



Analysing nature's experiment: Fisher's inductive theorem of natural selection

A.W.F. Edwards

Gonville and Caius College, Cambridge, CB2 1TA, UK



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ABSTRACT

The paper by Ewens and Lessard (2015) adds to the progress that has been made in exploring the discrete-generation analytical version of Fisher's Fundamental Theorem of Natural Selection introduced by Ewens (1989). Fisher's continuous-time theorem differs from the version described by Ewens and Lessard by using a different concept of fitness. Ewens and Lessard use the conventional 'viability' concept whereas for Fisher the fitness of a genotype was its relative rate of increase or decrease in the population. The sole purpose of the present paper is to emphasize the alternative inductive nature of Fisher's theorem, as presented by him in 1930, by placing it in the context of his contemporary development of the analysis of variance in agricultural experiments. It is not a general discussion of the theorem itself.

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1. Introduction

Ewens and Lessard (2015) 'On the interpretation and relevance of the Fundamental Theorem of Natural Selection' is a rigorous exploration of one way of approaching Fisher's Fundamental Theorem ('FTNS' Fisher, 1930). Here I argue that their approach is not a true reflection of Fisher's purpose and therefore that the 'problems' that they see in the theorem are particular to their own development, as they partly recognize.

Rather than as an attempt to model natural selection, Fisher's FTNS may be viewed as an analysis of the effect of selection on a character at a single moment in time, comparable to the analysis of an agricultural experiment. The major differences are (1) that nature's experiment of Darwinian evolution is not a designed one and (2) that the error terms which occur in an agricultural analysis are in the genetical case high-order effects, and the population is considered infinite. Tests of significance do not arise. These differences are irrelevant to the force of the analogy with agricultural experiments since the basic idea of Fisher's analysis of variance carries over into FTNS. Moreover, in one general respect the analogy is particularly appropriate: unlike the development in Ewens and Lessard the purpose of FTNS is inductive, drawing out information about the present effect of selection in just the same way as the analysis of a field experiment draws out information about the effect of, say, different types of fertilizer. Nature's experiment

is a factorial experiment and the genes (or gene-complexes) are the factors.

I present three types of evidence in support of this view. First, the evidence of what Fisher wrote, both in *The Genetical Theory of Natural Selection* (1930) and in subsequent publications and letters. Secondly, the background of his path-breaking developments in statistics at Rothamsted which were contemporary with the writing of *The Genetical Theory*. Thirdly, Fisher's later insistence that FTNS was not a potential theory to be compared with Wright's adaptive surfaces.

I disclaim any originality for this viewpoint. Naturally I believe it was Fisher's. Of the commentaries on FTNS prior to Price (1972), Bennett (1956) and Kimura (1958) understood it, while Kempthorne (1957) would have done had he not fallen at the last fence by failing to interpret his mathematics in Fisher's sense that FTNS referred to the increase in mean fitness attributable solely to the change in gene frequencies.

Price (1972), who was not familiar with Bennett (1956), was rather dismissive of 'The geneticists who have published derivations of what they thought was Fisher's theorem' because they 'have in most cases shown that the relation [total rate of change = genic variance] holds under special conditions'. Presumably this is a reference to Kempthorne (1957) and Kimura (1958), and while this may be fair to Kempthorne it is not fair to Kimura, whose paper, wrote Price, was 'based on the usual interpretation of Fisher's theorem as an equation for the [total rate of change]'. On the contrary, Kimura partitioned the rate of change into three components and came to the same conclusion as Price fourteen years later, that the additive genetic variance only contributed 'the part

E-mail address: awfe@cam.ac.uk.

of increase in fitness due to the improvement of the *genic* constitution of the species'. Ewens (1989) called this 'the partial change'. Price's is a valuable commentary with many supporting quotations from Fisher (1930, 1941), but it is not an ideal introduction for a first study of FTNS, and I myself have been more influenced by re-reading Kimura (1958). For further information on these historical points and an interpretation of Fisher's continuous-time original see Edwards (2014).

2. The analysis-of-variance structure

FTNS is a development starting from Fisher (1918) 'The correlation between relatives on the supposition of Mendelian inheritance' in which he wrote 'The contributions of imperfectly additive genetic factors divide themselves for statistical purposes into two parts: an additive part which reflects the genetic nature without distortion, ..., and a residue which acts in much the same way as an arbitrary error introduced into the measurements'. Here in embryo is the regression of genotypic value on gene number and the associated analysis of variance. In 1935 Fisher remarked in a letter (Bennett, 1983, p.260): '...we ordinarily count as genetic only such part of the genetic effect as may be included in a linear formula and ...we make a present to the environmentalists of such variation due to the combined action of genetic and environmental causes as is not expressible in such a formula' (an explicit recognition of his idiosyncratic use of 'environment' to include all the non-linear effects such as dominance and epistasis). We should note that Fisher's 1918 view that the 'additive part ...reflects the genetic nature without distortion' needs careful interpretation because the effects of the genes inherited by the next generation will depend on how they are distributed among the genotypes (see Falconer, 1985). A gene does not have a unique effect: in the presence of dominance its effect depends on the allele it is paired with, so one may only speak of its average effect in a particular population.

