The changeful fate of a groundbreaking insight: the Darwinian fitness principle caught in different webs of belief

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Abstract

Darwin's explanation of biological speciation in terms of variation and natural selection has revolutionised biological thought. However, while his principle of natural selection, the fitness principle, has shaped biology until the present, its interpretation changed more than once during the almost 150 years of its history. The most striking change of the status of the principle is that, in the middle of the 20th century, it transmutated from an often disputed, groundbreaking insight into a tautology. Moreover, not only the interpretation of the fitness principle, but the whole body of biological knowledge was subjected to significant modifications. In this paper, I relate modifications of the fitness principle to those of the respective body of biological knowledge. This body of knowledge is conceived as a Quinean web of belief. After an exposition of Darwin's conception of the principle, which equated fitness with adaptedness to the environment, several of its changes are analysed with respect to different webs of biological knowledge. It is concluded that the different interpretations and the reshaping of the fitness principle are rational responses to the modified systems of background knowledge, which saved the coherence of the web of biological knowledge in each single case.

Introduction

The evolutionary theories of Darwin and Wallace were the naturalists' answer to the question of the origin of species that was, until the 19th century, a domain for religious ideas and myths. The idea of a phylogenetic evolution was already around when these theories were developed, with, e. g., Erasmus Darwin and Lamarck being important proponents of such views and many philosophers of the enlightenment as supporters. However, before evolutionism could supersede the idea of special creation, questions about the mechanisms and driving forces of the evolutionary process had to be answered convincingly. Charles Darwin provided an answer by proposing the following: that the change of species takes place by natural selection of variant individuals, provided that the variation is inheritable to some degree. According to Alfred Russel Wallace's slightly different evolutionary theory, not only individuals but also whole groups of individuals are subjected to selection.[1] I will be dealing only with Darwin's version and some of its interpretations. Darwin's contemporaries regarded the principle of selection or of the sur-

[1] Charles Darwin, Alfred Russel Wallace, On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection, *Journal of the Linnean Society (Zool.)* 3 (1858), p. 45, reprinted in: Charles Darwin, Alfred Russel Wallace, *Evolution by Natural Selection*, Cambridge 1958.

vival of the fittest as a groundbreaking insight that was worthy of discussion and debate. But with the refinement of evolutionary theory, the principle was submitted to an amazingly wide spectrum of different interpretations not all of which would acknowledge that it had ever been disputed. In the course of the 20th century, it turned from the accepted basis of modern biology into a mere tautology, bare of any empirical content, and once more into an empirical claim that, despite its former importance, turns out to be wrong unless it is modified. The unaltered version, then, counted as belonging to an obsolete research program.

This changing interpretation is often regarded as a series that steps back and forth between misinterpretation and correction. Nevertheless, all interpretations turn out to be plausible in the context they belong to. Therefore, rather than judging some stages as correct and others as faulty, it is preferable to look for reasons for the changes. Often, a reason for a change of the interpretation of a component of a scientific theory can be found in the different bodies of knowledge to which it is assimilated in different times: The structure of the body of biological knowledge changes with time, and a changed structure may require embedding a component of a theory, like the fitness principle, in a modified way into the system of knowledge. Such a body of scientific knowledge is a web of belief in the Quinean sense. By standards of science and rationality, such a web has to be coherent and, with minor reservations, it also has to be consistent.[2] "Coherence" means that the parts of the body of knowledge do not fall apart and form unrelated "islands" of knowledge, but that various relations hold instead, connecting beliefs that belong to different parts, so that the body of knowledge constitutes a system with interdependent parts.[3] Inconsistencies gradually diminish coherence. To enhance coherence, a web of belief has to be adjusted by expelling contradictions and by modifying parts of the web to increase the degree of interrelatedness. Scientific culture is, in part, a culture of performing such adjustments in a controlled way, e. g., on the occasion of the integration of new results.

In the following, I will analyse such adjustments of the web of biological knowledge that involve a reinterpretation of the Darwinian selection principle, and thereby try to shed some light on an important trait of scientific culture. To do this, I will analyse several webs of belief that succeeded each other in the historical development of biology. Nevertheless, I do not intend to give a history of Darwinism here, on which excellent literature is easily available,[4] but will confine myself to certain prominent stages of the interpretation of Darwinism only. This selection does not form a linear sequence in which each interpretation supplants the previous

2 Willard Van Orman Quine, Joseph S. Ullian, *The Web of Belief*, 2nd ed., New York 1978, esp. pp. 42-53 and pp. 63-71. Accepting the notion of a web of belief entails accepting that the web as a whole influences the status that a particular component of a theory has within the body of knowledge in question. It does not entail the more demanding Duhem-Quine-thesis, which states that no component of such a web may have validity conditions that are independent of the web as a whole.

3 Paul Thagard, Chris Eliasmith, Paul Rusnock, Cameron P. Shelley, Knowledge and coherence, in: Renée Elio (ed.), *Common Sense, Reasoning, and Rationality* Vol. 11, New°York 2002, pp. 104-131.

one, though more recent webs obviously rely on earlier ones: a web of knowledge usually takes up certain components of older nets, but does not belong to the same interpretative framework. Finally, I will draw my conclusion on the underlying modus of change of biological knowledge.

I will reconstruct the different webs in a purely narrative way. This allows for a straightforward access to different interpretations of the fitness principle. Techni cal effort, in contrast, would be required for the reconstruction of the relations between the different webs,[5] which I will refrain from.

