Darwin's empirical claim and the janiform character of fitness proxies

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Ulrich Krohs

Department of Philosophy, Westfälische Wilhelms-Universität Münster
Domplatz 23, 48143 Münster, Germany
ulrich.krohs@uni-muenster.de
ORCiD: 0000-0002-5524-9626

Abstract

Darwin's claim about natural selection is reconstructed as an *empirical* claim about a causal connection leading from the match of the physiology of an individual and its environment to leaving surviving progeny. Variations in this match, Darwin claims, cause differences in the survival of the progeny. Modern concepts of fitness focus the survival side of this chain. Therefore, the assumption that evolutionary theory wants to explain reproductive success in terms of a modern concept of fitness has given rise to the so-called tautology problem. It is shown that the tautology problem reappears in the treatment of fitness proxies in today's experimental evolutionary biology when these proxies are considered to indicate fitness only. Taking Darwin's empirical claim seriously suggests, by contrast, that fitness proxies are first of all measures of the match between organism and environment, which I call the organism's 'fittedness'. At the same time, they are indeed related to reproductive success. Thus looking in both directions, at fitness and at fittedness, they are janiform. Acknowledging this situation not only allows for rejection of the tautology objection, but also for integration of Darwin's argument into current evolutionary biology. It is suggested that this helps reframe and alleviate the dispute between the Modern Synthesis and the Extended Evolutionary Synthesis.

Keywords: Darwin; Extended Evolutionary Synthesis; Evolution; Fitness; Fitness Principle; Modern Synthesis; Niche Construction; Origin of Species

1. Introduction

This paper combines a defense of Darwin against the so-called tautology objection with a critique of an understanding of fitness proxies that perpetuates a tautologous understanding of the principle of natural selection. It stresses that Darwin believed that the quality of the interaction of the organism with its environment could be judged from physiological traits. We do not need to infer this quality from reproductive success, which he claimed depended causally on the interaction of an organism's physiological traits and its environment. It is shown that the theoretical approaches of the Modern Synthesis (MS) and Extended Evolutionary Synthesis (EES) are each taking a different aspect of Darwin's theory as being the key aspect of evolutionary processes—MS reproductive success, EES the interaction with the environment—and neglecting or downplaying that it is an empirical question whether and to what degree the respective other one is linked to it. Returning to the Darwin's "On the origin of species by means of natural selection" (in the following: the *Origin*) as an origin of both approaches therefore helps to alleviate important differences that appear to hold between these approaches.

Disregarding the empirical, and therefore in any new case of application hypothetical, character of the link between physiological match and reproductive success might be suggested by Spencer's phrase of the *survival of the fittest* (Darwin 1872, p. 51), to which Darwin's insight into the mechanism of evolutionary change by natural selection is often reduced. Interpreting "the fittest" as "the organism with the highest number of surviving offspring," as suggested by the concept of fitness used in the MS framework (but not by Darwin himself, as is shown below), results in the view that evolutionary theory is based on a claim that is close to a truism. In this view, Darwin's insight thus seems to lack explanatory power. The first aim of my paper is to show that Darwin in fact makes a strong *empirical* claim about the mechanism of evolutionary change (section 2) and that the tautology-view mistakes his argument (section 3).

A derivative of the tautology problem reappears in the treatment of fitness proxies by today's experimental evolutionary biology—namely, when these are considered as indicating fitness only. For many research questions, this is reasonable. However, Darwin's empirical claim suggests that these fitness proxies are tightly linked to the initial part of the causal chain leading from environmental match to reproductive success. They are connected to downstream *and* upstream sections of this chain and can therefore be used at once both as indicators of the match and as predictors of reproductive success. In a second step (section 4), I demonstrate that a standard way to introduce and use fitness proxies in empirical research on evolution misses the opportunity to couple reproductive success to the relationship between the physiology of an organism and its environment, as Darwin did, and by this consolidates a tautologous picture of natural selection. It is shown that the most often used fitness proxies (e.g., for many species, the individual growth rate) are janiform, looking at the same time at the physiological-ecological match and at reproductive success.

In the third and last step (section 5), I show how this richer concept of a fitness proxy not only helps to understand, but also diminishes some important points of conflict between proponents of MS and EES. The dispute between MS and EES is reconstructed as the attempt to convince the proponents of the respective other side that only one of the faces of the fitness proxies is of empirical interest. Acknowledging the janiform character of fitness proxies thus may help reframe the debate.

2. Darwin's empirical claim

The assumption that Darwin's principle of natural selection is free of empirical content is not very plausible. I reconstruct his claim about natural selection from the first edition of the *Origin* (Darwin 1859) and thus from the argument as he gave it before Spencer's phrase was coined. His claim differs drastically from the reading of Spencer's phrase that became usual within the MS framework: It has strong empirical content. Although also a notion close to fitness as understood in MS and in population genetics can be found in Darwin, this notion is not even closely related to what he means when using the term "the fittest." As can be expected from a ground-breaking insight within empirical science, his claim is not tautological but refutable and in need of empirical support. This might be one reason why the *Origin* is so rich in reported observations and discussion of analogies.

2.1 Darwin's argument

Darwin's notion of natural selection is the basis for his argument about the generation of biological species (Darwin 1859; 1876). This notion combines three ideas:[1] first, the

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[1] I am concerned only with the claim about natural selection and not with the whole argumentation about speciation to which it contributes. In particular it is not relevant for

general observation that individuals differ, and that this holds for all species; second Darwin's empirical finding that, in the wild, most individuals die at early developmental stages or at a young age; and third, the theoretical insight that in populations of biological individuals of which each produces more than one offspring during its lifetime, not all offspring can possibly survive in the long run. Let me first recapitulate this tripartite point of departure, which provides the basis for Darwin's empirical claim about evolutionary change, in reverse order.

