The Price Equation and the Mathematics of Selection*

Amitabh Joshi

Fifty years ago, a small one and a half page paper without a single reference was published in the leading journal Nature. The paper laid out the most general mathematical formulation of natural selection that would work for all kinds of selection processes and under any form of inheritance (not just biological evolution and Mendelian genes), although the paper discussed the issue in a genetical framework. Written by a maverick American expatriate in England, with no prior background of studying evolution or genetics, the paper had initially been turned down by the editor of Nature as too difficult to understand. Largely ignored by the evolutionary biology community till the 1990s, the Price Equation is now widely recognized as an extremely useful conceptualization, permitting the incorporation of non-genetic inheritance into evolutionary models, serving to clarify the relationship between kin-selection and group-selection, unifying varied approaches used in the past to model evolutionary change, and forming the foundation of multi-level selection theory.

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Background: Charles Darwin, Natural Selection, and Population Genetics

To fully understand the significance of the Price Equation, we need to step back over a century and a half to Charles Darwin and the principle of natural selection. Darwin derived his concept of natural selection by analogy to plant and animal breeding, in which varieties of domesticated organisms with desired characteristics could be developed merely by choosing individuals with certain desired traits to breed from, generation after generation. Darwin realized that the ecological struggle for existence in na-

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ture, as a result of competition for limiting resources, would act as a natural analogue of the breeder selecting which individuals got to reproduce, based on whether they had the desirable traits, or not. Thus, individuals with traits that enabled them to function well in their environment would tend to be more successful at surviving to breed, and eventually produce more offspring than individuals that had traits less suited to the environment. The connection between greater reproductive success in the struggle for existence to longer term evolutionary change was provided by heredity, which implied that offspring would tend to resemble their parents. Selection, therefore, involved both the differential survival and reproduction of certain individuals, and the similarity in traits between those individuals and their offspring. Of course, Darwin did not know the mechanisms of either the generation or the inheritance of trait variations. Yet, he saw the important implication that, if offspring were relatively more likely to carry trait variations identical or very similar to their parents, and if individuals with certain trait variations were to routinely produce more offspring than others, then eventually those 'favourable' trait variations would become more common in the population, resulting in adaptive evolutionary change.

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After the 'rediscovery' of Mendel's Laws in 1900, a major focus of theoretical research in evolutionary biology was to reconcile the mechanism of natural selection with the principles of Mendelian inheritance, especially since it had been widely believed that natural selection would not be effective in mediating change in the face of the conservative force of heredity[1]. This naturally led to a focus on genic inheritance, leading to population genetic models of the process of adaptive changes in populations under the influence of natural selection. These were classic models of dynamic systems, making a number of simplifying assumptions, and focussing mechanistically on how genotype or allele frequencies would change over generations under the influence of various evolutionary forces like mutation, migration, selection, and random genetic drift. It was this blending of population genetics with the principle of selection that largely made

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[1] See *Resonance*, No.9, pp.3–5, 2000 and *Resonance*, No.6, pp.525–548, 2017; Boxes 1,2

up the so-called Neo-Darwinian Synthesis. The Price Equation took a very different approach, and sought to ask why various systems under selection changed in the manner they did, over generations, rather than focussing on how they changed. Thanks to this shift in focus, and its avoidance of traditional mechanistic modelling aimed at prediction, the Price Equation threw light on the underlying mathematical structure of selection itself, yielding insights of great originality and profundity into the evolutionary process.

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What is the Price Equation?

The Price Equation is simple and elegant, constituting a theorem encapsulating evolutionary change. In one of its commonly encountered forms, it is presented as

$$\Delta\bar{\phi} = \frac{1}{\bar{W}}\left[\mathrm{cov}(W, \phi) + E(W\bar{\delta})\right]$$

Here, in the familiar context of biological evolution by natural selection, W is Darwinian fitness (the number of offspring an individual having a particular phenotype leaves in the next time step), $\bar{W}$ is the population mean fitness i.e., the mean number of offspring produced per individual in the population, ϕ is the phenotype, $\bar{\delta}$ is the population mean of the difference between an individual's phenotype and the mean phenotype of its offspring, and $\Delta\bar{\phi}$ is the change in the mean phenotype in the population after one round of selection. Before we get into examining what exactly this equation means, and why, let us see where it is coming from. There are several different ways in which one can derive the Price Equation. We will follow the derivation in Chapter 6 of Rice (2004). Therefore, the notations used here are different from those originally used by Price, which are shown in the accompanying Article-in-a-box.