Ewens and Lessard observe that 'The relevance of the additive genetic variance in plant and animal breeding programs via the concept of heritability is central'. It is the same in FTNS. The analysis of variance identifies the 'main effects' of the genes with the additive genetic variance, Fisher treating the higher-order terms as environmental.

3. The inductive purpose of FTNS

At the 6th International Congress of Genetics at Cornell Fisher (1932) contrasted his approach to the study of evolution in the light of Mendelian genetics to that of J.B.S. Haldane. In 1924 Haldane had started publishing a long series of papers 'A mathematical theory of natural and artificial selection' (Haldane, 1924) in which he worked out the consequences of selection for a large variety of Mendelian models, usually with discrete generations and infinite population size. Fisher called this approach 'analytic and deductive': 'Genetic studies are regarded as revealing the mechanism connecting cause and effect, from a knowledge of which the workings of the machine can be deduced and the course of evolutionary change inferred' (p.165). His own approach, by contrast, was 'inductive and statistical'. That is, he was – by implication in *The Genetical Theory* and in particular FTNS – using statistical methods such as the analysis of variance and fixed- x regression to elucidate inductively the fundamental feature of the operation of natural selection. There was no intention to predict the course of evolutionary change by adopting a specific Mendelian model and none was implied by his analysis beyond the basic laws of Mendelian inheritance.

A more recent recognition of the inductive nature of FTNS is in 'The inductive theory of natural selection' (Frank, 2014). According

to Frank 'Fisher's fundamental theorem is a simple invariance. ...[It] shows that the change in mean fitness by selection is invariant to all details of variability in the population except the variance associated with the transmissible predictors'.

4. The influence of Rothamsted

From his appointment as statistician to Rothamsted Experimental Station in 1919 and throughout the 1920s Fisher developed the analysis of variance, randomization and experimental design at an astonishing rate, writing *The Genetical Theory* in the evenings. Already in 1925 the first edition of *Statistical Methods for Research Workers* (Fisher, 1925) had contained two sections 'Technique of Plot Experimentation' and 'The Latin Square', but the most convenient summary of the background to these developments is his later *The Design of Experiments* (Fisher, 1935) which grew out of the material in *Statistical Methods*.

Introducing FTNS in *The Genetical Theory* in 1930 Fisher explained (p.22) 'The object of the present chapter [II] is to combine certain ideas derivable from a consideration of the rates of death and reproduction of a population of organisms, with the concepts of the factorial scheme of inheritance, so as to state the principle of Natural Selection in the form of a rigorous mathematical theorem, by which the rate of improvement of any species of organisms in relation to its environment is determined by its present condition'. To interpret Fisher's word 'factorial' reference may be made to *The Design of Experiments* Chapter VI 'The factorial design in experimentation'. As Fisher remarked in his Bateson Lecture in 1951 (Fisher, 1952) '...the "factorial" method of experimentation ...derives its structure, and its name, from the simultaneous inheritance of Mendelian factors' (the usual word employed by the early Mendelians).

In FTNS the 'factors' are the genes themselves and their additive effects are the 'main effects' in a 'factorial scheme'. The treatment is that of the analysis of variance applied to the regression of genotypic measure on gene number. Concentrating on a single diallelic locus, Fisher called the change caused by substituting one allele by another as represented by the slope of the regression line 'the average effect of a gene substitution' on the measure (his example was human stature). With this definition the effect of changing from one homozygote to the heterozygote is the same as changing from the heterozygote to the other homozygote, so the average effect is this quantity too. Fisher called the variance accounted for by the regression the 'genetic variance' (using the word 'genetic' as the adjective from 'gene') as opposed to the overall 'genotypic variance'. His contrast in meaning between 'genetic' and 'genotypic' escaped some commentators and the genetic variance soon became the 'additive genetic variance' and latterly the 'genic variance', a phrase which incidentally had Fisher's approval.

By contrast, the 'average excess (in stature) associated with the gene substitution in question' was arrived at by imagining half the heterozygotes to be grouped with each of the homozygotes and taking the difference between the average statures of these imaginary groups. Unlike the average effect, this was an exact concept not dependent on regression. Of course if the genotypic values were themselves linear (the case of no dominance) then the two measures were the same, but Fisher did not assume this.

As to 'certain ideas derivable from a consideration of the rates of death and reproduction of a population of organisms', this is a reference to his development of Malthusian parameters of population increase, but it is a complexity not necessary for an understanding of FTNS, where, as we shall see, ordinary rates of increase can be used in the first instance (Edwards, 2014).

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