The theoretical insight at the basis of the argument is that unrestricted populations increase at a geometrical ratio, i.e., they grow exponentially (Darwin 1859, pp. 47–49, 58, 79, 332), and that, because the food supply cannot grow exponentially forever, not all individuals can possibly survive. Darwin borrows this idea from the economist Robert Malthus (1798, pp. 4, 6–7). In the third chapter of the *Origin*, he transfers the "doctrine of Malthus" from human social systems to "the whole animal and vegetable kingdoms" and stresses that there can be neither an artificial increase of food, nor "prudential restraint from marriage" in these kingdoms (Darwin 1859, p. 47). The situation therefore is that not all animals and plants can and will survive.[2]

This theoretical result is confirmed by Darwin's observation that plants and animals living under unfavorable circumstances leave fewer offspring (cf. next paragraph but one) and specified by the empirical finding that most individuals die at early developmental stages or at a young age and thus do not leave any offspring at all. Darwin points out several times that many seeds and seedlings, eggs and young are "destroyed" (1859, pp. 47, 48 *et pass.*).[3] Food shortage is not the only reason for these

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my present purpose whether there is indeed only one argument about natural selection in Darwin's *Origin* or whether there are parallel arguments (Hodge 1977, 1992; Sintonen 1990; Mayr 1991; Regner 2001).

[2] For a reconstruction of Darwin's reliance on Malthus see, e.g., Ospovat (1997) and Hodge (2009).

[3] In addition to Darwin's focus on selection at early developmental stages when citing empirical evidence, he also considers selection in the adult state; however, the drastic

deaths, although he counts it as important at least in the context of climate and seasonal changes; it is also relevant that many young individuals serve other animals as prey (p. 50).

Consequently, Darwin considers it inevitable that, in each species, many individuals die before their time—in particular, before they had a chance to propagate. This does not, however, say anything about *which* individuals among the young ones die and *which* ones survive. Survival could be a matter of chance, of intrinsic properties like body mass, strength or locomotive capability, of being the first or last born, or of any other account. Darwin prepares his answer to this question (which he does not ask explicitly) by referring to the general observation that individuals differ and that this holds for all species. Reference to variation is so important for his argument that he commences his *Origin* with two chapters on differences between individuals. In the first chapter, he describes variability as a phenomenon that allows breeders to form varieties of a species by selecting individuals for breeding that have traits deviating in the desired direction from other individuals. In the second chapter, he states that variation also occurs in the wild and is thus not an artifact of domestication. Darwin does not have a satisfying explanation of variation, but he tries to make its occurrence as plausible as he could by providing examples, both domesticated and in the wild. He discusses the proposals of other authors as to how variation comes about, namely that variation was induced by light, excess food, or other external factors. Darwin himself is cautious in ascribing these factors more than a minor influence, but he considers variation, whatever its origin might be, as a matter of fact and most variation as being heritable (1859, p. 10).

The theoretical result about the overproduction of offspring, confirmed by the empirical result that there is indeed overproduction of offspring regulated by the death mainly of young individuals, leads in combination with the observation of heritable individual differences (however induced) to Darwin's central claim that exactly those inheritable individual differences will make the difference in survival:

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losses of seeds, nestlings, or tadpoles might have been compelling evidence available to any reader.

> [A]ny variation, however slight and from whatever cause proceeding, if it be *in any degree profitable* to an individual of any species, *in its infinitely complex relations to other organic beings and to external nature*, will tend to the preservation of that individual, and will generally be inherited by its offspring. The offspring, also, will thus have a better chance of surviving. (Darwin 1859, p. 46, emphasis added)

So Darwin does not consider the inheritable difference *as such* as making the difference in survival. Relevant is whether a variation is profitable for the individual in how it can deal with the external world. (Eyes do not help very much in the dark, and a high body mass not on an island with restricted food supply in absence of predators.)

The quote given above is followed by the introduction of the term 'natural selection': "I have called this principle, by which each slight variation, if useful, is preserved, by the term of Natural Selection, in order to mark its relation to man's power of selection" (p. 46). Darwin conceives this process as being burdened with uncertainty:

> [I]f variations useful to any organic being do occur, assuredly individuals thus characterised will have *the best chance* of being preserved [...] and [...] *tend to* produce offspring similarly characterised. (Darwin 1859, p. 92, emphasis added)

Which individuals survive is essentially the outcome of a causal process. Unknown causal factors and/or chance merely impose a (probabilistic) weakening on the causal connection between survival and the "profitability" or "usefulness" of a certain variation in a particular environment.[4]

The persuasiveness of Darwin's claim depends on how convincingly individual differences are demonstrated to be linked to survival. Darwin conceives the link as consisting in the effects of a varying match between the individual's traits and its

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[4] For a discussion of Darwin's understanding of chance and of the different concepts of chance that can be discerned, see Shanahan (1991), Pence (2015) and Hodge (2016); for 'chance' in particular in Darwin's later writings: Beatty (2006) and Lennox (2010); for a more encompassing account, Johnson (2015).

environment, framed in terms of an economy of nature (Ospovat 1979; Hodge 2008):[5] Survival is supported by those variations of traits that are “profitable” for the individual “in its infinitely complex relations to other organic beings and to external nature”—that is, by variations that allow the individual to cope better with its biotic and abiotic environment. In the definition, this is abridged as “being useful.” Stripping the economic metaphor of its teleological content, Haeckel introduced the concept of ecology (Haeckel 1866); sometimes he explicitly took up the concept of an economy of organisms (vol. 1, p. 8) or of nature in his definition (Haeckel 1868, p. 539). So, from the present point of view, *natural selection* and its reference to the biotic and abiotic environment, which is understood as being more or less constant, can be seen as an ecological concept (cf. Bouchard 2011).

Natural selection on the basis of the match of the organism with the environment gains its evolutionary relevance only under two assumptions: first, the assumption of the heritability of variation, which is supported in later chapters of the *Origin* with a plethora of empirical examples, and second, the idea that the range of variation is not fixed, but always centered at the actual parameter value so that the limits of variability also grow or shift with each new variant. This shift allows for organisms departing further and further from the original type, as Wallace puts it in his version of a selection theory (Wallace 1858, p. 54).