Consider a set of N individuals in the parental generation, and let ϕ_i denote the phenotype of the ith individual ($0 < i \leq N$). Then, $\bar{\phi}$ denotes the population mean phenotype in the parental generation. Let $\delta_{i,j}$ denote the difference in phenotype between the parental individual i and its jth offspring. Then, $\bar{\delta}_i$ is the difference between the phenotype of parental individual i and the mean phenotype of all its offspring. Finally, let W_i denote the number of offspring of parental individual i, and $\bar{W}$ the mean number of offspring produced by individuals of the parental generation. Given the above, the phenotype of the jth offspring of the ith parent is given by $\phi_i + \delta_{i,j}$. The mean phenotype of all individuals in the offspring generation, $\bar{\phi}'$, is thus given by

$$\bar{\phi}' = \frac{\sum_{i=1}^{N} \sum_{j=1}^{W_i} \left(\phi_i + \delta_{i,j}\right)}{\sum_{i=1}^{N} W_i}$$

The numerator in this equation adds up the phenotype of all offspring of all N parents, and the denominator is the total number of all offspring.

Let us next examine the various summations in the above expression. Since the individual phenotype of the ith parent, ϕ_i, is first being summed over its own W_i number of offspring, rather than over the $i = 1...N$ parents, we can simply write this sum as the product of W_i and ϕ_i.

$$\sum_{j=1}^{W_i} \phi_i = W_i \phi_i \,.$$

Similarly, the summation of the difference in phenotype between each of the W_i offspring of the ith parent with the parental phenotype ($\delta_{i,j}$) can be written as the product of the number of offspring of the ith parent (W_i) and the difference between their mean phenotype and that of the parent ($\bar{\delta}_i$), as

$$\sum_{j=1}^{W_i} \delta_{i,j} = W_i \bar{\delta}_i \,.$$

And, finally, the summation of offspring number per parent over all N parents in the denominator can be written as

$$\sum_{i=1}^{N} W_i = N\bar{W}\,.$$

Substituting these three values into the equation for $\bar{\phi}'$, we get

$$\begin{aligned}\bar{\phi}' &= \frac{1}{N\bar{W}}\left[\sum_{i=1}^{N} W_i\phi_i + \sum_{i=1}^{N} W_i\bar{\delta}_i\right]\\ &= \frac{1}{\bar{W}}\left[E(W\phi) + E(W\bar{\delta})\right]\,.\end{aligned}$$

Let us briefly examine what these terms on the right hand side are. Within the square brackets are two expectations. If you are not quite familiar with the concept of an 'expectation' of a random variable, it is essentially very similar to the arithmetic mean (for details, see *Resonance*, February 1996 pp.55–68). For example, the first term in the square brackets is the expectation of the product of number of offspring (W) and phenotype (ϕ), which is equivalent to the mean of the offspring number × phenotype (product of fitness and phenotype) in the parental generation. Similarly, the second expectation is essentially the mean, in the parental generation, of the product of fitness and the difference between an individual's own phenotype and the mean phenotype of all its offspring.

Moving on with our derivation, we next use the standard relationship cov $(x, y) = E(xy) - E(x)E(y)$ to write the expectation of two random variables x and y in terms of their covariance (see *Box* 1) and the product of their individual expectations, respectively, as $E(xy) = cov(x, y) + E(x)E(y)$. Thus, we can write $E(W\phi) = cov(W, \phi) + \bar{W}\bar{\phi}$, yielding

Box 1. Covariance of Two Random Variables.

A covariance, as the name suggests, is a measure capturing the tendency of two random variables to vary together e.g., if one random variable shows a higher than average value, the other does too (positive covariance), or if one random variable shows a higher than average value, the other tends to show a lower than average value (negative covariance). Two random variables that are independent of one another will show zero covariance. The covariance between two random variables x and y is defined as $\mathrm{cov}(x, y) = E[(x–E(x)) \times (y–E(y))]$. If you are not comfortable with the notion of a mathematical expectation, you can also think of the covariance in terms of a sample of n measurements, in which on each individual you measure both x and y. Compute the arithmetic means, respectively, of the x values and the y values, across all n individuals. Next, for each individual, compute the quantity [(x – mean of x) × (y – mean of y)]. Sum up this quantity across all the individuals and divide by n. This average product of the respective deviations of x and y from their means is the covariance of x and y in this sample of size n.