1. Fitness and adaptation: Malthus's law, Darwin's insight, Spencer's phrase

Darwin's theory referred to the observation that not all individuals of the same biological species show the same morphology but that morphological variation occurs and that many variations are inheritable. Less obvious was that selection is going on in nature, and that natural selection could give rise to changes of species. Here, Darwin could not allege to any direct evidence. Instead, he argued for this by reference to Malthus's law as the basis of the mechanism of selection (as did Wallace). This law states that the growth of population, showing exponential increase of the number of individuals with time, quickly overruns any conceivable growth of nutritional supply.[6] In the long run, consequently, only a small fraction of individuals can survive to propagate. While Malthus was thinking of fairly stable populations as a consequence of the resulting "struggle for existence", the idea of inheritable variations opened up the possibility of another consequence. It seemed striking to Darwin that, under the conditions of limited resources, the composition

4 E. g., Peter J. Bowler, *Evolution. The History of an Idea*, Berkeley, 2nd ed. 1989; David J. Depew, Bruce H. Weber, *Darwinism Evolving*, Cambridge 1995; Jean Gayon, *Darwinism's Struggle for Survival*, Cambridge 1998. For the early development in German evolutionary biology, cf. Emanuel Rádl, *Geschichte der biologischen Theorien*, Leipzig 1909; for the time of the Modern Synthesis, cf. Wolf-Ernst Reif, Thomas Junker, Uwe Hoßfeld, The synthetic theory of evolution: general problems and the German contribution to the synthesis, *Theory in Biosciences* 119 (2000), pp. 41-91; Thomas Junker, *Die zweite Darwinsche Revolution. Geschichte des Synthetischen Darwinismus in Deutschland 1924 bis 1950*, Marburg 2004; Rainer Brömer, Uwe Hoßfeld, Nicolaas A. Rupke (eds.), *Evolutionsbiologie von Darwin bis heute*, Berlin 2000, where also the Russian evolutionists are considered.

5 That mainly the reconstruction of theory relations asks for formal methods is shown in: Ulrich Krohs, Wissenschaftstheoretische Rekonstruktionen, in: Ulrich Krohs, Georg Toepfer (eds.), *Philosophie der Biologie. Eine Einführung*, Frankfurt/Main 2005, pp. 299-316; anyhow, a simplified method is often sufficient to reconstruct biological theories: cf. Ulrich Krohs, *Eine Theorie biologischer Theorien: Status und Gehalt von Funktionsaussagen und informationstheoretischen Modellen*, Berlin 2004.

6 Thomas Robert Malthus, *Essay on the Principle of Population*, London 1798 (this 1st ed. appeared anonymously). Malthus assumed a linear growth rate for the supply. As one of the early critics, List has rejected this assumption: Friedrich List, *Das nationale System der poli tischen Ökonomie*, Stuttgart 1841, p. 143. Nevertheless, it is clear that exponential population growth would exhaust quickly even the resources of the whole universe.

of the population will change over the generations: The survivors will constitute neither a subset of individuals that represents the complete population, nor an arbitrary subset of individuals. Instead, there will be a biased selection: Survival should, according to Darwin, depend on differences in the viability of the variants. He regarded such differences in viability as a consequence of an unequally good fit of different individuals into their environment. Survival, then, relies crucially on the quality of this fit: the better the fit, the higher the probability for an individual to survive and to propagate. Darwin called this the principle of natural selection.[7]

Herbert Spencer named this principle with the phrase "survival of the fittest", which he had already coined as an economic phrase before Darwin's Origin was published.[8] Darwin used Spencer's phrase, from the 5th edition of the Origin onwards, synonymously with his original phrasing:

> "I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection, in order to mark its relation to man's power of selection. But the expression often used by Mr Herbert Spencer of the Survival of the Fittest is more accurate, and is sometimes equally convenient."[9]

The use of the superlative "fittest" is obviously not to be taken literally, since not only one species or one variety has survived. And nobody seems ever to have claimed that Darwin meant that exclusively the one single organism with the highest fitness would survive. So I agree to the view that he was talking about a comparison of fitness only, and that only local comparison of organisms competing for the same resources was meant.[10] Talk about "the fittest", even at the time when it was introduced, has to be taken as a slogan that characterises the basic idea of natural selection without caring much about the details. Nevertheless, I shall claim in the following section that things are different with respect to survival: that Darwin did not conceive survival in terms of a comparatively higher survival rate.

While Spencer's phrase was older than its application to biology, Darwin's explanation of the selection principle by reference to the fit between an organism and its environment was older than his adoption of Spencer's phrase, as I have mentioned above. However, more important than the question by which phrase the principle may be expressed most adequately is its intimate relation to the notion of adaptation. The degree of fit refers to the notion of adaptation of an individual to its environment. The latter point is crucial, since the explanation of the obvious adaptation, e. g., of the giraffe to feeding on tall trees or of fishes to locomotion in a liquid medium, was one of the key questions of 19th century biology. Adaptation

7 Charles Darwin, *On the Origin of Species by Means of Natural Selection*, London 1859, in: Paul H. Barrett, R.B. Freeman (eds.), *The Works of Charles Darwin* Vol. 15, London 1988, p.°80.

8 Herbert Spencer, *Social Statics*, London 1851.

9 Charles Darwin, *The Origin of Species by Means of Natural Selection*, sixth edition, with additions and corrections to 1872, London 1876, in: Paul H. Barrett, R. B. Freeman (eds.), *The Works of Charles Darwin* Vol. 16, London 1988, p. 49.

10 Frédéric Bouchard, Alex Rosenberg, Fitness, probability and the principles of natural selec tion, *The British Journal for the Philosophy of Science* 55 (2004), pp. 693-712.

was often a door for teleological arguments for the existence of God. Darwin rephrased the problem of being adapted in terms of a mere fit, which takes away any teleological connotation the term "adaptation" may have. Now he could use the term "adapted" synonymous to "fitting", and he uses both in very similar contexts. In the first edition of the Origin, his argument relies on this transition:

> "Let it be borne in mind how infinitely complex and close-fitting are the mutual relations of all organic beings to each other and to their physical conditions of life."[11]

Two pages later, Darwin takes up the relation of organisms to their environment, now substituting "adapted" for "close-fitting", when he points out that adaptation, i.e., fit, is never found to be perfect:

> "No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could anyhow be improved".[12]

Very much in this line of interpretation, Ariew and Lewontin write about Darwinian fitness:

> "The word 'fit' ('fittest', 'fitness') is a metaphorical extension of its everyday English meaning as the degree to which an object (the organism) matches a pattern that is pre-existent and independently determined (the environment)."[13]

2. Fitness and (human) fertility: historical precursors of 20th century interpretations

Darwin borrowed a central idea that contributes to his selection principle from the social sciences. Conversely, many biologists, mathematicians, and physicians were ready to apply Darwin's ideas to society.[14] The so-called biometricians claimed to do so.[15] On the one hand (the mathematical one), their work was the first attempt to quantify the parameters that Darwin had introduced. On the other hand (the socio-political one), the biometricians developed eugenicist ideas that had fatal impact on their Victorian society as well as on the politics of other countries, and which were developed by their successors into the most cruel euthanasia program

11 Charles Darwin, *On the Origin of Species by Means of Natural Selection*, London 1859, in: Paul H. Barrett, R.B. Freeman (eds.), *The Works of Charles Darwin* Vol. 15, London 1988, p.°81 (my italics).

