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► **To cite this version:**

Nicola Bertoldi. Adaptation and optimality in evolutionary biology: Historical and philosophical perspectives on the interpretations of R.A. Fisher’s “Fundamental theorem of natural selection” and the “Formal Darwinism” project. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, 2020, 81, pp.101285 -. 10.1016/j.shpsc.2020.101285 . hal-03490921

**HAL Id: hal-03490921**

**<https://hal.science/hal-03490921v1>**

Submitted on 22 Aug 2022

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**Title :** *Historical and philosophical perspectives on optimality and adaptation in evolutionary biology: the interpretations of R.A. Fisher's "Fundamental theorem of natural selection" and the "Formal Darwinism" project*

### **Acknowledgments.**

I am hugely grateful to Professor Jean Gayon, whose inspiration was key in launching this editorial project.

I am also indebted to my fellow guest editor, Professor Tim Lewens, and to Philippe Huneman for assisting me at various stages of this project.

This work has been funded by the ANR Grant "Explabio", #13 BSH3 0007, and by the Laboratoire International Associé CNRS Paris-Montréal ECIEB.

## **Historical and philosophical perspectives on optimality and adaptation in evolutionary biology: the interpretations of R.A. Fisher's "Fundamental theorem of natural selection" and the "Formal Darwinism" project**

Darwin's theory of evolution by natural selection is arguably a thorough attempt to provide a naturalistic interpretation of the prevalence of adaptation and design-like features in the organic world. Since the rise of the modern version of Darwinian evolutionary theory, i.e. the "Modern Evolutionary Synthesis", several attempts have been made to theoretically ground the tools through which evolutionary biologists regard, ascribe or explain design and adaptation in their daily practice. Such proposals are all dependent on the various mathematical frameworks elaborated by the founders of the Modern Synthesis, as well as by later contributors working in such fields as behavioural ecology or population genetics. This special issue is thus a contribution to the historical and philosophical clarification of the stakes that are involved in those attempts to formally define and ground such related concepts as adaptation, design and optimality within the framework of the current disciplinary matrix of evolutionary biology, which has arisen between the 1920s and the 1940s, as a synthesis of concepts, methods and models from multiple disciplines of the life sciences (Dobzhansky 1949; Mayr & Provine 1980). More precisely, such a framework has first stemmed from the synthesis of biometrics and Mendelian genetics (Gayon 1998, Provine 2001), based on a proof of the consistency of two different mathematical frameworks, i.e. the statistical analysis of the correlations between the heritable characters of relatives and the quantitative description of inheritance patterns provided by Mendel's scheme of allele transmission (Fisher 1918). Modern theoretical population genetics has expanded on this achievement, chiefly through mathematical modelling, by establishing the foundations for the rigorous analysis of the production and the selection of hereditary variations, which Darwin's theory of evolution had not been able to accomplish (Kimura & Crow 1970; Hartl & Clark 2007).

By supplementing evolutionary biology with genetic analysis, the synthesis of biometrics and Mendelian genetics has brought about a new understanding of evolution. In the light of population genetics, evolution is regarded as the process of modification of the genetic composition of a given population that is caused by natural selection and other evolutionary forces (Dobzhansky 1937). R.A. Fisher's "Fundamental theorem of natural selection" (Fisher 1930), or FTNS, has played a crucial role in enabling this view of evolution, by equating the rate of change of a population's mean fitness to its genetic variance in fitness. According to its "modern" interpretation (Edwards 1994), the FTNS implies a two-pronged causal analysis that elucidates the genetic basis of the

process of natural selection: on one side, the concept of genetic variance in fitness allows isolating the portion of fitness variance that is explained by the genetic composition of the population in question; on the other side, the positive change in mean fitness that the FTNS allows to quantify is nothing but the change caused by the action of natural selection on gene frequencies, as opposed to the one that is brought about by the influence of environmental conditions (in an extended sense of the term, i.e. including the genomic backgrounds of single alleles). The consequence of the theorem is the analytical derivation of a fitness increasing effect of natural selection. In this sense, Fisher's FTNS can be regarded as the first attempt to translate the design-yielding character of natural selection in a mathematical framework, thus conferring Darwin's principle an epistemological status that is akin to that of physical laws<sup>1</sup>. However, to what extent is such an interpretation of the FTNS justified? How relevant is this theorem for understanding recent attempts to ground the evolutionary concepts of selection, adaptation and optimality in a formal framework, such as the Price equation (Price 1970), Hamilton's kin selection theory (Hamilton 1964) or Alan Grafen's "Formal Darwinism" project (Grafen 2014)? In what respects do those attempts allow us to reevaluate some fundamental tenets of the Modern Evolutionary Synthesis and what are their broader implications for our understanding of evolutionary processes?