The covariance between two random variables is also related intimately to the linear regression of one upon the other. If we regress y upon x, for example, what we are doing is finding the line $y = a + bx$ that best fits the data, with a being the y-intercept and b the slope of the regression. Using expectations, it is straightforward to show that $\mathrm{cov}(x, y) = bVar(x)$, *i.e.*, the covariance is the product of the slope and the variance of the independent variable.

$$\begin{aligned}\bar{\phi}' &= \frac{1}{\bar{W}}\left[\mathrm{cov}(W,\phi) + \bar{W}\bar{\phi} + E(W\bar{\delta})\right] \\ &= \frac{1}{\bar{W}}\left[\mathrm{cov}(W,\phi) + E(W\bar{\delta})\right] + \bar{\phi}\,.\end{aligned}$$

Finally, we subtract $\bar{\phi}$ from both sides of the equation to get the Price Equation,

$$\Delta\bar{\phi} = \frac{1}{\bar{W}}\left[\mathrm{cov}(W,\phi) + E(W\bar{\delta})\right]$$

What Does the Price Equation Tell Us?

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“A good notation”, Bertrand Russell once wrote, “has a subtlety and suggestiveness which at times make it seem almost like a live teacher”. Another way of putting it is that a good ‘notation in the Russellian sense, is like a beautiful couplet or a haiku, in that it expresses a deep insight in a limited number of terms, singing to us of some fundamental truth. The beauty and strength of the Price Equation lie precisely in the fact that, unlike typical mathematical models of real phenomena, it does not make simplifying assumptions in order to attain predictive power with a mechanistic model. It takes an alternative approach of examining a real phenomenon (in this case, selection) and asking what mathematical structure emerges from a contemplation of the phenomenon itself. It is, thus, definitional rather than predictive, clarifying the inherent structure of the selection process in a particularly lucid and transparent manner, rather than predicting how a given system will change under selection. Moreover, it is independent of the specific system of inheritance involved: it is the most general expression defining any process involving selection.

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In the previous section, we had derived the Price Equation using a context that was explicitly one of biological evolution – we spoke of individuals, phenotypes, and Darwinian fitness, and of parents and offspring. However, the Price Equation is considerably more general than that, and we shall now examine this generality in some detail. When we refer to parents and offspring (or, as some authors do, to ancestors and descendants) in the context of the Price Equation, all that is implied is that there are two ensembles on which the same characteristic (or phenotype) can be defined, and that one can then understand from where the difference in mean characteristic between them arises. The individual entities making up the two ensembles need not even be of the same type, although they can be. The two ensembles can be separated in time (in any units) or even space. All that is required is that there be some one-to-one or one-to-many mapping between individual entities in one ensemble (arbitrarily labelled ‘parents’) and individual entities in the second ensemble (arbitrarily labelled ‘offspring’).

For example, in Price’s original formulation, ‘parents’ were diploid individuals, whereas ‘offspring’ were haploid gametes that successfully became part of the next generation. Parents and offspring were, thus, different types of entities, separated by one generation of time. The shared phenotype in Price’s formulation was the frequency of an allele within an individual parent or offspring, taking values of 0, 0.5, or 1 in parents and 0 or 1 in offspring. In some phenotypic models, the mean of the phenotypic values, say height, of the two parents and the phenotypic value of each offspring reflect the shared phenotype. The point to appreciate is that the same formulation would also hold true if the labels 'parent' and 'offspring' were to be applied to the same individual at different points in time, i.e., selection is acting through differential persistence rather than differential reproduction. For example, if some subset of a population were to migrate from one location to another, then 'parents' would refer to the individuals that were in the population originally, i.e., before the migration event, and 'offspring' would refer to the subset of the 'parents' that migrated during the event. Individuals among the 'parents' who did not migrate can be treated conceptually either as parents who produced no offspring, or offspring who died before migration. The covariance between phenotype and fitness here would be that between phenotype and the propensity of an individual bearing that phenotype to migrate and survive during the migration event. In this particular case, the individual that migrated would still be the same phenotype as it was pre-migration (it is the same individual, after all), and therefore the phenotypic difference between each 'parent' and its 'offspring' would be zero. It should be straightforward to see that the same logic would apply even to the 'migration' of items from a supermarket shelf ('parents') to a shopping basket ('offspring'), under the action of a conscious shopper. The key covariance here would be that between the phenotype of the item and its propensity to be chosen by the shopper for purchase. Once again, the phenotype of 'parent' and 'offspring' would not differ. Another way of thinking of the labels 'parent' and 'offspring' is as referring, respectively, to the 'original' group and the 'selected' group, regardless of the mechanism of selection and the details of how phenotypes of individual entities linked by 'parent-offspring' labels in the two groups differ or not. The latter is essentially 'inheritance', whereas the mechanism of selection, e.g., whether by differential survival and reproduction, or choosing to migrate, or being chosen by a shopper, distils the essence of