12 Ibid. pp. 82-83 (my italics). It should be observed that Darwin claims here explicitly that fit is always non-optimal. In contrast to this, modern analyses of adaptation often rely on optimality principles: cf. Steven Hecht Orzack, Elliott Sober (eds.), *Optimality and Adaptationism*, Cam bridge 2000.

13 André Ariew, Richard C. Lewontin, The confusions of fitness, *The British Journal for the Phi losophy of Science* 55 (2004), pp. 347-363, cf. p. 348.

14 Young goes a step further when claiming that biologists' and sociologists' writings were part of a single debate: Robert M. Young, Malthus and the evolutionists: the common context of biological and social theory, *Past and Present* 43 (1969), pp. 109-145.

in Nazi Germany. That this fact cannot be deleted from the history of the reception of Darwin's work is now widely accepted. It is thoroughly analysed, e. g., in the historic accounts of Darwinism that are referenced above in footnote no. 4. Relying on these accounts, I will examine the change of the interpretation of the selection principle within the programme of biometrics, and the dependence of the altered interpretation on the different elements of the biometricians' web of belief.

Part of this web of belief was a cluster of offensive political ideas about social welfare that was underpinned by meagre empirical data. The biometricians started from demographic data and tried to analyse them in the light of Darwinian principles. These demographic data were read in a way that is chauvinist on different levels at once. Gayon characterises the views of 19th century demographers as follows:[16]

> "The poor, said the demographers, marry earlier and, being feckless, have a large number of children. The 'upper' classes, on the other hand, being prudent and wishing to give their offspring the best possible education, limit their fertility."

Such a view, though not necessarily the eugenicist idea that is based on it, is in large part shared by Darwin himself, as chapter V of his Descent of Man witnesses. There, besides the views of his nephew Galton, he gives the following quote from Greg, to which he seems to agree:

> "The careless, squalid, unaspiring Irishman multiplies like rabbits; the frugal, foreseeing, self-respecting, ambitious Scot, stern in his morality, spiritual in his faith, sagacious and disciplined in his intelligence, passes his best years in struggle and celibacy, and leaves few behind him".[17]

For the biometricians, the consequence from such 'data' seemed to be twofold: first, within each society there will be a proletarisation, meant, nota bene, as a process of biological proliferation. And second, among different societies and "races" the more "primitive" ones would outrun the more "noble" ones.[18] Under this interpretation, which Darwin judged as erroneous since it did not take into account infant mortality,[19] the data seemed to prove that evolution would change mankind

15 I will not follow the wider field of Social Darwinism, which makes use of a fitness concept that has the connotations of strongness and efficiency and may be regarded as being based mainly on Spencer's rather than on Darwin's writings. For references cf. Robert J. Richards, *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior*, Chicago 1987, p. 5. Unfortunately, the most widespread German translation of the *Origin* by Carl W. Neu mann (Leipzig 1921/Stuttgart 1963) gives, very much in line with these connotations, "Überle ben des Tüchtigsten" for "survival of the fittest", while some earlier translations (e. g., J. V. Carus) have "Überleben des Passendsten".

16 Jean Gayon, *Darwinism's Struggle for Survival*, Cambridge 1998, p. 242.

17 Charles Darwin, *The Descent of Man*, 2nd ed., London 1877, in: Paul H. Barrett, R. B. Free man (eds.), *The Works of Charles Darwin* Vol. 21, London 1989, p. 138.

18 The conceptualisation of ethnic groups as human "races" is not only politically dangerous, but also untenable from the genetic point of view, cf. UNESCO Report, *The race concept. Results of an inquiry*, Paris 1952; Luigi Luca Cavalli-Sforza, *Genes, Peoples, and Languages*, New York 1999.

for the worse. To block this tendency, eugenics was set up as a program of the exclusion of people with politically unwanted traits, which were assumed to be heritable, from having children. Since eugenics was meant to counteract a supposed evolutionary process, it has to be classified as a breeding program rather than as a Darwinian approach.

Nevertheless, biometry had Darwinian roots and I shall therefore analyse how the meaning of the selection principle was changed so that it could be used as a reference of such a breeding program. The important Darwinian input was that Homo sapiens, as any other species, is subject to evolutionary change. In his Descent of Man, Darwin had explicitly extended the range of application of evolutionary theory to humans. Since there may be fitness differences between human individuals, natural selection may in principle influence the evolution of humankind. But Darwin's selection principle did not predict the result that humankind will evolve for the worse, of which the biometricians were afraid, since it did not refer to fertility, the crucial aspect of their approach. In Darwin's writing, survival meant the survival of an individual at least to the point of leaving offspring. Having in mind the analogy with selection in breeding, he did not care about the role that differences in fertility may have on the result of a selection process. He conceived the struggle for existence as an all-or-nothing process of having success or having no success in leaving progeny.

