

Scientific Understanding and Mathematical Abstraction

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Abstract This paper argues for two related theses. The first is that mathematical abstraction can play an important role in shaping the way we think about and hence understand certain phenomena, an enterprise that extends well beyond simply representing those phenomena for the purpose of calculating/predicting their behaviour. The second is that much of our contemporary understanding and interpretation of natural selection has resulted from the way it has been described in the context of statistics and mathematics. I argue for these claims by tracing attempts to understand the basis of natural selection from its early formulation as a statistical theory to its later development by R.A. Fisher, one of the founders of modern population genetics. Not only did these developments put natural selection on a firm theoretical foundation but its mathematization changed the way it was understood as a biological process. Instead of simply clarifying its status, mathematical techniques were responsible for redefining or reconceptualising selection. As a corollary I show how a highly idealised mathematical law that seemingly fails to describe any concrete system can nevertheless contain a great deal of accurate information that can enhance our understanding far beyond simply predictive capabilities.

Keywords mathematical abstraction · natural selection · population genetics

Introduction: Some Background, Examples and Generalities

As the title suggests my goal in this paper is to examine the relationship between mathematical abstraction and our understanding of natural phenomena/systems. It is tempting to think that the greater the degree of abstraction used in describing phenomena the less understanding we have with respect to its concrete features. I want to challenge that myth by showing how mathematical abstraction can aid us in understanding phenomena in ways that more empirically based investigation cannot. I have chosen to focus on the role of mathematics in biology, specifically population genetics, not only because we are often suspicious about the use of mathematical abstraction in biology but also because it provides a particularly nice example of how mathematics can change our understanding of biological

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phenomena/processes. But, before saying more about the specifics of my argument let me offer some philosophical background to situate the discussion.

Even without bringing mathematics into the equation the very notion of what it means to ‘understand’ is by no means straightforward. Philosophical attempts to ‘understand’ understanding are usually linked to the equally controversial notion of explanation, more specifically, the task of conveying information in a way that will answer a why- or how-question. Typically scientific understanding, especially in physics, is the result of applying both general principles and more specialized models that enable us to describe, predict and explain specific types of behaviour. This is not to say that an appropriate answer to every question must invoke both strategies but simply to recognize that certain kinds of questions demand certain kinds of answers. In other words, the idea that explanation and understanding can be achieved solely on the basis of fundamental laws and initial conditions, as described by the D-N model, is now thought to be insufficient for understanding much of the physical world. We need a variety of things, fundamental theory, different kinds of models as well as laws that constrain the kinds of behaviours that systems display.

One of the things that renders laws explanatory, as highlighted by the D-N model, is the fact that they are general enough to apply to a diverse number of phenomena. In other words, they enable us to understand specific features of phenomena as similar in certain respects; for example, universal gravitation shows that both terrestrial and celestial bodies obey an inverse square force law. Nancy Cartwright (1983) claims that this generality is a reason for thinking laws are false; their generality results in their being unable to fully describe the situations they reportedly cover, or they deliberately omit aspects of the situation that are not relevant for the calculation at hand. In that sense they don’t accurately describe concrete situations. Part of her reason for claiming that covering laws are false is to contrast them with phenomenological laws (or models) which supposedly do give us more accurate descriptions of the physical world. But, since all scientific description embodies a certain amount of abstraction it is difficult to know where to draw the line here. Ignoring the things that are seemingly irrelevant and idealising objects and relations that are too complex to describe in detail are necessary features of science and part and parcel of laws, theories and models as well. While it is certainly true that we distinguish between phenomenological and more fundamental laws it is usually the former that are thought of as giving an incomplete description of the situation at hand. Typically fundamental laws are thought to furnish a better understanding of why phenomena behave as they do because they appeal to underlying micro processes.

That issue opens the door to a related question: how does the abstraction built into theories and laws enable us, or indeed prevent us from, understanding physical systems. Initially one might think that understanding is inhibited by abstraction but we only need to look to scientific textbooks to see that this is clearly this is not the case. The kind of models that serve as exemplars in the Kuhnian sense (e.g., the harmonic oscillator, the potential well etc.) embody a great deal of abstraction yet are the corner stone of understanding essential features of certain kinds of physical systems. These models or exemplars enable us to conceive of systems as being of a particular type, exhibiting certain kinds of behaviour that allow us to classify them in terms of their general features. All of these factors enhance our understanding.

But, like explanation, understanding depends on the level of knowledge we seek and the kinds of questions we ask. For example, if we ask why a particular metal exhibits superconducting properties we can explain it in terms of zero resistivity and the accompanying thermodynamic phase transition, something that is only possible in certain kinds of metals. However, if we want to know the details of what happens at the subatomic level then we need to

invoke the BCS model complete with its description of electron–phonon interactions, Cooper pairing and the BCS wave function. From these models we can derive exact results like infinite conductivity, exclusion of magnetic fields, flux quantization and zero resistivity. But this is somewhat peculiar because how can one get exact consequences from models that are approximations. So, one now wants to understand why it is that the models work so well? The reason is because we can also understand a superconductor as a material in which electromagnetic gauge invariance is spontaneously broken and these models contain a breakdown of electromagnetic gauge invariance as a fundamental assumption. The detailed dynamical theories and models like BCS are required to explain why and at what temperatures this symmetry breaking occurs but not to derive the kinds of consequences mentioned above. In other words, these properties can be derived directly from the assumption of the spontaneous breaking of electromagnetic gauge invariance and so are consequences of general principles rather than specific approximations embodied in the model (Morrison, 2007). Regardless of whether you think of BCS as a theory or a model the point here is that there are different levels of generality that can be used to understand and explain the phenomena characteristic of superconductivity. The model provides more detail than general physical principles but still trades on a degree of abstraction and idealisation in order to be applicable to a variety of concrete cases of superconductivity.