The various contributions that are included in this special issue explore different facets of those questions. For instance, Alan Grafen focuses on the fundamental goals of formal Darwinism and its relevance for the understanding of the synthesis between Darwinism and Mendelism. His project aims, namely, to bridge the gulf between two different formal approaches to evolution, by grounding the naturalisation of design and teleology in terms of the "individual-as-maximising-agent" analogy – inspired by microeconomic reasoning – into the analytical framework of population genetics (Grafen 2014). To this aim, formal Darwinism develops a mathematical framework consisting in a meta-model that unifies two classes of mathematical models: population genetics models of gene frequency dynamics and adaptationist fitness-optimisation models. In this issue, Grafen insists on the fact that such an attempt should be regarded as a generalisation of Darwin's statement that natural selection functions as an improving process, the aim of which is to found Darwinism on Mendelism, in continuity with Fisher's FTNS. Philippe Huneman and Tim Lewens both expand on and provide some criticisms of Grafen's project. More precisely, Huneman offers an interpretation of formal Darwinism as a conceptual link established between population genetics and behavioural ecology's adaptationist models, without any empirical commitments, and

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<sup>1</sup> R.A. Fisher (1930) himself famously compared the FTNS to the second principle of thermodynamics.

argues that such a framework enables a Darwinian interpretation of both the design of organisms and the individual traits as adaptations. Lewens draws a comparison between traditionally “Paleyian” conceptions of natural design and “Neo-Paleyian” ones, rooted in a tradition of evolutionary theorising that proceeds from Darwin to Grafen. He thus argues that the most relevant forms of recent neo-Paleyianism are better understood as attempts to draw on Fisher’s FTNS to identify a “criterion of evolutionary design”, rather than to prove that selection reliably succeeds in increasing fitness and/or that selection reliably produces good design. In connection to the first three papers, Warren J. Ewens provides an alternative formulation of the FTNS, which he sees as “deficient” when understood as a quantification of the evolutionary effect of natural selection in a diploid Mendelian population. Consequently, he proposes a new theorem, which focuses on the changes in gene frequencies under natural selection and not, as does R.A. Fisher’s one, on changes in mean population fitness.

The remaining three papers address problems that are particularly relevant for the second prong of Grafen’s project, i.e. the attempt of making sense of adaptive behaviours through the lenses of fitness-maximisation models. Jonathan Birch lays out a distinction between two roles for a fitness concept in the context of explaining cumulative adaptive evolution, i.e. “fitness as a predictor of gene frequency change” and “fitness as a criterion for phenotypic improvement”. He then argues that Hamilton’s definition of inclusive fitness in the framework of his kin-selection theory is best understood as “a criterion for improvement and a standard for optimality”, rather than as a predictor. Johannes Martens provides another contribution to the understanding of both Hamilton’s theory and the theoretical importance of inclusive fitness by contrasting two mathematically equivalent way of modelling the evolution of altruistic behaviours, i.e. a “direct fitness”-based approach and an “inclusive fitness”-based one. Drawing on an analogy between the structure of inclusive fitness theory and that of causal decision theory, Martens argues that only the inclusive fitness framework can provide us with a proper and unambiguous causal partition of the relevant variables involved in the evolution of altruism. Cédric Paternotte reviews both Grafen’s formal Darwinism and Hamilton’s theory by focusing on the theoretical problems that are raised by the “individual-as-maximising-agent” analogy: does natural selection tend to maximise something? Does it produce individuals that act as if they maximised something? To clarify those questions, he compares local approaches to such an analogy with global ones and argues that the latter are conceptually on a par with the former, as well as heuristically advantageous in their own merit. As a result, this special issue brings together contributions from philosophy, history of science and evolutionary biology to discuss both the advantages and the shortcomings of various efforts to devise a naturalistic and rigorous explanation of design and purposiveness in living nature, while

analysing the relations, affinities and antagonisms that have existed between such attempts throughout recent conceptual history, discussing the whys and wherefores of optimisation models in the history of evolutionary biology, as well as clarifying the conceptual ties between adaptationism, microeconomics, teleology and Darwinism. In conclusion, we would like to dedicate this special issue to the loving memory of Professor Jean Gayon, whose contribution was essential to organising the workshop that served as a blueprint for this editorial project and who sadly passed away almost two years ago. Many of the contributors to this special issue have had the privilege to be inspired by him as an author, a colleague or a teacher and, for this reason, we are all indebted to him.

## Bibliography

- Crow, J., Kimura, M. (1970). *An Introduction to Population Genetics Theory*. Caldwell, NJ: Blackburn Press.
- Dobzhansky, T. (1937). *Genetics and the Origin of Species*. New York: Columbia University Press.
- Dobzhansky, T. (1949). Towards a Modern Synthesis. *Evolution*, **3**(4): 376-377.
- Edwards A.W.F. (1994). The Fundamental Theorem of Natural Selection. *Biological Reviews*, **69**(4): 443-474.
- Fisher, R.A (1918). The Correlation Between Relatives on the Supposition of Mendelian Inheritance. *Transactions of the Royal Society of Edinburgh*, **52**(2): 399-433.
- Fisher, R.A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Gayon, J. (1998). *Darwinism's Struggle for Survival: Heredity and the Hypothesis of Natural Selection*. Cambridge: Cambridge University Press.
- Grafen, A. (2014). The Formal Darwinism Project in Outline. *Biology and Philosophy*, **29**(2): 155-174.
- Hamilton, W.D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology*, **7**: 1-52.
- Hartl, D., Clark A. (2007). *Principles of Population Genetics*. Sunderland: Sinauer. (First published 1980)
- Mayr. E., Provine, W. (1980). *The Evolutionary Synthesis: Perspectives on the Unification of Biology*. Cambridge, MA: Harvard University Press.
- Price, G. (1970). Selection and Covariance. *Nature*, **227**(5257): 520-521.
- Provine, W. (2001). *The Origins of Theoretical Population Genetics*. Chicago: Chicago University Press. (First published 1971)