2.2 Fit(tedness)

Within the framework of his economic metaphor, Darwin speaks about the profitability or usefulness of certain variations for the individual’s coping with its living conditions, which I have characterized above as the quality of the match of the individual and its environment. However, he speaks neither about a match (he uses this word only in a different sense in the context of breeding), nor does he use the term ‘environment’.

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[5] Darwin relied on a long tradition of the metaphor of the economy of nature. It can be found at least since the mid-17th century and was established as an expression of the mutual connection of living beings (“nexus inter se”) by Linnaeus about one hundred years later (Toepfer 2011 vol. II, p. 688).

Sometimes he writes about the individual or its trait as being *adapted*, in particular when the stabile traits of a species are at stake (Darwin 1859, pp. 2, 45, 57 *et pass*.). But in general, and also with respect to new variations, he speaks of the *fit* between an individual and other beings or external nature. He also refers to an individual or a character as being fitted to, or being fitted for, *certain ends*: The flying lemur's wings are "fitted for gliding through the air" (p. 130); Darwin admires "how infinitely complex and close-fitting [...] the mutual relations of all organic beings to each other and to their physical conditions of life" are (p. 59). The fitting-relation is graded, so, for example, seeds are better or less well fitted for dispersal (p. 106). Better fit, Darwin claims, gives the individual that produces these seeds an advantage over other individuals (p. 106).

Darwin uses the metaphor of being fitted already in his essays from 1842 and 1844, respectively, where he speaks about recent and fossil organisms as being "fitted to wholely different ends" (Darwin 1842/1844, p. 30) and, referring to Rhinoceroses in former times, that "some of these ancient animals were fitted to very different stations" (p. 37). He writes about species being fitted to diversified means of subsistence (p. 146), "best fitted to its new habits and station" (p. 156), and for being "fitted to widely different ends in the economy of nature" (p. 160). He uses also negations and speaks of organisms being unfit for a new climate regime (p. 173) or being ill-fitted (Darwin 1859, p. 261).

To stay close to the terms Darwin uses and at the same time to disambiguate his use of "being fitted," I call the degree of match, of being fitted *to the biotic and abiotic environment*, the *fittedness* of an individual.[6] Darwin's notion of a trait being fitted *to*

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[6] The technical term I propose avoids the allusion of a particular way of how the fit is brought about, which seems unavoidable in terms like 'adaptedness'. Moreover, it overcomes the teleological connotation of Darwin's 'profitability`, which makes sense only within the overarching metaphor of an economy of nature. My concept of fittedness is wider than the concept introduced by Burns (1994), which also captures the embedding of an organism in its environment, but is restricted to ecological interactions with the other organisms that make up a network together with the organism in question and leaves out interactions with the abiotic environment. Burns is also more restrictive

ends or to habits, on the other hand, refers to how well the trait under consideration can perform its task. Such tasks are mirrored by the functional organization of an organism and their performance depends also on the environment. A trait being fitted in this other sense is thus a matter of its functioning. The fittedness of an organism obviously depends, though in a non-trivial way, on how well its traits are fitted; on how well it's whole set of traits performs in the actual environment.[7]

Focusing fittedness is very much in line with Stephen Jay Gould's claim that "criteria of fitness independent of survival can be applied to nature and have been used consistently by biologists" (Gould 1976, p. 100). It disentangles the two components intermingled in his somehow misleading reference to "criteria of fitness": the smoothness of the interaction of the organism with its environment (fittedness), which belongs to what Gould calls 'design', and their claimed connection to fitness (see below sec. 4.2).

A change in fittedness has consequences. Darwin points out that an increase of fit increases the "chance of surviving and of leaving offspring" (1859, p. 67). So, having "fitted" traits is what makes the difference with respect to survival. The better fitting individual (or, analogously, species) has greater chances of leaving offspring than the less well-fitted individual (or species), which runs a greater risk of dying too early in life to leave progeny. Under the presupposed heritability of variation—and when above the inherited characteristics also new variation occurs in the offspring—natural selection leads to a gradual improvement of fittedness in a given environment and to regaining fittedness after a change in the environment. So fittedness has an important explanatory role: differences in fittedness explain differences of (the chance of) leaving offspring.

According to this reconstruction, we have a two-step mechanism that leads from variation to the number of progeny and, consequently, a two-step explanation. Step one: Variation of traits modifies the capabilities and thus the fittedness of an organism. Step

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in conceiving fittedness as a heritable trait. I wish to thank Michael te Vrugt for referring me to this earlier concept of fittedness.

[7] Reference to the set of traits is meant to include the plasticity of the traits, their interactions, etc.

two: the individual with higher fittedness leaves more surviving offspring. Under the empirically supported assumption that, by and large, the progeny inherits the traits of the ancestors, re-iteration of these two steps yields the evolutionary result of natural selection.

That fittedness of the individual is a cause of, or at least a predictor for, differences in the survival of its lineage and the basis for gradual changes of a species is a strong empirical claim. It could easily turn out to be empirically wrong, either generally or for some species, and in the latter case, either in all settings or in some particular situations only. It might well be that, in some species, individuals that fit physiologically almost perfectly into their environment have fewer offspring than individuals with lower fittedness. One can think of manifold reasons in behavior and in physiology. The individuals might, for example, be too lazy or too busy to build nests, not engage in brood care, be unattractive to possible mates, be themselves too picky in choosing mates, or they might have a less functional reproductive system or even be sterile.[8] It is also not very likely that fittedness, which depends on a large set of parameters (of which many will be quite unstable), is a parameter that could be determined with such high precision that one could indeed order individuals unambiguously according to their fittedness. Anyway, the estimation of fittedness needs to take into account that there is a sophisticated interaction between different traits (Pistón et al. 2019). Nevertheless, Darwin has developed a highly plausible explanatory scheme and shows that it can be applied fruitfully in many cases.

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[8] One might wonder whether these reproduction-relevant characteristics should not be counted among the traits that make up fittedness. However, they are not identifiable as relevant by looking at the interaction and physiological match of the individual with the environment, but only by judging them from their fitness effects. Such a move counteracted Darwin’s idea that reproductive success depends on match by making match conceptually dependent on reproductive success. It should also be noted that, even if some of the behaviors mentioned above could justifiably be considered as increasing the match of the organism with its environment, others will decrease it: brood-care often increases the risk of being predated, has energetic costs etc.