Explanation that makes use of abstraction, idealisation and general laws is thought to be common-place in physics. However, the degree of complexity associated with biological phenomena is largely thought to rule out these kinds of explanatory strategies on the grounds that they are inappropriate for explaining and understanding what goes on in biological contexts. The inappropriateness has two distinct sources. There are those who claim that explanations that embody abstractions are simply uninformative, they don't tell us the kinds of things we need to know in order to understand the behaviour of biological phenomena. The other source is those who claim that the reductionist assumptions that underscore many explanations in physics are simply the wrong kind of methodology for biology. By ignoring the individual nature of biological phenomena we draw the wrong kinds of conclusions about complex living systems, which in turn can be used to justify undesirable social and political practices. Instead, biological explanations need to be “closer to the ground,” as it were, and appeal to the specific nature of individuals or species and their interaction with their environment.

A notable exception to this population genetics, a highly mathematical branch of biology that deals with the genetic basis of evolution. The objects of study are primarily the frequencies and fitnesses of genotypes in natural populations. Some population geneticists even define evolution as the change in the frequencies of genotypes over time, something that may be the result of their differences in fitness. Or to put it more accurately, we can model evolution by assigning fitnesses to genotypes and then following the changes in allele frequencies. The problem is that while genotype or allele frequencies are easily measured their change isn't. Most naturally occurring genetic variants have a time scale of change that is on the order of tens of thousands to millions of years, making them impossible to observe. Fitness differences are likewise very small, less than 0.01%, also making them impossible to measure directly. What this means is that although the state of a population can be observed, the evolution of a population cannot be directly studied. Hence the need for mathematics.

Like most systems that are not directly accessible one investigates them by constructing mathematical models of the evolutionary process and then comparing their predictions with the behaviour or states of the system, in this case populations, that can be directly observed.

But because one can't know the genetic structure of a species (not only would we need a complete description of the genome but also the spatial location of every individual at one instant in time which would then change in the next instant) the models need to incorporate certain idealizing assumptions that ignore the complexities of real populations. They focus on one or a few loci at a time in a population that mates randomly or has a simple migration pattern. The success of these idealised models has been remarkable and indeed the birth of population genetics itself resulted from the application of mathematical techniques and idealisations that invoked infinite populations and ideas from statistical physics. To that extent then the methods of population genetics look very much like the methods of physics. And indeed the claim by many population geneticists is that allele based models is what constitutes our *understanding* of much of the mechanics of evolution. What this seems to suggest is that, at least in the domain of population genetics, understanding in physics and biology is very similar. My claim however is a stronger one, specifically, that much of our contemporary understanding and interpretation of natural selection has resulted from the way it has been described in the context of statistics and mathematics. The implication here is that mathematical abstraction can play an important role in *shaping* the way we think about and hence understand certain phenomena, an enterprise that extends well beyond simply representing those phenomena for the purpose of calculating/predicting their behaviour.

In what follows I show how this claim is realised in attempts to understand the basis of natural selection from its early formulation as a statistical theory to its later development by R.A. Fisher, one of the founders of modern population genetics. Indeed, it was only by using the abstract mathematics of statistical mechanics that Fisher was able to show that selection was operating in Mendelian populations. Not only did this put natural selection on a firm theoretical foundation but its mathematization changed the way selection became understood as a biological process. It is perhaps important to point out that it wasn't the case that the definition of selection simply needed to be made more precise and a mathematical representation helped to clarify its status. Rather, a mathematical model was responsible for *redefining* or *reconceptualising* selection. This is important because in many cases we think of mathematical models as tools for making things precise or for representing phenomena in a mathematical way. Here the mathematics was more than a technique for achieving a specific technical result, although it did do that. This is not to say that issues regarding selectionist explanations are now settled. There is still much philosophical (and perhaps scientific) debate about the nature of these explanations, for example, can they explain the presence of individual traits and at what level does selection operate (gene, organism, etc.). My point here is just to show that the very basis of these questions depends to a great extent on an understanding of natural selection that emerged from the introduction of mathematical models in the 1920s and 1930s.

Before embarking on the details of my argument I want to first consider a very simple example of a fundamental law in biology, one that is certainly highly idealised and makes assumptions not realised in any natural population. However, what the Hardy–Weinberg law shows is how embedded in what Cartwright would call a 'false' law is a great deal of accurate information about biological populations, information that forms the basis for the synthesis of Mendelian heredity and natural selection. To that extent it reveals how some simple mathematics can enhance our understanding far beyond predictive capabilities.

Laws and Understanding

The question of whether the kinds of models used in population genetics provide explanation and *understanding* of biological processes is intimately linked to the question

of whether biology is, in any respects, similar to physics. Does the mathematical nature of models and explanation in biology provide us with understanding of populations in the same sense that mathematical laws and models in physics provide information about physical systems? As we shall see below the Hardy–Weinberg law enables us to understand fundamental features of heredity and variation by establishing a mathematical relation between allele and genotype frequencies that embodies the very gene conserving structure that is the essential feature of Mendelism. Hence, the claim that the law is false in some sense misses the point if our concern is understanding and conveying information. What is important for my purposes here is to show that the unrealistic nature of its assumptions in no way affects the significance of either the conclusions it provides or the information implicit in its formulation.