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the context. This is the strength of the Price equation: it manages to succinctly lay before us the underlying formal structure of the selective process, in a form that is invariant to changes in context or systems of inheritance! It is the most accurate and elegant codification of Darwin's original insight.

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Phenotype in the context of the Price equation simply means some characteristic that can be assessed on both 'parents' and 'offspring' and expressed as a number, such that each individual can have only one corresponding number denoting its phenotypic value. It could even be a 'complex phenotype' e.g., height^2/weight. Multiple individuals, of course, may share the same phenotypic value, but one individual cannot have more than one phenotypic value. Moreover, unlike the models used in population genetics that track changes in the frequency (relative abundance in the population) of individuals or alleles sharing a phenotypic value, ignoring which offspring arise from which parent, the notation in the Price Equation tracks individuals and their offspring, regardless of whether the parent and offspring phenotypic values coincide or not. All the remarkable insights bestowed upon us by this formulation stem from this innovative and highly original notational shift, compared to the standard population genetic models.

Multiple Interpretations of the Terms in the Price Equation

A friend of mine, an accomplished poet in multiple languages, is fond of saying that a good poem should have at least seven inherent layers of interpretations. The idea is that the core image or metaphor of a good poem or couplet, when projected onto different axes of experience, yields varied relevant insights. Indeed, this is what gives great poetry its universal appeal, because different people, with very varied experiences, can nevertheless derive some helpful insight from it. On this count, too, the Price Equation ranks very high. In the above discussion, we have been interpreting the two terms on the right hand side of the Price Equation, respectively, as a 'selection' term, representing adaptive change, and a 'transmission' term, representing non-adaptive change. In other words, total change in mean phenotype over one step of selection includes change due to the covariance between fitness and trait (the 'selection' term) and due to the fact that offspring and parent phenotypes need not be identical (the 'transmission' term). In many simple population genetic models, the transmission term is not easily recognized as its effects are implicitly embedded in the calculation of the next generation's allele or genotype frequencies. Actually, the situation is a bit more subtle than just that. The covariance term encompasses all factors that can drive a relationship between phenotype and fitness, not just selection but also random chance, or drift. Similarly, the expectation term encompasses multiple factors that can contribute to parent-offspring differences, some of which are not immediately intuitively obvious. For example, it is immediately clear that genetic assortment and recombination in diploid sexual species can drive differences between parent and offspring phenotypes. In addition, mutation occurring in the process of gamete formation is another factor that can contribute to parent-offspring differences in phenotype. Likewise, the breeding system (who tends to mate with whom) can also alter patterns of parent-offspring phenotypic similarity, giving rise to non-adaptive evolutionary change even in the absence of selection [In this context, readers familiar with simple one locus, two allele population genetic models may wish to see *Box* 2; those unfamiliar with such models can safely skip it].

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Box 2. ‘Selection’ and ‘Transmission’ in Simple Population Genetic Models.

Most of us with any exposure at all to evolutionary genetics are familiar with the Hardy-Weinberg Equilibrium, wherein allele and genotype frequencies in a one-locus two-allele system remain unchanged from one generation to the next in a very large population with random mating, in which there is no net mutation, migration or selection with regard to the locus under consideration (see *Resonance*, No.10, pp.951–970, 2008). From the perspective of the Price Equation, in this situation of an ideal large population, $\Delta\bar{\phi} = 0$, *i.e.*, the population is at equilibrium: there is no change in mean phenotype from one generation to the next. Since we have assumed no selection, $\mathrm{cov}(W, \phi) = 0$, since all individuals have the same Darwinian fitness, regardless of phenotype. Similarly, $E(W\bar{\delta})$ is also zero, in part because the ‘no selection’ assumption also rules out gametic selection, and we have assumed no mutation, but also because of the fact that the population is assumed to be a random mating one. In fact, if we look at individual genotypes, their offspring are not necessarily identical to parents in type. For example, when an $\mathrm{A_1A_1}$ individual reproduces via random mating, a fraction p_1 of its offspring will be $\mathrm{A_1A_1}$, whereas the remaining $1 - p_1$ will be $\mathrm{A_1A_2}$, where p_1 and p_2 are the frequencies of the alleles $\mathrm{A_1}$ and $\mathrm{A_2}$, respectively, in the population. However, at the Hardy-Weinberg Equilibrium genotypic frequencies ($f_{A_1A_1} = p_1^2; f_{A1A2} = 2p_1p_2; f_{A2A2} = p_2^2;$), the deviations of offspring from parental type for the three parental genotypes cancel out exactly, leading to the average deviation being 0.