> "If such [useful variations] do occur, can we doubt (remembering that many more individu als are born than can possibly survive) that individuals having any advantage, however slight, over others, would have the best chance of surviving and of procreating their kind?"[20]

So the advantage or surplus in fitness may be great or small. But Darwin conceives surviving and procreating as an all-or-nothing process that happens with a certain probability ("chance" and "probability" to be taken in a non-technical sense). This means that the degree of fitness leads to a certain chance of survival rather then to a certain grade of survival. So Darwin saw the effect of natural selection in making the difference between survival and destruction. As he wrote in the famous letter to Asa Gray from September 5th 1857:

> "Only a few of those annually born can live to propagate their kind. What a trifling difference must often determine which shall survive, and which perish!"[21]

Nevertheless, the all-or-nothing result of individual survival contributes to the relative survival rates on the level of populations, and to fully account for these, fertility had to be included. But Darwin, in contrast to Wallace, was thinking in terms of

19 Charles Darwin, *The Descent of Man*, 2nd ed., London 1877, in: Paul H. Barrett, R. B. Freeman (eds.), *The Works of Charles Darwin* Vol. 21, London 1989, p. 138.

20 Charles Darwin, *The Origin of Species by Means of Natural Selection*, sixth edition, with additions and corrections to 1872, London 1876, in: Paul H. Barrett, R.B. Freeman (eds.), *The Works of Charles Darwin* Vol. 16, London 1988, p. 63.

21 Cf. p. 265 of: Charles Darwin, Abstract of a letter to Professor Asa Gray (1857), in: Charles Darwin, Alfred Russel Wallace, *Evolution by Natural Selection*, Cambridge 1958, pp. 264-267.

individuals as contributing to populations rather than in populations as wholes and therefore could keep fertility out of his concept of fitness. Nevertheless, it has to be acknowledged that Darwin's thinking was not as simple as just presented. He points out that

> "of those which do survive, the best adapted individuals, supposing that there is any variability in a favourable direction, will tend to propagate their kind in larger numbers than the less well adapted."[22]

He seems to have seen this as an effect that may in some cases affect the evolutionary process in addition to the survival-destruction-result of natural selection, not as its basic mechanism.

The biometricians disagreed, and in 1877 Galton introduced productiveness in leaving offspring as another factor that influences the survival rate, besides natural selection and sexual selection that Darwin had identified.[23] Consequently, Pearson included reproductive selection, a supposed fitness-enhancing effect of high fertility, as a third component of fitness when he redefined the concept in the 1890s.[24] Without such a redefinition, no consistency could have been achieved between the offensive ideas about human society, wrong presuppositions about human biology, and the Darwinian view of humankind as being involved in the evolutionary process. It was a means to overcome Darwin's dispassionateness with respect to the future evolution of humankind without giving up any component of the biometricians' own web of belief, especially without giving up their interpretation of the unreliable data on fertility.

However, the chauvinist and racist worldview as articulated by Greg in the quote given above was not new and co-existed before its merger with Darwinism with a Malthusian view on the struggle for existence. But why did the integration of the new biological knowledge with these social ideas have such a horrible consequence? In contrast to Darwin's view, Malthus regarded the structure of the society as fairly stable. Evolutionary theory suddenly seemed to pinpoint a possible instability of the society: If evolution is going on, the biometricians concluded, then only the fittest will survive and society will change. The fear was nourished that the 'higher class' will be reduced in number and in the long run even be eradicated. This fear could be rationalised by integrating a modified fitness principle into the web of belief, a principle that allowed to delegate all supposed shortcomings in the fitness of the upper class to the fertility component, without touching the prejudice about other differences in quality between the classes.

22 Charles Darwin, *The Origin of Species by Means of Natural Selection*, sixth edition, with additions and corrections to 1872, London 1876, in: Paul H. Barrett, R.B. Freeman (eds.), *The Works of Charles Darwin* Vol. 16, London 1988, p. 68.

23 Jean Gayon, *Darwinism's Struggle for Survival*, Cambridge 1998, p. 245.

24 Ibid. pp. 245-246.

3. Fitness and classical genetics: steering through rough sea

With the beginning of the 20th century, Darwinism came in trouble for empirical reasons. In 1900, Mendel's work was rediscovered and integrated into the web of biological knowledge. The new genetics, nowadays called "classical genetics", stated three rules about the inheritance of traits in sexually reproducing species. The threat to Darwinism was that, according to Mendel's results, variant traits may become invisible in the first generation, and show up again only in the second generation of a crossing experiment. The consequence within the Darwinian framework is that an organism that is better adapted than other members of its species does not always produce offspring that has a similar fitness advantage. This find ing was in contrast to Darwin's assumption that variations are inherited as morphologically visible traits.[25] Mendel had shown that instead some factor that brings about the modified trait, dubbed "gene" by Johannsen in 1909, may be silently present in the offspring: It may give rise to the variant trait in the subsequent generation, when two silent carriers of the factor mate. So, initially, Mendelism was a threat to Darwinism, and it was not at all clear how and whether at all both could be made coherent.

Mendel discerned the genetic constitution of an organism from its physiological constitution, the genotype from the phenotype (these, again, being Johannsen's terms). This distinction allowed substituting the concept of a genetic mutation for that of a Darwinian variation. This contribution of Mendelism to evolutionary theory can be regarded as the most important step of the integration of Darwinism and population genetics in the synthetic theory of evolution, or the "modern synthesis" as the new theoretical framework was baptised by Julian Huxley.[26] The new framework uncoupled to some extent the mutation of a gene and the modification of the phenotype: Any particular gene may occur in different forms, called alleles. Each cell has two copies of every gene, one from each parent, and in many cases a phenotypic effect is seen only when both of the copies carry a mutation. In these cases two genotypic carriers of a mutated allele of a gene have to mate before the mutation has any phenotypic effect. However, it remained a mathematical task to show whether the propagation of mutated alleles can in principle give rise to evolu-

[25] For a Mendelian critique of Darwin's blending theory see chap. 1 of: Ronald A. Fisher, *The Genetical Theory of Natural Selection*, Oxford 1930. The last chapters of Fisher's book show that he, like many other geneticists of this time, was a strong eugenicist. Nevertheless, since the eugenic background was made compatible with the fitness principle already by the biome tricians, it did not seem to have much influence on the research program of the synthetic the ory. The Nazis did not rely on evolutionism but overtly claimed their own values that they ascribed to or denied humans ("lebensunwertes Leben") and used these as well as overt racism as a justification of what they intended to do. They even purged the works of Darwinists from the libraries, see p. 234 of: Diane B. Paul, Darwin, social Darwinism and eugenics, in: Jonathan Hodge, Gregory Radick (eds.), *The Cambridge Companion to Darwin*, Cambridge 2003, pp. 214-239. For reference to historical analyses of the relationship of German biolo gists to Nazi ideology, see footnote 51 below.