The Hardy–Weinberg law is often described as a consequence of Mendel's law of segregation, or a generalization of Mendel's laws as applied to populations. It relates allele or gene frequencies to genotype frequencies and states that in an infinite, random mating population in the absence of external factors such as mutation, selection, sampling error and migration, one generation of random mating will produce a distribution of genotypes that is a function solely of allele frequencies and does not change over subsequent generations provided all conditions are held constant. In other words, if we have a pair of alleles Aa at a particular gene locus and the initial ratio of A to a is p to q then for every succeeding generation the ratio will be p to q , and regardless of the distribution of genotypes in the initial generation the distribution for all succeeding generations will be

$$p^2 AA + 2 pq Aa + q^2 aa.$$

p^2 is just the probability of getting an AA homozygote which is the probability that the egg is A_1 times the probability that the sperm is A_1 (by the product rule for independent events). Both of these probabilities are p because in its simplest form the law assumes that the species is hermaphroditic. Since the heterozygote can be formed in two different ways the probability is $2 pq$ (by the addition rule for mutually exclusive events). So, if you know the value for p then you know the frequencies of all three genotypes. Since random mating does not change allele frequencies all one needs to calculate the genotype frequencies after a round of random mating is the allele frequencies before random mating. In populations where each individual is either male or female with different allele frequencies it will take two generations to reach Hardy–Weinberg equilibrium. One can see then the relation between the stability of the frequencies and Mendel's law of segregation. With random cross-fertilization there is no disappearance of any class whatever in the offspring of the hybrids, each class continues to be produced in the same proportion.¹

But, and here is the important point, what is significant about the Hardy–Weinberg law is not so much the binomial form of the genotype frequency and the prediction of genotypes based on the stability of the population, but rather what the stability actually shows or presupposes. Despite the idealizing assumptions the stability allows us to understand something about Mendelian populations that is crucial for understanding heredity and variation. In other words, certain conditions must be present for the stability to be possible. Thus, the predictive success of the law is intimately connected with certain basic claims about genetic structure. What the Hardy–Weinberg law says is that if no external forces act then there is no intrinsic

¹ The law of segregation refers to the fact that the characters that differentiate hybrid forms can be analysed in terms of independent pairs; that is, each *Anlagen* acts separately – they do not fuse. We can also understand this as stating that any hybrid for a given character produces an offspring distributed according to definite proportions. If the pure parental forms are A and a and the hybrid Aa then the offspring of the hybrid will be distributed according to the ratio $1A:2Aa:1a$. Pearson (1904) was probably the first to show the relation between the law of segregation and the stability of a population in the absence of selection.

tendency for the variation caused by the three different genotypes in a population to disappear. It also shows that because the distribution of genotype frequencies is independent of dominance, dominance alone cannot change genotype frequencies. In other words, there is no evidence that a dominant character will show a tendency to spread or a recessive one die out. Instead the genotypes frequencies are maintained in constant proportions. The probabilistic genetic structure is conserved indefinitely; but should it be influenced by an outside force, e.g., mutation, the effect would be preserved in a new stable distribution in the succeeding generation.

This was crucial for understanding the debate between the Darwinians, who advocated blending inheritance and the Mendelians. Under blending inheritance variation was thought to decrease rapidly with each successive generation, but Hardy–Weinberg shows that under a Mendelian scheme it is maintained. This pointed to yet another fundamental aspect of Mendelism, namely the discontinuous nature of the gene, and why it was important for the preservation of variation required for selection. How was it possible for the genetic structure to be maintained over successive generations? The reason for the stability could be traced directly to the absence of fusion which was indicative of a type of genetic structure that could conserve modification. In that sense then one can see the Hardy–Weinberg law as the beginnings of a completely new understanding of the role of mutation and selection and how they affect our understanding of evolution. A simple mathematical law that held only under highly idealised conditions could be seen as an integral part of the conceptual revolution in the understanding of heredity. To that extent the claim that the law is false in some sense misses the point if your concern is understanding and conveying information.

Re-Conceiving Natural Selection

Biology Becomes Statistics

While the Hardy–Weinberg law is based on extremely simple mathematics (basically just multiplication and probability) the conceptual revolution it began was extended by R.A. Fisher who introduced not only the analysis of variance but also the more abstract mathematics of diffusion theory, Markov chain models and branching processes into genetics. Clearly there are some results in population genetics that could not have been arrived at non-mathematically such as results in the multilocus and the stochastic theory. While this is important for increasing our understanding of certain kinds of genetical processes my focus is the impact of certain kinds of mathematical techniques on our understanding of natural selection. The process began with Karl Pearson and the development of statistical analysis as a way of framing evolutionary problems. Fisher's more abstract mathematical approach built on this statistical foundation and revolutionized our thinking about selection and the compatibility of Darwinism and Mendelism.

Despite remarkable theoretical success some eminent biologists and philosophers have voiced criticisms about the mathematical nature of the models used in population genetics. For example, in responding to R.A. Fisher's first technical paper on the topic in 1916, a paper which marks the origin on the synthesis of Mendelism with Darwinism, Punnett the referee complained that it displayed the hallmarks of treating weightless elephants on frictional surfaces.² Ernst Mayr has complained that population genetics, to the extent that it treats evolution as mere changes in gene frequency (as an input or output of genes), is like bean bag genetics involving the addition and removal of beans from a bag (1959). Here Mayr was

² As quoted in Norton and Pearson (1976).

echoing an earlier remark made by Waddington (1957) who claimed that the mathematical theory of evolution had not led to any noteworthy quantitative statements nor did it reveal any new types of relations or processes that could explain phenomena that were previously obscure. Mayer has also remarked that one cannot really understand the workings of natural selection unless one understands the uniqueness of the individual, something that population genetics clearly ignores (1982). Moreover, in a new afterward to his classic book *The Origins of Population Genetics* Provine stated that “the models of the 1930s, still widely used today, [are] an impediment to the understanding of evolutionary biology.”