3. Fitness: The transformation of the principle of natural selection

3.1 Making a tautology

The debate about Darwin's principle of natural selection is linked to the so-called fitness principle, the phrase claiming the *Survival of the Fittest*, which Darwin added in the fifth edition of the *Origin* and that we find in the most popular sixth edition. He took it up from Herbert Spencer (Spencer 1864) and inserted it right behind the definition of the concept of natural selection quoted above: "But the expression often used by Mr Herbert Spencer of the Survival of the Fittest is more accurate, and is sometimes equally convenient" (Darwin 1872, p. 51). Spencer's phrase gave rise to several severe misunderstandings and was repeatedly reinterpreted within varying contexts (cf. Krohs 2006). Because of its ambiguity, Thomas Henry Huxley considered it an unlucky substitution for "natural selection" (Huxley 1890). Nevertheless, it became *the* catchword for Darwin's theory, and it—rather than Darwin's extensive use of "fit" and "being fitted"—gave rise to the concept of fitness that has become so important in population genetics.

The abovementioned numerical fuzziness of any measure of fit and fittedness might have been one reason why MS reframed and transformed Darwin's talk about fit. Spencer's phrase, at least, seemed to offer a starting point: If a certain individual can be said to be the "the fittest," then obviously others have lower fitness. It is also clear that the phrase is not to be read in the sense that only one, "the fittest," individual survives, so grades of fitness map onto grades of the survival of lineages. Such grades could be given and compared by the number of individuals occurring in the lineage in future generations. On the level of population genetics, the relevant measure is the abundance of alleles in the population gene pool. Depending on the context, fitness is therefore taken to be the number of surviving offspring (including future generations), or as the (relative) contribution of a genotype to the gene pool (cf., Byerly and Michod 1991; Krimbas 2001; Ariew and Lewontin 2004). Fitness comes in numerical values and is thus nicely graded. The concept perfectly met the needs of MS: Within its framework of explanatory adaptationism (cf. Godfrey-Smith 2001), adaptedness can be directly inferred from the fitness value: the higher the number of surviving offspring, the better the adaptation.

Karl Popper prominently claimed what others had complained about before: that the fitness principle is (almost) a tautology: If survival is meant as survival of a lineage, and fitness is measured by the number of offspring, then the phrase the survival of the fittest understood in terms of fitness merely states that those individuals with the highest number of surviving offspring have the highest number of surviving offspring, or that the survivor survives (Popper 1974).[9] Popper concluded that evolutionary theory, being based on a tautology, is at its core not empirically refutable, so he took it to be a metaphysical research program (non-pejoratively used). His intention was thus a re-classification of evolutionary theory with respect to its type, whereas many other authors considered the tautology being fatal for the theory.[10] This line of objections began with F.M. Müller in 1887 (Toepfer 2011 vol. 1, pp. 46–47) and did not end with Tom Bethell in 1976 (cf. the reply by Gould 1976).[11]

3.2 Fitness as a propensity

After having been convinced that even evolutionary biology is empirical science, Popper's way to deal with the principle was to take fitness not as the actual number of offspring, but as the propensity, objective probability, or stochastic disposition to leave a certain number of offspring (Popper 1978).

Popper is right, of course, that this grants empirical content to the fitness principle. The propensity view therefore abounded in the philosophy of biology (Mills and Beatty 1979; Richardson and Burian 1992; Bouchard and Rosenberg 2004, Roffé and

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[9] Popper later on considered his view having been influenced by Waddington, Fisher, Haldane, and Simpson (Popper 1978, p. 344).

[10] To mention a counter-example: Waddington (1960), who also diagnosed the tautology, didn't consider it being problematic.

[11] For more recent comments and reviews of the tautology problem, cf. (Grene and Depew 2004; Rosenberg and Bouchard 2005; Hunt 2014; Roffé and Ginnobili 2020).

Ginnobili 2020). The difference between the expected and actual number of offspring is considered to be relevant for evolutionary explanations (e.g., Pence and Ramsey 2013), so fitness as a propensity is a good candidate for figuring in these explanations. However, it is no *independent* measure of adaptedness, fit, or fittedness, but still based on data about, or estimates of, surviving offspring, corrected by a – possibly large – number of other parameters determined with the help of other theories (Rosenberg 1992). These other theories might include theories about the interaction of the organism with its environment, so systematic differences of fittedness come into play, at least. This is the case when fitness as a propensity is estimated with the help of optimality models,[12] which allow assessing the quality of the solution to a design problem realized by a certain trait (Brandon & Beatty 1984). The parameter used to assess the design variables, however, is considered to be ideally fitness, and alternatively some variable that is proportional to fitness (Beatty 1980, p. 535). This choice does make optimality models useful in explaining selective processes. However, the degree of fit between organism and environment depends conceptually on fitness-related variables, which means that an inference from optimality to fitness merely replicates the structure of the model. Consequently, Brandon and Beatty still consider the principle of natural selection to be "without empirical biological content" (1984, p. 343), with an emphasis on "biological". The empirical content of the principle, and hence the solution for the tautology problem, is restricted in this approach to the empirical content that a law governing probabilistic inferences may have in general (Brandon 1981, p. 432), i.e., the empirical difference between the propensity and the actually realized value.

The ongoing debate about fitness being the actual number of offspring (or contribution to gene pool, etc.) or the corresponding propensity does not tackle this issue of a missing or at least incomplete disentanglement of optimality and fitness, but focuses on the other important question of whether there can be cases in which propensity and actual outcome could differ systematically. It was shown that such cases can be construed (Drouet and Merlin 2015), so that the issue whether fitness-as-a-propensity can replace the standard concept of fitness is still under debate.

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[12] A different use of optimality models is discussed in the next section.