[26] Julian S. Huxley, *Evolution: The Modern Synthesis*, London 1942.

tionary processes. Even if Darwin should have known about Mendel's work, an issue that is not settled, he would hardly have been able to tackle the mathematical problem. Only in the 1920s did population geneticists have reason to claim that the question has to be answered in favour of genetics being the basis for evolution. But this synthesis required another adjustment of the notion of fitness.

Population genetics describes the distribution of alleles in a population in a quantitative way. Only basic statistical and combinatorial methods are needed to deduce some basic rules of allele distribution, like the Hardy-Weinberg law.[27] But as long as such equations do not refer to natural selection, they do not describe Darwinian selection. At this level, Mendelism and Darwinism still were two independent bodies of knowledge. They were mutually compatible, but isolated, and therefore cannot be regarded as constituting one coherent web of belief. Introducing the notion of fitness into population genetic equations bridged the gap between both fields. This was done in the 1920s by Ronald A. Fisher, Sewall Wright, and J. B. S. Haldane. The way this integration was achieved may be regarded as a two-step process: The population genetical equations dealt with genotypes only. So the first step was to assign fitness no longer to the phenotype, but to the genotype. This was plausible because the genotype was thought to determine the phenotype completely. (The nature-nurture and other debates challenged this view later on.) And since Mendel had shown that genes for different traits are inherited independently (segregation rule), it seemed to be plausible to deal not only with the fitness of whole genotypes, but to assign to each allele a share of the fitness value by which it contributes to the overall fitness of an organism. These shares were regarded as being additive (which was an educated guess at best, in analogy to the segregation rule).[28]

In addition to this first step, a measure for fitness was needed. The second step established such a measure, which could easily be gained from the selection principle. According to this principle, the fitter will survive; the less fit will die before it can reproduce. So fitness may be estimated by survival rates. How are these rates to be determined? The biometrician's legacy was to include a fertility component into the survival rate. Therefore, evolution-relevant survival can be measured by counting the number of offspring. Accordingly, the number of offspring that an individual leaves under given conditions is an estimate of its fitness under these conditions. By comparison of the fitness of individuals differing in the allele of one gene only, relative fitness values can be ascribed to each allele, as required. Survival data may now be used to ascribe fitness-contributions of single genes that are under comparative investigation. Fitness, initially being a synonym for adapted ness of an organism, became an additive property of the alleles a genotype consists of.

By this move, the notion of fitness was reshaped to integrate genetics and Darwinism into one single coherent web of knowledge. The argument leading to the

[27] See, e. g., Elliott Sober, *The Nature of Selection*, Chicago 1984, pp. 32-38.

[28] Ibid. pp. 179-178; cf. Ronald A. Fisher, *The Genetical Theory of Natural Selection*, Oxford 1930.

redefinition is perfectly sound within the framework of the modern synthesis. The empirical content of the equations includes, e. g., the prediction that fitness values of the alleles of any particular gene are independent from the genetic context, and that they are additive. However, the next two sections of my paper will deal with problems that arise as to the empirical content of the principle when the web of belief changes, or when the argument is read, beyond its scope, as a proof of Darwinism.

4. The fitness principle and general knowledge: a strange consequence of canonisation

By the middle of the 20th century, Darwinism as it was shaped by the synthetic theory had made its way into general knowledge. However, what was taken up by general knowledge was a digest of evolutionary theory only, focused around the mechanism of mutation and selection and the phrase of the survival of the fittest. In particular, it seems to have been part of general knowledge that fitness was measured by survival rates. At least, that is what can be found in accounts of Darwinism that were given by intellectuals of that time, most prominently by Karl Popper. It certainly does some injustice to Popper to concede only general knowledge of Darwinism to him, and for sure he studied the literature more carefully than many others may have done. But as he was neither directly involved in evolutionary research nor did count himself among the specialists in biological topics,[29] I hope one will forgive me classifying Sir Karl like this. Anyhow, it shall not be con cealed that Popper later on recanted the objection against Darwinism that this section of my paper will deal with.[30]

The eclectic integration of only some aspects of Darwinism into the web of general knowledge entailed another reinterpretation of the fitness principle; a reinterpretation biology still has to deal with. It resulted in an objection against Darwinism that is historically most astonishing: While Darwin's theory was hardly compatible with the web of belief of many of his contemporaries,[31] 100 years later it has not only been conceded that it gives the correct account of natural history, but that this account is even obviously true and that Darwinism collapses into a mere tautology. The tautology argument runs as follows: (i) Darwinism claims that only the fittest will survive; (ii) fitness equals the survival rate of the offspring; (iii) substituting (ii) into (i) turns (i) roughly into the claim that the survivor will survive. Consequently, the objection is raised that Darwinism is based on a mere tautology and therefore is empirically empty. (The premises, however, do not do justice to Darwinism, see below.)

29 Karl R. Popper, Natural selection and the emergence of mind, *Dialectica* 22 (1978), pp. 339-355. Excerpts are reprinted as: Natural selection and its scientific status, in: David Miller (ed.), *A Pocket Popper*, London 1983, pp. 239-246.

30 Ibid.

31 Things are similar with the web of belief of present-day creationists, who are unable to inte grate evolutionary theory into their belief in the translation of the bible they grew up with.