As I mentioned above, what motivates many of these criticisms is the view that the methods of population genetics, with their emphasis on reduction and gene selection, simply ignore many of the important factors that figure in evolutionary development. They just aren’t explanatory in the sense that provides us with a proper *understanding* of the evolutionary process. All of this seems to presuppose that the uniqueness of biological individuals must be taken account of in ways that the uniqueness of physical objects needn’t. Idealisation and abstraction can be informative and aid our understanding of physical systems but not in the case of biological populations. A closer look reveals that not only is this *not* the case, but it is difficult to see how it *could* be the case. The fact that the mathematics of population genetics has established results that were impossible using direct observation and other types of empirical methods is certainly sufficient for claiming that it has increased our understanding of evolutionary processes. However, in order to argue my point about the changes that occurred in our understanding of selection I need to say a little about how it was understood in the context of the early statistical analyses initiated by Francis Galton and how that changed with the more sophisticated techniques introduced by Karl Pearson and later Fisher. All of these men were Darwinians. But it was Fisher’s mathematization of selection that created a new framework in which its operation was understood as an *irreducibly* statistical phenomenon, a reconceptualisation that emerges in conjunction with the evolution of specific mathematical, as opposed to purely statistical, techniques.³

To appreciate these differences we need to briefly mention the main features of natural selection as formulated by Darwin. The basic assumption is that for selection to operate there must be variability that is individually based and inherited. Natural selection itself is referred to as a power brought into play under nature through the struggle for existence and the consequent survival of the fittest. Without variability nothing can be affected; but one needs only small individual differences and these are most likely the sole means of the production of new species. So, the general process of selection involves the accumulation of variations provided by nature through the reproduction of individuals possessing those variations. To put it briefly, natural selection consists in the modification of species through an accumulation of infinitesimally small differences. But, most importantly, selection does not create variation it *requires* it. It is an ‘agent’ or a ‘power’ that either eliminates or

³ As I have argued elsewhere (Morrison, 2000) the synthesis of Mendelism and Darwinian selection was accomplished through the employment of mathematical techniques that allowed its founders (Fisher, Sewall Wright and J.B.S. Haldane) to establish the operation of selection in Mendelian populations. To that extent the synthesis produced an enhanced understanding of selection as something compatible rather than at odds with Mendelism. But, the interesting aspect of the synthesis was that while its authors, particularly Fisher and Wright, agreed on the general conclusion each had a very different account of *how* selection functioned and the conditions under which it would be most effective. I have discussed this at length elsewhere (Morrison, 2006) so I won’t rehearse those arguments here, nor do I want to go into detail about the different mathematical approaches of Fisher and Wright and the extent to which those differences influenced their interpretation of selection. Instead my concern here is with the way that the mathematical approach used initially by Fisher was responsible for restructuring our ideas about selection in ways that have informed contemporary population genetics.

diffuses variation in a population or species. As Darwin himself remarks: “Natural Selection acts by life and death – by the preservation of individuals with any favourable variation, and by the destruction of those with any unfavourable deviation of structure” (Darwin, 1859, p. 194). What is significant here is that natural selection is defined in terms of the individual. The individualistic nature of selection refers to the preservation of *individuals* that possess favourable variations that natural selection acts on.⁴ While it acts on the small inherited variations that are passed down through generations it is important to point out that this is in no way an indication that Darwin favoured a particulate theory of heredity. In fact, there was no account of heredity and variation within the Darwinian theory, consequently it lacked a firm scientific foundation.

Through the development of biometry in the late nineteenth and early twentieth centuries in the hands of Karl Pearson the growth of statistics became intimately connected with an attempt to establish Darwinism as the correct theory of evolutionary development. The biometricians saw statistics as a way of establishing a scientific ground for Darwinian natural selection. They advocated Darwin’s account of blending inheritance and even after the rediscovery of Mendel’s work in 1900 continued to oppose Mendelism as a theory of heredity. If selection could be established statistically that would obviate the need to explain the mechanisms of heredity; hence this became the goal of the biometric approach.

As I mentioned above, the statistical account of heredity began with Francis Galton (1865) who invented the statistical tools of regression and correlation and formulated a law of ancestral heredity (1889) which described the inheritance of traits from ones ancestors as a decreasing geometric ratio.⁵ Galton’s lack of a proper account of multiple correlation and regression required the correction and extension of these notions by Pearson (1895) who saw Galton’s work not as “a biological hypothesis, but the mathematical expression of statistical variates...[which] can be applied...to many biological hypotheses”(Pearson, 1930, p. 21).⁶ This law became for Pearson a purely *statistical formula* for predicting the value of a trait from ancestral values (rather than a representation of the separate contribution of each ancestor to the offspring, both of which were assumed equivalent by Galton). In other words, the emphasis was on establishing statistical facts rather than claims about individuals. The correlation of a somatic character in a great-grandparent and grandchild was not in any sense a real measure of what the former contributed to the latter, nor was the corresponding regression coefficient such a measure. Rather, what was being tested was what could be predicted, on average, about somatic characters of the offspring from what the germ plasms had produced in the past (Gayon, 1998). Hence, “contribution of an ancestor” was not interpreted literally, it was merely a tool for prediction. Pearson claimed

⁴ It is perhaps important to point out here that while Darwin thought in terms of species defined as collections of individuals he didn’t have a well worked out notion of a population in the statistical sense of the term.

⁵ The law of ancestral heredity stated that “the share a man retains in the constitution of his remote descendants is inconceivably small. The father transmits, on average, one-half of his nature, the grandfather one-fourth, the great-grandfather one-eighth; the share decreasing step-by-step in a geometrical ratio with great rapidity.”

