamics have clearly been major breakthroughs in the evolutionary biology of the last 40 years. However, the precision obtained from these modeling approaches does not permit us to make general claims about adaptation, which require more abstract descriptions.

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