Popper, though he was a little bit more cautious and wrote about Darwinism as "almost tautological" only, held this view at least until 1974.[32] And though many biologists and philosophers of biology disputed this view,[33] he felt in company even with Darwinists in holding the tautology-view.[34] In Popper's thinking, Darwinism as an almost tautological theory had to be classified as a metaphysical research programme rather than as a theory with empirical content. He conceived Darwinism as an "applied situational logic".[35] This classification acknowledges that the realm of life on earth has arisen contingently. But given that the realm of biological objects is structured as it empirically has turned out, all propositions of evolutionary theory followed just from applying logical principles to the description of biological reality. So Popper accepted that evolutionary theory is based on empirical data, but denied that it can yield other propositions about this field than truisms. It should be noticed that this need not be regarded as an objection to Darwinism. Reconstructing a scientific theory as an applied logic was exactly what Carnap, in a sense an antagonist of Popper's, aimed for. He reconstructed scientific theories as axiomatic systems. According to him, theories are based on the definition of a number of concepts and their relations in the set of axioms expressed in the language of predicate logic. The theory itself then becomes an applied logic. And this in no way hinders that theorems of the system might conflict with empirical data, showing need to modify the axiomatic basis of the system.[36] Since the applicability of a theory to a range of phenomena is a matter of empirical ade quacy, a scientific theory may be tautological without being an empirically empty metaphysical research programme for this reason.

Many critics who understood the fitness principle tautologically were less concerned about giving a philosophically interesting reconstruction than Popper was, and claimed that Darwinism is scientifically useless in the end. Again, this was done mostly by non-specialists and therefore may be regarded as a view based on the deprived version of Darwinism that entered general knowledge.[37] This criti

32 Karl R. Popper, *Objective Knowledge: An Evolutionary Approach*, Oxford 1972; Karl R. Pop per, Darwinism as a metaphysical research programme, in: Paul A. Schilpp (ed.), *The Philoso phy of Karl Popper* Vol. I, La Salle 1974, pp. 133-143.

33 For reviews of the dispute, see Costas B. Krimbas, In defense of Neo-Darwinism: Popper's "Darwinism as a metaphysical research programme" revisited, in: Rama S. Singh, Costas B. Krimbas, Diane B. Paul, John Beatty (eds.), *Thinking About Evolution: Historical, Philosoph ical, and Political Perspectives*, Cambridge 2001, pp. 292-308, and Richmond Campbell, Jason Scott Robert, The structure of evolution by natural selection, *Biology and Philosophy* 20 (2005), pp. 673-696.

34 Karl R. Popper, Natural selection and the emergence of mind, *Dialectica* 22 (1978), pp. 339-355. Excerpts are reprinted as: Natural selection and its scientific status, in: David Miller (ed.), *A Pocket Popper*, London 1983, pp. 239-246.

35 Cf. pp. 134-135 of: Karl R. Popper, Darwinism as a metaphysical research programme, in: Paul A. Schilpp (ed.), *The Philosophy of Karl Popper* Vol. I, La Salle 1974, pp. 133-143.

36 Rudolf Carnap, *Einführung in die symbolische Logik, mit besonderer Berücksichtigung ihrer Anwendungen*, Wien 1954; engl. ed. New York 1958; cf. Ulrich Krohs, Wissenschaftstheore tische Rekonstruktionen, in: Ulrich Krohs, Georg Toepfer (eds.), *Philosophie der Biologie. Eine Einführung*, Frankfurt/Main 2005, pp. 299-316.

37 Cf. the examples given by Elliott Sober, *The Nature of Selection*, Chicago 1984, p. 61.

cism is justified within the body of general knowledge as it was extracted from Popper's writings, involving a deprived version of Darwinism only, as long as the applicability of the basic concepts of Darwinism is not questioned. Nonetheless, this criticism clearly misunderstands Fisher's account of fitness in terms of sur vival. The equation that relates fitness and survival was never meant to be a definition of fitness, it should help to measure it. As I have reviewed in the last section, Fisher did not define fitness by survival, but used survival as an estimate of fitness.[38] It is not astonishing at all that the estimate of fitness that relies on the selection principle cannot give an independent proof of the principle. It is useless to overstress the Fisher equation in this way. The equation shows merely how fitness adds up from contributions of particular genes (and needs to make grossly simplifying assumptions to yield this result). Since the web of general knowledge neither integrates the rationale of Fisher's definition nor acknowledges that fitness was initially defined as adaptedness, it becomes coherent upon the tautological interpretation of the fitness principle.

However, Popper's way out was more elegant and in fact gave an important push to the debate, which lasts to the present. He defined fitness as the propensity to leave offspring instead of equating fitness with the actual survival rate or the probability to survive.[39] Propensity and probability differ conceptually and the average survival rate may differ from the one to be expected from a certain propensity. Therefore, this definition escapes any suspicion of having a tautological structure.

5. Fitness and the renunciation of adaptationism: the fruitful political incorrectness

In the preceding section, we have seen how an oversimplification of Darwinism has lead to a reinterpretation of the fitness principle as a mere tautology. The tau tology occurred when the survival rate, being used as an estimate for fitness, is mistaken as its definition. Pointing at this shortcoming, however, leaves unanswered the question for a proper definition of fitness as it comes up within biology. The issue is not yet settled and my task will not be to enter the ongoing discussion about a formally correct definition, to which I will give some clues only. Most of these definitions refer to ones belonging to older webs of belief, but more interesting in the present context are the modifications they show. These are due to the modified theoretical background. I will therefore discuss in the present section the modified theoretical background that demanded, from 1979 on, a new definition of fitness to adapt the concept to the changed web of biological knowledge.

In 1979, Steven J. Gould and Richard Lewontin published their seminal paper with the flowery title "The Spandrels of San Marco and the Panglossian Para-

[38] The status of being an estimate rather than a definition is stressed by Sober, ibid. p. 43.