Consider, next, a similar ideal large population, except for the fact that reproduction is by self-fertilization, not random mating. When the two homozygotes self-fertilize, they produce offspring that are identical to themselves. But when the heterozygotes self-fertilize, half their offspring are homozygous for one or the other allele, and only half remain heterozygous. Therefore, each generation, the frequency of the heterozygotes will be reduced to half of what it was in the preceding generation, while those of both homozygotes will proportionately increase. Here, too, there is no selection ($\mathrm{cov}(W, \phi) = 0$), as in the previous case, but there is a non-zero $E(W\bar{\delta})$ term, due to the heterozygotes producing all three types of offspring. This non-zero ‘transmission term’ drives an evolutionary change in genotypic frequencies which is, however, non-adaptive since the mean fitness of the population does not change in consequence.

Let us now move to ideal large population models of selection. If w_{ij} be the Darwinian fitness of genotype A_iA_j, let us consider a case where $w_{11} > w_{12} > w_{22}$ (directional selection). In this scenario, as long as the A_1 allele is not fixed, its frequency, and that of the $\mathrm{A_1A_1}$ genotype, continues to increase in the population, over generations. Here, both the right hand side terms of the Price equation are non-zero and positive, and both contribute to change in mean phenotype over generations.

Finally, let us consider a case where $w_{12} > w_{11}, w_{22}$ (heterozygote superiority), a situation typically exemplified in textbooks with the example of sickle cell anaemia in malaria endemic areas. We know that this system attains an equilibrium for allele and genotype frequencies in which both alleles are maintained stably in the population. Of course, even at equilibrium, the differences in fitness between phenotypes remain and, therefore, selection is still occurring, i.e., $\mathrm{cov}(W, \phi) \neq 0$. However, since there is no change in genotype frequencies, $\Delta\bar{\phi} = 0$. At the equilibrium frequencies of alleles and genotypes, the change due to parent-offspring difference in type, $E(W\bar{\delta})$, exactly cancels out the change due to selection ($\mathrm{cov(W, \phi)}$).

An even more non-intuitive and far-reaching interpretation of the 'transmission' term in the Price Equation is that, if the context is one of selection acting between individual organisms, this term also includes any differences between offspring and parent phenotype that can arise as a result of selection acting at a level below that of the individual.

An even more non-intuitive and far-reaching interpretation of the 'transmission' term in the Price Equation is that, if the context is one of selection acting between individual organisms, this term also includes any differences between offspring and parent phenotype that can arise as a result of selection acting at a level below that of the individual, even as selection is acting between individuals. Consider, for example, the well known phenomenon of meiotic drive, first described by M. M. Rhoades in 1942. In meiotic drive, when individuals heterozygous for a single locus, or for a multi-locus haplotype, reproduce, one of the two alleles or haplotypes is differentially represented in the gametes formed, as opposed to the 1:1 ratio of the two gametic types expected under Mendelian principles. This phenomenon, in terms of its effects on allele or haplotype frequencies in the next generation, is a subset of gametic selection, in which not all gametic types have equal fertilization success, because of either disproportionate production, or disproportionate pre-fertilization mortality, or disproportionate fertilization success and zygote viability of different gametic types. Now, imagine a situation where all individual diploid genotypes have equal survivorship and reproductive output, i.e., there is no selection among individuals and, consequently, $\mathrm{cov}(W, \phi) = 0$. However, if there is gametic selection, there will be mean phenotype change over the course of one generation, i.e., $\Delta\bar{\phi} \neq 0$, and this will be entirely due to the 'transmission' term, $E(W\bar{\delta})$, because selection, acting among gametes rather than individuals, is driving a difference, on an average, between offspring and parent phenotypes. Thus, if selection were simultaneously acting at two levels, both between individuals and between gametes, the Price Equation would permit a neat partitioning of the relative contribution of selection at the two levels to total phenotypic change over one generation.

