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ARTICLE

Population Thinking, Price's Equation and the Analysis of Economic Evolution

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Abstract

In this paper it is argued that evolutionary economics needs general statistical tools for performing the analysis of the aggregate effects of evolution in terms of the underlying population dynamics. These tools have been developed within biometrics, and they have recently become directly applicable to economic evolution due to the development of what may be called a general evometrics. Central to this evometrics is a method for partitioning evolutionary change developed by George Price into the selection effect and what may be called the innovation effect. This method serves surprisingly well as a means of accounting for evolution and as a starting point for the explanation of evolution. The applications of Price's equation cover the partitioning and analysis of relatively short-term evolutionary change within individual industries as well as the study of more complexly structured populations of firms. By extrapolating these applications of Price's evometrics, the paper suggests that his approach may play a central role in the emerging evolutionary econometrics.

Keywords: population thinking, statistical analysis of economic evolution, Price's equation, multi-level selection.

1. Evometrics: A statistical approach to economic evolution

In the accounts for economic evolution by classical and neoclassical economists like Adam Smith, Marx, Menger, Marshall and Schumpeter, we find clear elements of evolutionary economics as a historical science. The historical character of this old evolutionary economics is obviously due to the fact that economic evolution is a unique process in historical time. But economic evolution is based on a number of evolutionary mechanisms that cannot be handled systematically by historically oriented studies. Instead the evolutionary mechanisms have to be analysed theoretically, and this analysis has been performed by a new evolutionary economics that started with Nelson and Winter's (1982) analysis of Schumpeterian competition and the reactions of economists to the Maynard Smith's (1982) analysis of the evolutionary games of biological life.

JEL: O30, O40.

Since these pioneering works, the new evolutionary theorising has deepened and widened the theoretical understanding of the mechanisms of economic evolution (see e.g. Nelson, 1995; Dopfer, 2001; Foster and Metcalfe, 2001). But it is fair to say that the relationship to historical and statistical analyses of economic evolution has been rather weak. For instance, historically oriented researchers like Freeman and Louca (2001) have had little help from theoretical evolutionary economics. Since the connection between theoretical and historical work on economic evolution is crucial for the further development of evolutionary economics as a science, a core research issue is to link theory and history by means of a quantitative evolutionary economics. To be more specific, we need an evolutionary metrics — or evometrics — that is operational for both theoretical analysis and empirical studies of economic evolution.

Theoretical analysis has revealed that the most important prerequisite for evolutionary economic theorising is to take serious the differences that exist within and between populations of economic agents. This may seem a trivial requirement, but in practice it is not at all easy to perform this kind of analysis. Many have learnt to think in terms of statistical ‘populations’ when analysing the significance of empirical data, but it is less common to use the changing statistical properties of real populations to obtain a basic understanding of their evolution. Instead, there is a widespread tendency to treat such real populations as classes that can be characterised by a few common characteristics. Since Plato, there have actually been standard philosophical arguments for abstracting from the myriad of ‘superficial’ variations in order to concentrate on the underlying ‘idea’ or ‘type’ that basically characterise the population. But this typological thinking is a major obstacle for an adequate treatment of evolution. Instead we need a population thinking that means that we deal with heterogeneous populations and to consider outliers as even more important than normal agents (Metcalfe, 2001). This heterogeneity of populations is upheld by the behavioural inertia that characterises boundedly rational agents. If we study the distribution of behaviour (like strategy or productivity) in such a population, we normally observe that this distribution evolve over time. We also recognise that this evolution may be ascribed to two main forces. Selection is the force that implies that firms with different values of the characteristic have different growth rates. Thus selection presupposes variance with respect to a particular characteristic, and this characteristic must be important in each member’s environment (including the other members of the population). Selection means that the mean value of the characteristic of the population will change. But this mean may also change because of innovation, imitation, learning and random drift. The latter factors of change may be grouped under the heading of innovation and they can, at least conceptually, be distinguished from selection.