[39] Karl R. Popper, Darwinism as a metaphysical research programme, in: Paul A. Schilpp (ed.), *The Philosophy of Karl Popper* Vol. I, La Salle 1974, pp. 133-143.

digm."[40] They blamed the received view of Darwinian evolution, which saw an adaptation in each and every trait of a biological organism, for missing the goal to explain evolutionary history. All too often, instead of giving an explanation, Darwinists were contented with a demonstration of the mere compatibility of the fossil record and of the structure of recent organisms with the theory of evolution. Since it was regarded as impossible to close all the gaps that the fossil record leaves open with respect to the phylogenetic processes, this seemed all that could be achieved. Being content with the possible, many biologists merely aimed for showing that there might have been a plausible evolutionary way that in principle could have resulted in what can be observed, to tell an "adaptive story". The best-known example of such a story is Darwin's account of the possible evolution of the eye.[41] Gould and Lewontin pointed out that such adaptationist stories, by referring exclusively to the external conditions an organism is subjected to, ignored most important constraints of internal organisation and of historically contingent organismic structures. These constraints not only restrict evolvability, at the same time they may direct evolutionary processes as much as adaptational demands do. Therefore, adaptive stories that should make plausible the evolution of a trait may in many cases be grossly faulty. Such stories were accused of in fact explaining nothing – not because adaptationism[42] was trivially true as the tautology-objection suggests, but because trivially any trait could be explained in some way as being adaptive, independent of whether this explanation is historically correct or not and even whether the trait is adaptive at all. Gould and Lewontin argued that the organisation of an organism is as dependent on inner constraints as on adaptation to the non-living and to the living environment. And the constraints influenced survival as much as the degree of adaptation to the environment.

This view has roots, e. g., in theories of morphological self-organisation, but also in the 'neutral theory' of evolution.[43] It does not deny that adaptation plays a major role in evolution, but it demands an account of what actually occurred instead of story telling, explanation instead of sketches of what might have been possible. If nevertheless the notion of the survival of the fittest should be retained as an evolutionary principle, the informal Darwinian definition of fitness as well as

40 Stephen J. Gould, Richard C. Lewontin, The spandrels of San Marco and the Panglossian par adigm: a critique of the adaptationist programme, *Proceedings of the Royal Society London B* 205 (1979), pp. 581-598.

41 Charles Darwin, *On the Origin of Species by Means of Natural Selection*, London 1859, in: Paul H. Barrett, R.B. Freeman (eds.), *The Works of Charles Darwin* Vol. 15, London 1988, chap. VI.

42 It is an oversimplification to speak of "the" adaptationism as I do here for the sake of conve nience. Godfrey-Smith discerns different levels of adaptationism, cf. Peter Godfrey-Smith, Three kinds of adaptationism, in: Steven Hecht Orzack, Elliott Sober (eds.), *Optimality and Adaptationism*, Cambridge 2000, pp. 335-357.

43 Cf. D'Arcy W. Thompson, *On Growth and Form* (1917/42), Cambridge 1961; Motoo Kimura, *The Neutral Theory of Evolution*, Cambridge 1983. A predecessor of the neutral theory is Wagner's migration theory. Here, the sampling error that occurs upon the splitting of a popula tion replaces Darwinian selection as the determinant of which variations survive: Moritz Wag ner, *Die Entstehung der Arten durch räumliche Sonderung*, Basel 1889.

the geneticists' refinements had lost their validity. In the light of the new theoretical approach, these old definitions decoupled biological theory from the historical facts. A decoupling of the different components of a body of knowledge decreases its coherence, since high coherence requires a strong interdependence of the components of the set of beliefs.[44] So integration of knowledge about constraints as evolutionary factors caused a decrease of the coherence of the body of biological knowledge. If Darwinism should not completely be expelled from this web, the concept of fitness needed to be redefined to increase coherence of the web of belief. Usually, the original tautology objection and the triviality objection just mentioned are not regarded separately by the defenders of the fitness principle, so their attempts to overcome a tautological structure may be regarded as defending an adaptationist view against both objections at once.

The most common re-integration into the web of biological knowledge followed Popper's propensity view as mentioned in the last section. This view is not committed to the adaptationist programme and may include a component that is due to constraints. Nevertheless, most approaches put forward versions of the fitness principle that do not explicitly refer to constraints. Some authors return to fitness as adaptedness, proposing ways to avoid a tautological structure of the definition and to find a measure for this kind of fitness,[45] while others want to abandon ecological fitness altogether.[46] While some approaches discern different notions of fitness that have to be kept separate,[47] others see the need to combine different aspects within one single concept of fitness.[48] As I have promised, I will not go into detail. I wanted to show merely that the change of the web of biological knowledge that was induced by the renunciation of adaptationism entailed another need for a redefinition of the concept of fitness. This new discussion about the proper definition of fitness has emerged mainly among philosophers of biology. Notwithstanding the challenge to find a definition that is theoretically satisfying,

44 Paul Thagard, Chris Eliasmith, Paul Rusnock, Cameron P. Shelley, Knowledge and coherence, in: Renée Elio (ed.), *Common sense, reasoning, and rationality* Vol. 11, New York 2002, pp. 104-131.

45 Frédéric Bouchard, Alex Rosenberg, Fitness, probability and the principles of natural selec tion, *The British Journal for the Philosophy of Science* 55 (2004), pp. 693-712.; Alex Rosen berg, Frederic Bouchard, Matthen and Ariew's obituary for fitness: reports of its death have been greatly exaggerated, *Biology and Philosophy* 20 (2005), pp. 343-353; Richmond Camp bell, Jason Scott Robert, The structure of evolution by natural selection, *Biology and Philoso phy* 20 (2005), pp. 673-696.

46 Mohan Matthen, André Ariew, Two ways of thinking about fitness and natural selection, *The Journal of Philosophy* 99 (2002), pp. 55-83; Mohan Matthen, André Ariew, How to under stand casual relations in natural selection: Reply to Rosenberg and Bouchard, *Biology and Philosophy* 20 (2005), pp. 355-364.

47 André Ariew, Richard C. Lewontin, The confusions of fitness, *The British Journal for the Phi losophy of Science* 55 (2004), pp. 347-363; Cf. pp. 699-700 of: Frédéric Bouchard, Alex Rosenberg, Fitness, probability and the principles of natural selection, *The British Journal for the Philosophy of Science* 55 (2004), pp. 693-712.