⁶ This new law took the form of a multiple regression equation of offspring on mid-midparental ancestry:

$$P_0 = 1/2(\sigma_0/\sigma_1 P_1) + 1/4(\sigma_0/\sigma_2 P_2) + 1/8(\sigma_0/\sigma_3 P_3) \dots$$

P_0 is the predicted deviation of an offspring from the generation mean, P_1 is a linear function of the deviation of the mid-parent from that generation mean, P_2 similarly for the mid-grandparent and $\sigma_0, \sigma_1 \dots$ the standard deviation of the appropriate generations of the offspring. From this formula Pearson derived theoretical values for various regression and correlation coefficients between relatives. He also generalized the geometric series of partial regression coefficients which raised the parental correlations.

that the law of ancestral heredity was simply a statement of a fundamental theorem in statistical theory of multiple correlation applied to a particular type of statistics. If the statistics of heredity are themselves sound, the results deduced from the theorem will remain true regardless of which biological theory of heredity is in place. The proper method was the statistical theory of multiple regression – empirical knowledge of the nearer coefficients of correlation would suggest the more distant ones, which would probably be expressible as a geometric series. And, as long as the sample was large enough once could expect a reasonably accurate result. What this entailed however was that the notion of a population had become, to a great extent, a mathematical construct due to the difficulties finding populations of individuals large enough to satisfy the constraints required by biometrical statistics.

This commitment to the statistical methodology of biometry is further evidenced in Pearson's debate with the Mendelian, Bateson (1901). Pearson (1902) refused to accept any biological arguments or evidence not grounded in biometrical techniques; in other words, biology, based on experiment (other than the collection of sample data) had in some sense ceased to become a source of scientific knowledge for Pearson. Without dealing with the vital statistics of large populations it would be impossible to make any progress in the theory of evolution since no tabulation of individual instances could possibly lead to definite conclusions. So, how does this emphasis on statistical methodology distance us from Darwin's notion of selection as grounded in individual differences? Put differently, how does the reliance on statistics as a justification for the selection hypothesis change our understanding of selection itself?

Pearson had firm beliefs about the nature of individuals as well as how those individuals should be represented in the context of a proper statistical analysis. Remarks in *The Grammar of Science* (Pearson, 1900) and elsewhere reveal his belief that no two physical entities are exactly alike; instead they form a class with variation about a mean character. Hence, even in physics the ultimate basis of knowledge is statistical and the notion of sameness applied to molecules is only statistical sameness (Pearson, 1900, p. 156). Because the category of causation seems to require absolute sameness, something which does not hold even in science, it needs to be replaced with the statistical idea of a correlation between two occurrences, which is, in effect, capable of "embracing all relationships between absolute independence to complete dependence." Because science itself could not survive describing only individual experiences, its conclusions are based on average experiences, no two of which exactly agree. The variability that is characteristic of experience may be attributed to errors in observation, impurities in specimens, physical factors in the environment etc. But, when these are removed by a process of averaging, one passes from the perceptual to the conceptual and so from the real world to a "model" world (Pearson 1911, p.153). The process of statistical analysis then involved the construction of models that could, in the case of biometry, be used to predict the inheritance of certain traits from parent to offspring. Important here is the notion of sample size. Biometrical statistics was designed to apply to large samples drawn from human, plant and animal populations. And, if the samples were large enough then one could supposedly substitute the sample statistics for the population parameters.⁷

How, exactly, did Pearson's faith in statistical methodology, affect his views about Darwinism? On his view the elements of the theory – blending inheritance and selection –

⁷ Pearson himself argued in his work on the χ^2 test that the sample and population constants differed on average by terms of the order $1/\sqrt{n}$, where n is the sample size, with the difference tending to zero as n became large. Small samples simply did not provide the proper basis for statistical work.

could only be established using statistical methods since that was the only route to reliable knowledge. Does this mean that he viewed Darwinism as a statistical *theory*? Yes, but this was because he redefined the concepts in terms of a statistical methodology that for Pearson captured the essence of scientific knowledge. Variability and a modification of the mean character were important indices of a selective process. So, deviations from the populational mean type needed to be measured; that is, small innumerable variations were now defined in terms of a frequency distribution. If natural selection existed it should affect the frequency distribution of the character on which it acted, and, in order to demonstrate natural selection the mortality rate had to be shown to depend on variations in a given character. So by accumulating comparable data on the correlation between mortality rate and variation one could establish natural selection on the basis of statistical inference.

What this meant was that selection was understood in terms of heredity which was explicated in terms of a correlation coefficient, that is, the correlation between a characteristic that occurs in parent and offspring.⁸ If the correlation between the parental character and that of the offspring was zero, selection could not alter anything in the population because the composition of the offspring population would be independent of that of the parents who survived and reproduced. Using the theory of multiple correlation, Pearson hoped to incorporate all the facts of heredity and selection. He developed what he termed a ‘fundamental theorem’ that involved correlated characters measured in successive generations of the same population which made it possible, in principle, to predict the character of the offspring given an exhaustive knowledge of the character’s distribution among ancestors. He went on to distinguish natural selection from what he termed reproductive selection which was an analogue of human artificial selection, something that he thought would be one of the most powerful modification forces.⁹ The theory of selection became then a theory about a plurality of interacting agencies, where agencies simply refers to different kinds or descriptions of selective behaviour. But, at the heart of this was the power of statistics as a predictive tool. As Pearson remarked to Galton “the problems of evolution were in the first place statistical, in the second place statistical, and only in the third place biological” (1930, p.128). In other words, no attempt to *understand* selection as a causal, biological process was either possible or desirable.