3.3 Fitness and fittedness

None of the two concepts of fitness captures what Darwin was after in the *Origin*, but at least none contradicts what Darwin says about fit. First of all: nowhere in the *Origin* does he use the term “fitness”. Even “fittest” he uses exclusively as a part of Spencer’s phrase, never independently. It does not occur in the first edition. In the sixth edition it occurs fifteen times, of which two are in chapter headings, and, as said, in all cases as component of the ever-identical phrase. This means that no passage in the *Origin* allows reading fitness, or even the abundantly used “fit,” as a label for leaving offspring (first and sixth edition were checked). This he calls descriptively “to yield offspring,” “success in leaving progeny,” “leaving” or “producing offspring” (e.g., Darwin 1859, pp. 40/47/67; 1876 pp. 44/52/74/75), or more specifically, “producing seeds” (Darwin 1859, p. 106), and so forth.

The situation does not improve when we take alternative proposals into account, like considering fitness not to be attributable to individuals, but to types of organisms (Ettinger et al. 1990) or to traits (Walsh 2010; Sober 2020). Besides saving formal soundness of the concept, both conceptions have some historical plausibility.[13] Nevertheless, these approaches simply modify the population-genetical concept of fitness, which has been shown to be too narrow. They do not capture the role of Darwin’s reference to better or worse fit as a physiological and ecological relation.

Fit in this sense comes into focus with the concept of ecological fitness (Bouchard and Rosenberg 2004; Ginnobili 2016). After a less satisfactory earlier attempt (see below), this concept was operationalized by embedding it in a modified understanding of the optimality models mentioned above, in which physiological effectiveness of a trait rather than fitness parameters serve as the scale of optimality (Roffé and Ginnobile 2020, sect. 5). Optimality in this sense is conceptually independent from fitness, so that the connection between optimality and fitness is an empirical matter (Roffé and

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[13] As can be seen from the references quoted above, Darwin indeed talks about species fitting well to the environment—whether or not this is meant literally—and Wallace draws a picture of group selection. Darwin also refers to well-fitted traits.

Ginnobili 2020, p. 284), in contrast to Brandon and Beatty's (1984) understanding of optimality models. Moreover, like my proposed concept of fittedness, the ecological fitness approach is supported by a reconstruction of Darwin's understanding of natural selection (Ginnobili 2016). Fittedness and ecological fitness are thus strongly related.[14] Reference to optimality models, however, is a restriction that is not always welcome. It makes ecological fitness operationally dependent on a certain class of models. These models are very convenient whenever a certain set of parameters can change continuously. Roffé and Ginnobili (2020) explicitly stress this aspect, because it allows them to infer fitness values in a straightforward way from the optimality parameter. However, the models will not be applicable when comparing two organisms with a trait present in one and absent in the other. The price for securing quantitative predictability of fitness via optimality models is thus the restricted applicability of the ecological fitness concept.

Another attempt to spell out the concept of ecological fitness does so in terms of 'solutions to design problems' (Bouchard and Rosenberg 2004). — in opposition to previous harsh critique of any such 'lock and key' model (Lewontin 1978). The proposed operationalization involves a pairwise comparison of organisms, such as white-coated and dark-coated arctic prey. Differences in ecological fitness are then evaluated in terms of success in solving a design problem that is conceived of as given. In the example, the problem is to evade predators, which is solved by camouflage. This concept stresses the empirical content of claims about the fit of an organism to its environment (ibid., p. 709). Problematic, however, is supposing that natural selection aims at solutions to design problems. The authors are willing to bite the bullet of accepting the 'suggestion of teleology' inherent in this notion (ibid., p. 700). The crucial difference between the design problem operationalization of ecological fitness and the concept of fittedness proposed in this paper lies in the unidirectionality of design problem considerations. This unidirectionality includes the assumed fixedness of the situation: the environment poses a problem, natural selection needs to solve it.

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[14] As an aside, it should be mentioned that the term "ecological fitness" is a misnomer since the concept is explicitly not meant to be a concept of fit*ness*, which consensually captures, in one way or another, reproductive success.

Fittedness, in contrast, does not refer to pre-posed problems. It rather describes the interaction of the organism with its environment resulting in different degrees of match. My descriptive approach neither assumes that a low degree of match is the result of any problem being posed, nor assumes that this low degree "needs" to be overcome. A low degree just might have consequences with respect to survival.

The notion of fittedness that I propose abstains from referring to design problems and has a wider scope than optimality approaches. While any explication of the concept of ecological fitness models the relation between organism and environment in a particular way, the concept of fittedness is independent of any particular way of modeling. Developing a case-specific scale for comparing organisms with respect to their fittedness into a certain environment is to be left to biology.[15] This is not a shortcoming of the conceptual approach. In contrast, I consider this not only adequate for a conceptual approach, but also an even more adequate reconstruction of Darwin's fairly general empirical claim than the already operationalized concept of ecological fitness. Despite the differences between these two closely related concepts, fittedness and ecological fitness will be equivalent in many cases. In cases of equivalence, the concept of ecological fitness provides a valuable tool to straightforwardly assess fittedness, the match between organism and environment. In other cases, biology first needs to establish a method of assessing fittedness.

Let's take stock. (1) In Darwin, we find the concept of a *fit* between an individual and its biotic and abiotic environment, or of the individual *being fitted to* its environment. To disambiguate it from denoting the related, but different relation of being fitted to habits or to ends, I use "fittedness" for the match of the individual to its environment. Fittedness is an ecological, or rather, a physiologico-ecological concept that is shaped to

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[15] Singling out relevant aspects of the environment and the in-principle need to include not only "subenvironments" but the "whole environment" is notoriously difficult (e.g., Abrams 2009). A general solution to this problem doesn't seem to exist. Biologists rather have to judge in each single case which aspects are important when modeling the organism-environment interaction – a task to be solved in any modeling approach that aims to focus on relevant aspect of the modeled system, be it in biology, physics, or the social sciences.