48 Elliott Sober, The two faces of fitness, in: Rama S. Singh, Costas B. Krimbas, Diane B. Paul, John Beatty (eds.), *Thinking About Evolution: Historical, Philosophical, and Political Per spectives* Vol. 2, Cambridge 2001, pp. 309-321;

biologists are using operational definitions that satisfy the requirements of local arguments, e. g., based on hatching rates or even on mating numbers. By such definitions, the local coherence of a section of the web of belief is increased, which allows circumventing the remaining problems with the intimately related larger issue of the global concept of fitness.

6. Conclusion: How webs of belief are adjusted

The different interpretations and the reshaping of the fitness principle that occurred during the last century were reconstructed in the preceding sections as rational responses to the modified systems of background knowledge, which saved the coherence of the web of biological knowledge in each single case. In the first example, the eugenicist web of belief of the Victorian biometricians, the most important uptake of a fertility component into the selection principle was not sufficiently motivated by empirical results. Instead, it increased the coherence of the biometricians' web of belief by linking their biological and their socio-political beliefs. The next example, the web of belief of the population geneticists, initially showed inconsistencies between its Mendelist and its Darwinist components. This required not only a reinterpretation of the Darwinian concept of variation in terms of mutations; it demanded as well the division of fitness into contributions of individual alleles to overall genotype fitness. Third, the web of general biological knowledge in the mid-20th century embraced a deprived version of Darwinism. This gave rise to the tautology interpretation of the fitness principle and consequently to a critique of the synthetic theory, which increased the coherence of the web of belief, though it made Darwinism fairly uninteresting. And, finally, the renunciation of the research programme of adaptationism caused a decrease of the coherence of the web of biological knowledge that initiated a new debate on the issue. Several of the different recent approaches attempt to overcome the loss of coherence by specification and redefinition of the concept of fitness, thereby trying to re-establish adaptationism in a way that escapes the criticism, or by expelling the concept of fitness completely.

This survey shows that the fitness principle was not stable with respect to changes of the embedding context. Gayon stresses the context dependence even of the acceptability of the original Darwinian hypothesis:

> "Today's Darwinism was indeed founded by Darwin, but the theoretical and experimental context of the Darwinian hypothesis had to be utterly changed for it to become even plausible."[49]

The theoretical and experimental context Gayon talks about has to be conceived rather widely, as a whole web of biological knowledge and often even embracing non-biological beliefs. Anyhow, his statement has to be supplemented by the observation that not only has the context of the Darwinian hypothesis changed; the

[49] Jean Gayon, *Darwinism's Struggle for Survival*, Cambridge 1998, p. 398.

hypothesis itself has changed as well—which happened partly in response to modifications of the context it was embedded into. Such context sensitivity has often raised the question whether internal or external explanations hold, whether the changes of a scientific theory were introduced for scientists' own rational reasons, or as effects of the conditions science was subjected to in different times. To refer to the increase of coherence of a web of belief by rational reasons as an explanation of scientific change does in a way commit to the internalist view. It is the web of a scientists' own beliefs that requires rational changes of some of its elements. On the other hand, a web of belief may involve significant non-biological components, including socio-political beliefs, and it is not private, but shared by a scientific community. Therefore, the approach that I have followed seems to involve some commitment to externalist explanations of theory dynamics as well. This may appear to be problematic: David Hull, e. g., has recently criticised the externalist explanation that attributes the competitive approach of Darwin's evolutionary theory to the Victorian society and own social status,[50] and I completely agree with his view. Pointing out that the development of the conceptions of fitness in different countries paralleled each other, under completely different socio-political conditions, might even strengthen the critique: The views of the German biologists Wilhelm Ludwig and Nikolai Timoféeff-Ressovsky in the 1930s were very close to those of Fisher, Wright, and Haldane, though they worked in Nazi-Germany, under politically and socially completely different conditions than those holding for their British and American colleagues.[51] Anyhow, since there is no doubt that different causes may have similar or even identical effects, such a comparison cannot prove external explanation wrong. A proof against external explanations would need to demonstrate instead that identical external causes give rise to different results, but this can hardly ever be achieved. So a strict refutation of any relevance of external explanations will not be possible. However, the view of a complete disjunction of explanation by external causes or internal reasons seems to be simplis tic anyway.[52] The analysis based on webs of belief allows for a more differentiated view. Though a coherentist approach puts forward an internalist explanation, it is

50 David L. Hull, Deconstructing Darwin: evolutionary theory in context, *Journal of the History of Biology* 38 (2005), pp. 137-152.

51 Some recent work reconstructs the situation of the Modern Synthesis in Germany: Thomas Junker, *Die zweite Darwinsche Revolution. Geschichte des Synthetischen Darwinismus in Deutschland 1924 bis 1950*, Marburg 2004, pp. 306-328. Nevertheless, many German Biolo gists strongly supported the Nazi ideology, cf. Thomas Junker, Uwe Hoßfeld, The architects of the evolutionary synthesis in national socialist Germany: science and politics, *Biology and Philosophy* 17 (2002), pp. 223–249; Uwe Hoßfeld, Staatsbiologie, Rassenkunde und Moderne Synthese in Deutschland während der NS-Zeit, in: Rainer Brömer, Uwe Hoßfeld, Nicolaas A. Rupke (eds.), *Evolutionsbiologie von Darwin bis heute*, Berlin 2000, pp. 249–305; Thomas Junker, Synthetische Theorie, Eugenik und NS-Biologie, in: Rainer Brömer, Uwe Hoßfeld, Nicolaas A. Rupke (eds.), *Evolutionsbiologie von Darwin bis heute*, Berlin 2000, pp. 307–360.

52 This was pointed out several times with respect to the development of Darwinism, e. g., Robert M. Young, Malthus and the evolutionists: the common context of biological and social theory, *Past and Present* 43 (1969), pp. 109-145; David L. Hull, Deconstructing Darwin: evolutionary theory in context, *Journal of the History of Biology* 38 (2005), pp. 137-152.

not committed to rejecting external influence altogether. It accounts for the influence of external factors on theory formation indirectly, in so far as they are reflected in socio-political and biological beliefs of an individual or of a scientific community.

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