Finally, how does this emphasis on statistics provide a firm theoretical foundation for selection? Using the theory of multiple correlation Pearson was able to predict, in principle, the character of offspring given knowledge of the character’s distribution among the ancestors. And, because heredity was reduced to a correlation coefficient it was capable of ‘grounding’ selection. This grounding was not understood in terms of a causal process; instead both heredity and selection were given a purely descriptive, phenomenal basis. For Pearson this was the correct methodology for science because in the end science itself was a ‘conceptual description and classification of our perceptions.... not an explanation of anything. It is not a plan which lies in the phenomena themselves” (Pearson, 1900, Ch. 7, sec. 6, p. 205). Natural selection was simply a descriptive fact that was established using a statistical argument. In that sense both our understanding of selection as a biological process and the methods appropriate for biological investigation changed dramatically with the introduction of statistical analysis. What this represented was a rejection of not just the Darwinian notion of selection as a type of causal process but also a naturalist based

⁸ The problem with this definition of course is that the correlation coefficients are extremely variable depending on both the character studied and the species.

⁹ Here Pearson’s eugenics becomes important because natural selection was thought to no longer guarantee progress in civilised man because there was no correlation in the upper classes between viability and fertility.

approach to biological investigation. Conceived of in the Darwinian way a justification of selection and indeed a science of biology would simply not have been possible according to this new methodology.

Biology between Statistics and Physics

The situation changed when Fisher entered the picture. Not only was he an advocate of Mendelism as a way of answering many of the questions about heredity and variation but he developed new mathematical/statistical techniques for representing selection in Mendelian populations. In order to synthesize Mendelism and Darwinism two things were required: (1) a statistical methodology to deal with populations that would allow for the incorporation of Mendelian genes (something biometrical statistics could not handle, cf. Morrison (2002) and (2) a new understanding of what selection was and how it operated. The latter was a consequence of the mathematics Fisher used, rather than simply an incorporation of a Mendelian theory of heredity per se. As I mentioned above, Fisher viewed Mendelism as an acceptable theory of heredity; a belief that put him at odds with Pearson and the biometricians. While the phenotype was clearly a statistical entity as measured by the biometricians and defined at the level of a population, the gene or genotype was not definable in terms of statistical parameters. Fisher's statistical account of selection would dramatically change that picture by showing that Mendelism and selection acting together could produce a successful theory of evolutionary change.

Although Mendelism was capable of predicting with certainty the possible types of children of given parents, biometry was more vague but capable of wider application. The probable measurement of particular characters of the offspring could be calculated from those of the parents and those of the general population, but large numbers of families of similar parents in that population were required before the prediction was accurate. What was needed was some way of incorporating a Mendelian model of inheritance with the appropriate kind of statistical methods. Fisher's (1911) solution was an analogy between populations construed in terms of Mendelian factors (genes) and the populations of molecules that constitute a gas. The agencies of selection always act amidst a multitude of random causes, each of which may have a predominant influence if we fix our attention on a particular individual. Yet, these agencies determine the progress or decline of the population as a whole. In the case of the kinetic theory molecules are moving freely in all directions with varying velocities, yet we can obtain a statistical result that is a perfectly definite measurable pressure. Knowledge of the nature and properties of the atom is inessential and independent of our knowledge of general principles in the way that our ability to predict and control the way populations evolve is independent of particular knowledge of individuals.

But why did Fisher think that the kinds of probabilities associated with kinetic theory would be appropriate for modelling populations of genes? The answer comes from the way in which he conceived of a Mendelian system and his views about what kinds of probabilities were appropriate for scientific inference. Fisher's gas theory analogy suggested a new way of conceptualising populations of genes that were significantly different from the way in which biometric analysis attempted to characterise populations. Pearson's requirement concerning the amount and kind of information required to describe a population made it impossible to incorporate anything more than two or three Mendelian factors (genes); the mathematics was simply too cumbersome. By introducing sophisticated diffusion techniques and relaxing the kinds of assumptions required for specifying the population structure Fisher was able to achieve a synthesis of Darwinism and Mendelism that was simply impossible using

the statistical techniques of the biometricians. In other words Fisher produced a statistical interpretation of selection that was different from Pearson's, not only because it included the notion of a gene but because the population structure was different from the kinds of populations considered by the biometricians.¹⁰ The key to understanding this difference relates not only to the kind of statistical model implicit in Mendelism but how its union with the kinetic theory model was significant for this further reconceptualisation of Darwinian selection.

If we think about the notion of chance embedded in statistical physics the probabilities concern our ignorance of causes, they are epistemic and provide descriptions that compensate for the fact that there are simply too many molecules to have knowledge of individuals. Although we think of the motions of molecules as random this is because we have insufficient knowledge to predict how any individual molecule will behave. In the case of Darwinian theory as formulated by Pearson chance was involved in the origin of inherited variation but again this was because we had no knowledge of the causes that governed these events. Because the biometricians eschewed any appeal to causes, heritable variation was expressed in terms of statistical correlation. Where Mendelism is concerned however, the situation involved a chance *mechanism* that generated with probability 1 a set of clearly defined outcomes. To that extent the genetic probabilities could be considered *objective features of the world* rather than a measure of ignorance. In other words, the randomness expressed in a Mendelian system of inheritance isn't a reflection of our lack of causal knowledge; instead it is a measure of the possible outcomes. And, once one is required to take account of genes as the mechanism of heredity, the constitution of the 'population' changes from collections of individuals in the Darwinian/Pearsonian sense to collections of genes. Consequently we need a different kind of statistical methodology to characterise the ways in which selection would operate in Mendelian populations due to the sheer numbers of genes (or factors) involved and how they distribute across the population.¹¹ Fisher's genius was to combine the *methods* of statistical physics with the inherent randomness of Mendelism to arrive at model of heredity and selection that grounded in the notion of objective chance.