describe the quality or degree of the match between the organism and its environment. Although it is not usually possible to order such degrees on a numerical scale, pairwise comparisons might often be feasible, sometimes even with obvious results. (2) In MS and in population genetics, by contrast, we find the concept of fitness, or several related concepts of fitness, as the number of surviving offspring or as the contribution to a gene pool. This numerical concept helps explain and predict changes in the gene pool directly, starting from gene frequencies. Sober recognizes both the ecological (1) and the population genetical (2) aspect. He considers them being combined in the concept of fitness: *fitness as an ecological descriptor* and *fitness as a mathematical predictor* (Sober 2001).[16] However, combining both into one concept neglects that the link between these supposed "aspects" is not conceptual, but empirical, and that it might have different strengths in different systems. It is thus more adequate to consider them as being different concepts rather than different aspects of only one concept. Darwin had other epistemic goals than MS. He did not want to predict—or at least was not content with predicting—the number of surviving offspring. Instead, he wanted to explain how variation leads to differential reproduction. His explanation, while given in terms of an economy of nature, can nowadays be understood basically as an ecological one. (3) The philosophy of biology has brought up the concept of fitness as propensity. The aspect of propensity occurs in Darwin as *chance* to survive and to propagate. Fitness in this reading is not identical to, but is to some degree a causal consequence of, fittedness. According to Darwin, the fit(tedness) predicts the chance of having surviving offspring. The better the fit(tedness), the higher the chance. Fitness as propensity is a theoretical term that captures this chance: The better the fit(tedness), the higher the fitness-as-a-propensity. (4) Darwin's empirical claim is not that this propensity will, on average, be more or less realized, but concerns the step before this one. His empirical claim is that fit, in my terminology fittedness, i.e., the relation between the organism and the environment, gives rise to this propensity.

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[16] For a review of the even larger family of fitness concepts and their respective role in evolutionary genetics, see Orr (2009).

4. Fitness proxies

4.1 Establishing fitness proxies

Fitness in the sense of actual contribution to the gene pool is an important parameter in evolution research. It is often estimated using fitness proxies such as individual growth rate or annual reproductive success. It might be demanding to establish whether a performance measure like growth rate reliably indicates fitness (Franklin and Morissey 2017), but the general idea of using such proxies is straightforward. In this section, I want to show how the conceptual distinctions made above apply to research that relies on fitness proxies and how the concept of fittedness helps in understanding the role of these proxies.

Proxies are important in experimental evolution research because determining fitness directly is often unfeasible. Only in cases where generation time is short with respect to the observation period can fitness be measured directly or at least estimated on the basis of data directly related to the survival of offspring. To mention just two scenarios, the contribution of an organism to the gene pool can be reconstructed by counting offspring through several filial generations, or the changing abundance of a genetic marker in the gene pool can be measured (Orr 2009, p. 536–538). In organisms with a long generation time and long reproductive phases, things become more complicated. Measuring or estimating fitness directly is prohibited by the mismatch of the experimental and the reproductive timescales. Researchers then resort to fitness proxies—parameters that are somehow linked to fitness and allow its estimation.

The connection between reproductive success in a particular year (where this is an appropriate time scale), which was above mentioned as a proxy, and fitness seems to be fairly direct: The proxy of short-term success serves as an indicator of long-term success. This might be plausible, but needs empirical confirmation in each case. Growth rate, to pick out another proxy, is less clearly linked to fitness. It is easy to imagine a counterexample in which faster growing organisms leave fewer offspring than slower growing ones, which means that the relation between the two parameters first needs to be established empirically for a species; only then can the growth rate be taken as a proxy of fitness. In some cases, it turns out to play this role quite well (Lampert and Trubetskova 1996), but not in others (Foster et al. 1999; Edmunds 2017). Also measures of body condition (Milenkaya et al. 2015) have been found to make up good fitness proxies in some species. In any case, the appropriateness of a proxy needs to be established by demonstrating that the value of the proxy co-varies with the fitness value.[17]

To understand the roles of fitness proxies, it is helpful to look at why they co-vary with fitness and can thus serve as proxies. Systematic co-variation may, in principle, have different reasons. Fitness proxy and fitness could be either causally or constitutively linked. In the case of a causal link, the proxy could be among the direct or among the indirect causes of fitness, it could be a direct or indirect effect of fitness, or both could be among the effects of a common cause. In the constitutive case, one could be among the constituents of the other: the proxy could be part of the basis of the emerging phenomenon called fitness, a proxy might be emergent on a basis that includes fitness,[18] or both could emerge from a shared basis.

With some of the proxies mentioned, fitness depends causally on the proxy: the contribution to the future gene pool depends on the success of camouflage or on the body condition, not the other way around. With growth rate, one might not want to postulate a direct causal dependence, but perhaps a correlation brought about by a complex common cause; for example, the number of surviving offspring often depends on food intake, as does the individual growth rate. Effective foraging behavior, if it is genetically or culturally heritable, may lead to a high individual growth rate and to the survival of offspring that also shows this behavior, though a correction is required for the energy spent for foraging (Lemon 1991). But certainly, total offspring number at the end of life will neither cause nor constitute growth rate in early life.

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[17] This might, of course, require a sophisticated argument in species where fitness is not measurable on an experimental time scale.

[18] Think of a proxy that measures the overall activity of a whole lineage, e.g., modification of some environmental parameter. Differences in the structure of soil in adequate experimental settings could be taken as an indicator of the respective fitness of different subpopulations of earthworms.

4.2 The two faces of fitness proxies

Many fitness proxies are physiological parameters that depend on environmental conditions, as is obvious in the cases of individual growth rate, or, for example, hormonal status. These proxies not only face fitness as a downstream effect, but also indicate the physiological condition and might be a measure of how well the individual copes with its environment—that is, they face also upstream to the fittedness of the organism.

Let me first concentrate on the fitness side. In the case of a proxy that is a cause contributing to fitness or an indicator of such a cause, it is easy to see why it could be a good proxy and thus faces fitness: As long as no other causal contributions systematically interfere, the proxy will map onto fitness as its effect, or as an effect of a common cause. Interference might easily occur, as might a lack of specificity, so not every causally relevant parameter is a good candidate for a fitness proxy. Breathing, for example, is a causal precondition for any offspring production in terrestrial animals, so this parameter would hardly be a valid proxy of fitness. But many other factors will be of more specific relevance for reproduction and for survival of the offspring than breath rate. In the end, the usefulness of a parameter as a proxy needs to be established empirically in each case. Many proxies can assume their role because fitness depends on the parameter chosen as its proxy. The proxy is part of the causal mechanism that brings about the contribution to the gene pool. Due to this involvement, the proxy can be used as a predictor of fitness. This is one role of many fitness proxies.