In fact, the Price Equation has the flexibility to do even more than that. The 'transmission term', or expectation, on the right hand side of the equation can be recursively expanded into a covariance term and an expectation term, for as many hierarchical levels of selection as one may wish to consider. Thus, in an analysis of group selection, where selection acts both between groups and among individuals within groups, we get (for details of the derivations, and nuances of the notation, the interested reader is directed to Chapter 10 in Rice (2004)):

$$\Delta\bar{\phi}_g = \frac{1}{\bar{w}_g}\mathrm{cov}(w_g, \phi_g) + \frac{1}{\bar{w}_{iT}} E\left[\mathrm{cov}(w_i, \phi_i)\right] + \frac{1}{\bar{w}_{iT}} E(w_i\bar{\delta}_i)\,.$$

Here, $\Delta\bar{\phi}_g$ is the mean change in group phenotype, over one step of selection, in a collection of groups of individuals that are experiencing selection at both the group and the individual levels. Group phenotype is simply the mean phenotype of all individuals in that group. On the right hand side of this equation, we can see that the classic 'transmission term' has been split into a covariance term and a transmission term. The first term, $\mathrm{cov}(w_g, \phi_g)$, on the right hand side reflects the change in mean group phenotype due to selection between groups. The second term, $\mathrm{cov}(w_i, \phi_i)$, captures the change in mean group phenotype due to selection between individuals within groups. The third term, $E(w_i\bar{\delta}_i)$, reflects the change in mean group phenotype due to factors relating to individual reproduction, and/or selection at a level below the individual. This third term could again be similarly split into a covariance term, reflecting selection among entities below the level of individual (e.g. gametes), and a 'transmission term', reflecting the effect of factors relating to the reproduction of these lower-than-individual level entities, and/or selection at an even lower level. This particularly evocative and flexible recursive expansion of the 'transmission term' in the Price Equation is the foundation of multi-level selection theory.

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A Unifying Principle for Evolutionary Theory

Chronologically, the Price equation entered into evolutionary theory relatively late, several decades after the Neo-Darwinian synthesis – itself coming almost seventy-five years after Darwin's book – had successfully welded together Mendelian genetics and the Darwinian principle of natural selection into a fairly comprehensive theory of evolutionary change within populations. Yet, from the conceptual perspective of the formalism of evolutionary theory, the Price Equation is like the 'mother lode', closely mirroring Darwin's original insight in its simplicity and generality, spinning off practically every preceding theoretical result in population and quantitative genetics almost as a by-product, and also rooting many aspects of evolution, biological and otherwise, previously treated piecemeal in an ad hoc manner, into one grand generalization.

From the conceptual perspective of the formalism of evolutionary theory, the Price Equation is like the 'mother lode', closely mirroring Darwin's original insight in its simplicity and generality, spinning off practically every preceding theoretical result in population and quantitative genetics almost as a by-product.

For paucity of space, and because some of these aspects are fairly sophisticated and technical, I will not discuss these myriad ramifications of the Price equation in great detail, but merely mention them briefly. Interested readers are directed to the excellent expositions to be found in the writings of Steven Frank, Andy Gardner, Sean Rice, Alan Grafen, and Tobias Uller, among others.

In the domain of classical population genetics, all the marginal allelic fitness models, as well as models requiring a focus on genotypes or mating pairs, such as sexual selection and fertility selection models, can be derived from the Price Equation. Thanks to the relationship between covariance and regression (*Box* 1), the Price Equation can also be formulated in regression terms, thereby recovering all major results from quantitative genetics as well, showing that the Price Equation also underlies Fisher's original insight that led him to focus on average effects of alleles, breeding values, and regressions of fitness on allelic content to develop a phenotypic theory of evolutionary change, though rooted in Mendelian genetics across multiple loci. Fisher's Fundamental Theorem, the univariate and multivariate Breeder's Equations, Robertson's theorem, and Li's theorem all turn out to be special cases of the Price Equation, though preceding it by decades. Even the rich field of sex-ratio evolution, originally pioneered by Fisher and subsequently refined by Hamilton and others, is also most clearly understood through a Price Equation approach.