What Fisher wanted to do was determine the extent to which characteristics such as stature were determined by a large number of Mendelian factors. Studies had shown that in the case of brothers the correlation coefficient is around 0.54, (amount of variance due to ancestry) which leaves 46% of the variance to be accounted for in some other way. Fisher wanted to determine how much of the total variance was due to dominance, how much resulted from other environmental causes and how much from additive genetic effects. If one could resolve observed variance into these different fractions (i.e., expressing these fractions as functions of observed correlations) then one could easily determine the extent to which nature dominated over nurture. Using the analysis of variance Fisher (1918) succeeded in distinguishing between genetic and environmental variance but also between the different components of genetic variance itself (additive and dominance).

In order to perform this kind of statistical analysis Fisher made a number of explicit assumptions that were clearly at odds with some of Pearson's (1904, 1909a, b) earlier investigations regarding a possible compatibility of Mendelism and Darwinism. Although

¹⁰ By population 'structure' I mean not just how the population was constituted but also the conditions necessary for describing that population.

¹¹ This also has important implications for the differences in interpreting probability in Pearson's and Fisher's work but that is a much longer story and one that I won't go into here.

Pearson believed that biology differed from physics in the sheer number of variables one needed to take account of in any single case of inheritance, he did think that there were certain features of a population that needed to be specified in order to arrive at a proper statistical description. Perhaps the most important difference between Fisher and Pearson was Fisher's assumption of an indefinitely large number of Mendelian factors which seemed not only out of the region of experiment using Mendelian methods but was also mathematically intractable for biometrical statistics. In the context of the latter the mathematical difficulties arose because Pearson assumed that for each Mendelian factor one needed to know certain specific information:

- Which allelomorph was dominant
- To what extent did dominance occur
- What were the relative magnitudes of the effects produced by different factors
- In what proportion did the allelomorphs occur in the general population
- Were the factors dimorphic or polymorphic, to what extent were they coupled etc.

One can begin to see then that an analysis involving a large number of genes was virtually impossible using biometrical techniques. In addition to the information above there were more general considerations that also needed to be taken account of such as the effects of homogamy (preferential mating) as opposed to random mating and selection vs. environmental effects; all of which needed to be treated separately if one was to determine the genetic basis of the inheritance of particular characteristics. Pearson thought that if one assumed an indefinite number of Mendelian factors then the nature of the population could not be specified in any complete sense; thereby undermining any statistical result that might follow. In other words, we need certain kinds of information about individuals that make up a population in order for our methodology to give us reliable results.

However, if one takes as a model the velocity distribution law in statistical physics, then just as a sufficiently large number of independent molecules would exhibit a stable distribution of velocities, a sufficiently large number of Mendelian factors or genes in a population should enable one to establish general conclusions about the presence of particular traits. Contra Pearson, Fisher did not assume that different Mendelian factors were of equal importance so all dominant genes did not have a like effect. In order to simplify his calculations Fisher also assumed random mating as well as the independence of the different factors. Finally, because the factors were sufficiently numerous some small quantities could be neglected. So, not only did Fisher differ from Pearson with respect to specific assumptions about the *nature* of Mendelian factors (that all were equally important, etc.) but assumptions necessary to characterise a Mendelian population were much more general. By assuming an indefinite number of factors it was possible to ignore individual peculiarities and obtain a statistical aggregate that had relatively few constants. Underwriting these results is, of course, the central limit theorem.

Once the causes of variance were determined Fisher (1922) went on to specify the conditions under which variance could be maintained. This was especially important since in a Mendelian system loss of genetic variability would be infinitely less than with blending inheritance and due only to finite population size and consequential stochastic losses. So, how would the rate of loss compare with the gains through mutation under differing assumptions about selection? How would gene frequencies change under selection pressures and environmental conditions? To answer these questions Fisher began with a discussion of equilibrium under selection. He first demonstrated that the frequency ratio for the alleles of a Mendelian factor was a stable equilibrium only if selection favoured the

heterozygotes. He then showed that the survival of an individual mutant gene depended on chance rather than selection. Only when large numbers of individuals were affected would the effect of selection override random survival, and even then only a small minority of the population would be affected. To do this he introduced stochastic considerations and examined the survival of individual genes by means of a branching process analysed by functional iteration and then set up the ‘chain–binomial’ model and analysed it by a diffusion approximation.¹² He was able to calculate the amount of mutation needed to maintain the variability given a specific amount of selection and found that to maintain variability in the case of equilibrium in the absence of selection, the rate of mutation had to be increased by a very large quantity. So the presence of even the slightest amount of selection in large populations had considerably more influence in keeping variability in check than did random survival. Consequently, the assumption of genotypic selection balanced by occasional mutations fit the facts deduced from the correlations of relatives in humans.

So, by making simplifying assumptions about the large size of the population and its high degree of genetic variability, Fisher was able to demonstrate how his stochastic distributions led to the conclusion that natural selection acting on genes (rather than mutation, random extinction, epistasis etc.) was the primary determinant in the evolutionary process. He found that mutation rates significantly higher than any observed in nature could be balanced by very small selection rates. The distribution of the frequency ratios for different factors was calculated from the assumption that the distribution was stable. The kind of statistical independence that figured prominently in the velocity-distribution law was applicable to the effects of selection in Mendelian populations.