As suggested above, however, there is another role, because many fitness proxies at the same time indicate fittedness. Growth rate, production of offspring, and similar parameters obviously depend on the environment in which the organism lives. But of course, a focus on the environment alone would be too narrow a perspective. At stake is the *relation* between an organism and its environment. What counts as food or as shelter, though provided by the environment, depends on the organism. How much of the food supply an organism can use depends on its traits and on their individual characteristics. An individual bird that has a stronger beak than its conspecifics will be able to feed on certain seeds better than others. An eagle with weaker eyesight will gain less weight, or will gain it more slowly, than one with keen vision. So, it is not the environment, but the ease of interaction between the individual and the environment that causes quicker growth. Growth rate can thus be an indicator of how well the individual copes with the environment. In other words: in these cases it is a direct or indirect causal effect of the match of the individual with its environment, of its fittedness. The fitness proxy thus measures the fittedness of the organism. This is the other role of janiform fitness proxies.

Population geneticists adhering to explanatory adaptationism (see above) may interpret the observation that a fitness proxy has this double role in the following way (several did so in personal discussions): *Of course, the fitness proxy measures match, but only because match is judged in terms of fitness anyway*. According to this position, there is no fitness-independent measure of match, because survival of the offspring or of the genes is the one and only currency in the game. This anecdotal evidence reflects the wide-spread approach to take only reproductive success as the criterion to judge the interaction of the organism with the environment, and thus disregard physiological criteria as an indicator of how well an organism copes with its environment (e.g., Lampert and Trubetskova 1996; Parvinen and Metz 2008; Metz and Leimar 2011). It is followed even by some authors who consider fitness proxies explicitly as performance measures (Franklin and Morrissey 2017).

This argument, however, mistakes the status of the proxy. The proxy assesses first of all how well the individual copes with its environment on the physiological level. The scale of coping well is not derived from reproductive success: It is a physiological measure in its own right. When Darwin considers a strong beak fitting for hard seeds, this holds even when the individual does not propagate. Fittedness can be observed and investigated empirically on the physiological and ecological level. It neither needs to be nor could it possibly be derived from successful propagation. Biology is used to analyze and evaluate even highly complex interactions within the cell, within an organ, within an organism, and between organism and the environment. Think of switching metabolic pathways as in the case of the *lac* operon (Jacob and Monod 1961). We need not first look at whether the switch has a fitness effect before we understand its physiological relevance, namely, that it helps the bacterium to feed on different sugars. We have criteria to judge fittedness. Sometimes the integrity of the organism or of crucial metabolic pathways may play a role: snails match with feeding on toadstools, mammals do not. We can judge this by a physiological criterion: It is a matter of whether the organism keeps its functional integrity, not an evolutionary or population-genetic question. Selection comes only secondarily; the better matching organisms leave, on average, more surviving offspring—in many, but not in all cases. If a systematic relation between proxy and reproductive success can be established, the proxy *indicates*, but is not equal to, fitness as a propensity. The parameter thus serves as a predictor of fitness, by measuring not fitness, but rather some aspect of the fittedness of an organism. I take this as being the reason why Sober (2001) says that fitness *as a propensity* was a physiological descriptor. According to my proposal, not fitness itself is the descriptor; *the proxy* is the descriptor. The proxy, empirically confirmed rather than by definition, at the same time serves as an *indicator* of fittedness and as a *predictor* of actual fitness. Not fitness has, but fitness proxies have two faces. Granting Darwin's claim empirical content, this content is reflected exactly in the janiform character of the proxies.

5. Fitness proxies and the MS/EES debate

The insight about the two faces of fitness proxies helps improve our understanding of the differences between MS and EES and even overcome, in part, those differences. In this last section I first sketch how the differences between both approaches are presented by their respective proponents, and then discuss how acknowledging the janiform character of fitness proxies can help clarify these differences and conciliate the positions.

5.1 Explanation in MS and EES

Proponents of EES stress the importance of the impact of environmental factors on evolutionary processes. Mutations do not come first, but rather phenotypic variation resulting from environmental conditions. Variations are only secondarily fixed in the genome by genetic adaptation (Waddington 1942), after having been brought about by organism-environment-interactions. Therefore, EES regards plastic changes as important drivers of evolution. In general, its proponents recognize "processes by which organisms grow and develop [...] as causes of evolution" (Laland et al. 2014, p. 161).

Proponents of MS, by contrast, believe that their classical approach, in which phenotypic variation is largely driven by genetic variation, accounts adequately for all of these points. While they accept the mechanism of genetic adaptation, they state a lack of empirical examples of its action beyond processes generated experimentally. They stress that phenotypic plasticity, niche construction, inclusive inheritance, and developmental bias, which were claimed by proponents of EES as being not adequately accounted for in MS, “are already well integrated into evolutionary biology, where they have long provided useful insights” (Wray, Hoekstra et al. 2014, p. 163); however, they see these processes as “‘add-ons’ to the basic processes that produce evolutionary change: natural selection, drift, mutation, recombination and gene flow” (p. 164). While none of the additions is considered to be essential for evolution, it is accepted that “they can alter the process under certain circumstances” (p. 164). A more differentiated view is possible, in particular when accepting that Sewall Wrights *adaptive landscape* (Wright 1932), or a variation of it, allows us to account for niche construction proper within an adaptationist framing as well. This includes granting ecology evolutionary relevance *via* feedback loops rather than just by being part of the extended phenotype (Lewontin 1983; Tanaka et al. 2020).