Most spectacularly, the Price equation has greatly enhanced our nuanced understanding of kin selection and the evolution of altruism, clearing up many of the confusions that swirled around in the wake of Hamilton's path-breaking papers on social evolution. Among other things, the Price Equation also yields a much more general and accurate formulation of the so-called Hamilton's rule that lays out the conditions for the evolutionary increase of altruism within a population. In this context, the Price Equation makes clear that the evolution of altruism within a population involves processes of selection, both among individuals and among groups, and that kin-selection was merely one special way of trying to model this phenomenon at the individual level by focussing on within-population groups based on genetic relatedness. Through its property of recursive expansion, the Price Equation also provided the first clear formalism for understanding group selection, and its relationship with individual selection, a topic that had been controversial for several decades before George Price turned his attention to it. Moreover, the expansion of the Price Equation is the foundation for multi-level selection theory, permitting the analysis of selection simultaneously acting at multiple hierarchical levels of organization. An important and potentially very useful contemporary application of multi-level selection theory is in understanding tumour progression in cancer, one more reminder of how advances in basic understanding can have profound, often unexpected, practical implications in the future.

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At present, there is also considerable interest in the role of non-genic inheritance in evolution, both biological and cultural. Cultural inheritance – the acquisition of behavioural phenotypes via learning – is now recognized as playing an important role in the evolution of behaviours, in humans and other animals alike. Ecological inheritance – in the sense of shared environmental factors driving parent-offspring similarity in phenotype – is also receiving increasing attention in evolutionary biology, as is epigenetic inheritance, or the trans-generational persistence of added chemical 'marks' on DNA that can affect levels of gene expression. The Price Equation, once again, plays an important role in formulating the effects of such non-genic forms of inheritance on the evolu-

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tionary process because of its general form that does not restrict itself to any specific mechanism of inheritance.

In the 1860s, shortly after Darwin's book 'The Origin of Species' was published, the German biologist Ernst Haeckel had predicted that evolutionary thinking would unify not only diverse sub-areas of biology, but also bring into its domain many fields considered separate from biology, such as human behaviour, psychology, anthropology, sociology, and linguistics. Today, we are in the midst of such an expansion of the domain of evolutionary biology to include many areas not traditionally considered a part of it. Evolutionary psychology and evolutionary medicine are now active research fields internationally, though not yet in India. Evolutionary economics is a more recent, but rapidly growing field. One of the key developments that some researchers hope will truly unify the biological and social sciences is the development of a general theory of intertwined biological and cultural evolution. If and when that happens, George Price's eponymous equation will have played a central role in the realization of Haeckel's dream.

Evolutionary psychology and evolutionary medicine are now active research fields internationally, though not yet in India. Evolutionary economics is a more recent, but rapidly growing field.

Conclusion

Among those who can be said to have had a truly deep and intimate understanding of the process of natural selection, George Price would rank very high indeed, alongside Darwin, Haeckel, Weldon, Fisher, and Hamilton. He had an interesting but troubled life and, like the mathematician Srinivasa Ramanujan and the philosopher Ludwig Wittgenstein, made profoundly original and fundamental contributions to a field he had no formal training in, something he had dreamt of doing for much of his adult life (see Article-in-a-box in this issue). It is worth remembering, especially in these times of pragmatic and professionalized science, that passionate and dedicated amateurs have a lot to contribute to the growth of human knowledge; both Charles Darwin and Gregor Mendel were amateurs, too. Similarly, it is important to stress breadth and imagination in science education, in addition to depth and technical detail. It is equally important to appreciate the role

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played in the lives of Ramanujan, Wittgenstein and Price by the likes of G. H. Hardy, Bertrand Russell, and William Hamilton, respectively, who recognized and encouraged these ‘outsiders’ who brought their own unique, often seemingly incomprehensible, insights to the fields officially straddled by their mentors. It takes a certain combination of confidence, open-mindedness and generosity to be able to recognize genius when it shows up at one’s door. It is hard to imagine today that someone with no experience or degree in the field could be appointed as a Research Fellow in a major department simply because he or she had come up with a really interesting equation. Yet, this is what happened to Price when he went to show his covariance equation to leading statistical geneticist Cedric A. B. Smith at University College London in 1968. Cultivating and maintaining such confidence, open-mindedness and generosity is also an important aspect of science that we need to preserve, nurture and inculcate.

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