What can we say then about our understanding of selection that emerges from Fisher’s analysis? The distribution of the gene ratio provided the ultimate expression of selective effects because the gene remains the only trace of the existence of an individual in a population. (i.e., The Mendelian mechanism ensures that although a population may be said to have continued existence the individuals that comprise it do not. The variability that passes from one generation to the next through reproduction is related to but not identical to phenotypic variability.) Given that selection acts on the heritable what is important is the mean effect of each allele. Although we can’t know the state of each of the genes in the population we can know the statistical result of their interaction in the same way that gas laws can be deduced from a collection of particles. Selection is mass selection, taking into account only the additive effects of genes, stochastic factors can be ruled out because of population size. Selection became irreducibly statistical because: (1) It applies only at the level of large populations and is defined in terms of gene frequencies; (2) This kind of (large) population was necessary if one’s statistical methodology was to be objective and guarantee the appropriate kinds of results. Evolution consisted in the modification of genetic structure with the gene ratio constituting the real state of the species.

Indeed one can think of all observable processes of evolution as described in the language of the statistical distribution of genes. The natural population is simply an aggregate of gene ratios. The differences with Pearson are, to be sure, differences that result from bringing Mendelism into the equation, but these differences go well beyond any dispute about its status as a theory of heredity. For Pearson selection is still about the kind of individual differences that were important for Darwin; however, because we cannot have a proper science of individuals selection has to be established by an application of statistical techniques to analyse the occurrence of traits in a population. Because the occurrence of selection is *established* statistically and because statistical knowledge is the only kind of

¹² For more on these techniques see Edwards (1994) and Ewens (2004).

knowledge that can justify the principle of natural selection a redefinition was necessary. But this is largely a methodological issue about what constitutes proper scientific investigation rather than a substantive one about the way selection *operates*. That is to say, although selection has become absorbed into the theory of correlation we still have the fundamental notion that it *operates* at the level of individuals and explains why individuals, understood as members of a population, have the traits they do. However, in the hands of Fisher selection becomes irreducibly statistical because the mathematics used to describe it no longer allows it to explain the occurrence of individual traits. It now has truly become a population level phenomenon understood in terms of changing gene frequencies. The mathematics used to describe how selection operates dictates the way it should be understood.

Conclusion: The Debate Goes on

To summarise then: For Pearson selection was statistical for what appears to be *methodological* reasons, the fact that we could only have statistical knowledge of individuals resulted in the need for large populations to guarantee the legitimacy of his conclusions. For Fisher the source was *scientific*, once Mendelism was accepted as a theory of heredity then the analysis of selection demanded the type of statistical approach used in the kinetic theory; there was simply no other way to treat the large numbers of genes required to establish facts about evolutionary change. Consequently the statistical nature of selection had two sources: (1) the chance mechanism inherent in Mendelism and (2) the kind of mathematics required to model populations of genes. But, unlike the mechanistic foundation that underscores classical statistical mechanics Fisher's analogy was not mechanistic. Natural Selection or selective tendencies were not analogous to physical forces and could not be derived, like forces in a conservative system, from a simple potential function. Natural selection could only be understood and formalised by reference to a domain defined by the field of gene frequencies. Of course other factors involving environmental conditions (allelic interactions, i.e., dominance; epistatic interaction) played a role in evolution but they acted on the *outcome* of selection; they were not part of the process itself.

A good deal of Fisher's methodology, including his understanding of selection, forms the foundation of modern population genetics. There remain, however, debates about whether selection operates most effectively in large populations, and role that random drift (sampling error), migration and genetic interaction play in affecting gene frequencies. However, what is most important is that selection is now defined in terms of changes in gene frequencies and that this reconceptualisation resulted largely from the impact of mathematics in describing that process. A full discussion of the details surrounding the nature of selection would require a more in-depth study of the claims of people like Mayr who argue that the methods of population genetics provide little in the way of understanding evolutionary development. However, what I take my analysis to have shown is that this is at least *prima facie* incorrect. While it is true that our understanding of selection has departed from the traditional Darwinian one, it is also the case that this departure was necessary in order for selection to be given a properly quantitative formulation. In addition to these methodological concerns there are also questions about how the neutral theory figures in contemporary debates about selection as well as the relation between selection and the various accounts of fitness on offer in the literature. Add to this the philosophical disagreements regarding the proper the unit of selection and whether selection is a force or

simply a bookkeeping device for tracking gene frequencies, and we quickly see that a full understanding of selection is a lengthy and complex affair.¹³

What I have tried to do here is two things, first to highlight the way in which the use of statistics and mathematics to characterise the role of natural selection has changed our understanding of it in ways that are significantly different from its Darwinian origins. My purpose in telling that story was to show how abstract mathematics can function in ways that go well beyond simply representing phenomena for the purposes of exact calculation and prediction. The mathematical representations themselves are capable of providing a conceptual understanding of the phenomena that is sometimes much richer than what can be achieved using strictly empirical forms of investigation and description. This point was made not only with respect to natural selection but also in the case of the Hardy–Weinberg law where a number of literally ‘false’ assumptions nevertheless contain a great deal of accurate information that allows us to understand *why* the law functions as a successful predictive device. What I take these cases to show is that even in biological contexts, where details of complex phenomena seem to be important for theoretical understanding, mathematical abstraction and idealisation can function as the source of concrete information about the behaviour of these systems that goes well beyond the type of prediction-oriented knowledge we typically expect from mathematical representation.¹⁴

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¹³ This debate is represented in the literature by Sober (1984) who advocates the force view and Walsh (2004) who argues for the “bookkeeping” account. For other interesting aspects of the debate see Walsh, Lewens and Airew (2002) as well as Matthen and Ariew (2002)

¹⁴ A version of this paper was presented at the international conference on scientific understanding held at the Free University in Amsterdam in August 2005.

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