From an external perspective, the differences stated so far seem to be merely about the abundance and importance of certain mechanisms for evolution. There is genetic adaptation, and there is phenotypic plasticity—but how important are they? There is niche construction, but is the extra-genetic inheritance it allows for strong enough to gain evolutionary relevance over and above its genetic basis? There are mutations, and they are important for evolutionary processes, but are there not other processes driving evolution as well? Despite the vigor of this debate, these differences appear to be first of all quantitative disagreements, which might be better solved by empirical research than by conceptual wrangling.

But things are not that easy. First, quantitative differences might result in qualitative ones so that theories starting from MS and EES assumptions, respectively, could still be fundamentally different. Second, and much more importantly, the picture is not yet complete. What I left out so far is what both sides are considering as an evolutionary explanation.

The classical view of MS regards evolution as the change of gene frequencies. Accordingly, it is claimed that "what matters ultimately is not the extent of trait variation, nor even its precise mechanistic causes. What matters is the heritable differences in traits, especially those that bestow some selective advantage" (Wray, Hoekstra et al. 2014, p. 164). These proponents of MS explicitly abstain from referring in their evolutionary explanations to mechanistic explanation of trait variation.[19] While not denying that there might be a causal story to be told about some evolutionary processes, as in genetic adaptation, these are classified as irrelevant. Only heritable differences in traits are important, not how they come about. This is not as narrow-minded as it might look. If evolution is the change of gene frequencies, this change seems to be fully explained by assigning a fitness value to each allele and calculating the outcome, or by counting the outcome and calculating the fitness values of the alleles. From statistical mechanics it can be seen that such a stance might have explanatory power: According to the molecular chaos hypothesis, one does not need to know the places and momenta of the particles: To describe or to predict what is going on in a volume of freely moving particles, one needs to know the number, collision diameter, and mean energy of the particles, but not the details of how exactly a collision takes place in terms of fundamental interactions.

EES, on the other hand, is interested exactly in the causal processes that are going on in the background of population-level evolution. Here, "the processes by which organisms grow and develop are recognized as causes of evolution." (Laland et al. 2014, p. 161). This side also stresses the difference and states that, for MS, "these phenomena [i.e., development, environmental plasticity and extra-genetic inheritance] are just outcomes of evolution. For the EES, they are also causes" (p. 162). Even if it might be too restricted an account of MS to assume that it takes these phenomena *just* as outcomes, it is clear that such causal processes play no explanatory role in MS, because they are

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[19] This does not mean that the debate between a statistical and a causal understanding of natural selection, drift etc. (cf. Pence 2020; Sterpetti 2021) would be decided in favor of the statisticalists. One may well be a causalist in this sense without considering causal explanations of the mechanism of the generation of specific variations being relevant for understanding natural selection.

considered only in their role of bringing about variation, as enabling evolutionary processes, but not influencing the direction and dynamics of evolution. The latter is left to the selective regime. EES, by contrast, aims at mechanistic explanations of how evolutionary events are brought about and acknowledges that systematic influences on, for example, developmental processes may bias or direct evolutionary processes.

At stake in the dispute, however, is not what field the approaches are interested in, but what is disputed. MS does not deny that there are causal processes that bring about part of the variation, but merely that these processes are relevant for explaining evolution. EES does not deny that gene frequencies change, and that random variation may lead to evolutionary change, but only that all variation is random and that consequently the direction of variation needs not to be explained causally. Part of these differences can be reduced to an empirical question: is there a relevant number of cases where causal accounts of the generation of variants yield better explanations than explanations that rely fully on random variation? Linked to this quantitative question is the disagreement between the approaches about what should count as an evolutionary explanation. Only on this level, MS and EES appear to be irreconcilable.

5.2 Fitness proxies as mediators between the two syntheses: A proxy of a conclusion

A look at the janiform character and double role of fitness proxies is helpful to better understand and perhaps even resolve this dispute. As we have seen, a proxy can be applied either as predicting fitness, or as measuring the fittedness of an organism to its environment. Analogously, each trait can just be accepted as being there (showing a certain range of variation so that each variant has its specific fitness value) or else be regarded as the outcome of causal interactions between the individual and its environment. If we follow Darwin and consider the fittedness of an organism as explaining its survival and reproductive success, it seems natural to count causal processes that alter fittedness as influencing evolution, over and above simply changing the selective regime—on the condition that this variation is heritable, be it genetically or for example by inheriting the environmental conditions that bring the variant about. Genetic adaptation follows later. The aspect added by EES to the classical picture of MS is thus in considering fittedness as resulting in part from the interaction between the environment and the individual. This includes changes in the environment by niche construction, but also changes in the organism by environmental influences, that may include, for example, heterochronic effects as well as phenotypic plasticity (Alberch and Alberch 1981; Gilbert 2010). In Darwin's case of the earthworm (Darwin 1881), which exemplifies what we now call niche construction (Odling-Smee et al. 2003; Sultan 2015), both perspectives are already present.

MS is extremely successful in focusing on evolution understood as the alteration of gene pools and omitting the aspect of causal mechanisms that systematically give rise to variation because of its disregard of any physiological account of fittedness. If the measure for the interaction of the organism with its environment is taken to be reproductive success, as methodological adaptationism tends to do, looking at the causal interactions that constitute fittedness seems to be superfluous. One can concentrate on the causality of selection. MS has shifted what I call fittedness out of the scope of evolutionary biology into the realm of ecology. Evolutionary biology therefore could view everything through the pinhole of fitness. This divorces the Darwinian unity of ecology and evolution. The fittedness-side is now put forward separately as the EES alternative to MS, which considers fitness as being fully explained by fittedness. In coupling the outcome of evolution directly to the mechanisms that alter the environment-organism relation, this position also disregards the empirical character of Darwin's claim and takes it as something like a truism: a better match, if brought about by systematic influences, is preserved, and it leads quasi-automatically to higher fitness. MS looks exclusively for explanations on the one side of the proxy, while EES stresses the unequaled importance of explanations on the other side. Both work with one face of the janiform fitness proxies only and treat the other side as being simply a conceptual extension (MS) or an automatic outcome (EES) of the process assumed to be central to evolution. It is time to acknowledge that contingent empirical facts reside on both sides of the proxies and that evolutionary explanations neither start nor end in the middle.

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