Even from this short account of population thinking, it becomes obvious that this form of thinking has a statistical orientation. This fact is a source of both the unity and the difficulties of modern evolutionary economics. We have to apply some sort of statistical analysis in any kind of evolutionary study — from the evolution that takes place within a large firm via evolution of an industry to evolution at the regional, national and global levels. In all cases, we have to specify populations, behavioural characteristics, and the changing distributions of these characteristics. Whether we like it or not, we thus see that statistics enter even at the ground level of our thinking, where we define what to look for. The problem here is that few are accustomed to this kind of statistical thinking — partly because of poor support from commonly known analytic tools. To promote the unity of evolutionary economics there is thus a need for providing basic tools for population analysis. The potential of such tools is not only to unify different theoretical approaches but also to unify theoretical and empirical analyses of evolution.

The tools that support population thinking are to a large extent available, but they have mainly been developed within evolutionary biology. Therefore, there is a need to consider to which extent these tools are not only relevant for biostatistics, or biometrics, but also for an evometrics that study all forms of evolution. That this is actually the case has become increasingly clear (Frank, 1998). It was R. A. Fisher (1999) who formulated the foundations for evometric analysis through his combined efforts of developing modern statistics and modern evolutionary analysis. These foundations were largely formulated as a general theory of selection. At the very core of this theory is Fisher's so-called fundamental theorem of natural selection that says that the speed of evolutionary change is determined by the behavioural variance within a population. Fisher's immediate topic was biological evolution, but his analysis has full generality. He was actually proposing to treat selection in terms of what has later been called replicator dynamics or distance-from-mean dynamics. Thus the biologically oriented Fisher theorem may be seen as the application of a general Fisher Principle that is relevant for all forms of evolutionary processes (Metcalfe, 1994; 1998). However, Fisher's analysis is excluding what in the present paper is called localised innovation. Therefore, his equations do not cover the general case in which this phenomenon is present to a smaller or larger degree. George R. Price (1970; 1972a) solved this problem by developing a general method for partitioning of evolution. Thereby he not only clarified Fisher's main result about natural selection (Price, 1972b) and helped to lay the foundation for evolutionary game theory (Maynard and Price, 1973). He also developed a general and very fruitful decomposition of *any* evolutionary change, and thereby he formulated the core of a general evometrics (Frank 1995; 1998).

The simple Price equation serves to formalise what may be called *intra-population thinking* by focussing the attention on selection and localised innovation. His analysis is very basic and it has, to some extent, been rediscovered in Metcalfe's (1998; 2001) statistically oriented evolutionary economics and even in Nelson and Winter's (1982) pioneering contribution. However, the historical and statistical study of real processes of economic evolution is confronted with the problem of defining the units of selection. Since these units can both be national economies, regional industries, corporations, plants, work groups and individual employees, there is obviously a need to move from simple intra-population thinking to *multi-level population thinking*. Somewhat surprisingly, Price's approach can immediately be applied to the formalisation of the thinking in terms of multiple levels of selection. Thereby the approach serves to overcome the controversy within evolutionary biology between the majority view that only individual organisms are selected and the minority view that emphasises group-level selection (Hamilton, 1996; Frank, 1998). But Price's method of analysis is even more helpful in evolutionary economics. Here we simply start by partitioning of aggregate evolutionary change in terms of higher-level units (like corporations). Thereby we obtain a selection effect and a preliminary innovation effect. The preliminary innovation effect can be partitioned in terms of Price's equation. Thereby it becomes clear that it includes both selection within the units (e.g. selection between plants) and a more narrowly defined innovation effect. This analysis of the innovation effect can go on until we reach units of selection with no meaningful intra-unit selection. Obviously, it is not the same type of selection that takes place at the different levels of selection. At some levels the selection comes close to what biologists call natural selection and at other levels we may be dealing with conscious or artificial selection. But this is no problem for Price's approach that operates in terms of a fully general concept of selection.

The first beginnings of an evolutionary economic exploitation of the simple and the multi-level versions of Price's equation can be found in evolutionary game theory. Here Price's equation is used to analyse the emergence of cooperation in small to medium-sized human groups — irrespective of whether cooperative behaviour is genetically or culturally determined (Gintis, 2000, Ch. 11; Henrich, 2004). This analysis immediately leads to the study of the emergence of the institutions (i.e. higher-level selection environments) that make it advantageous to perform the 'altruistic punishment' necessary to uphold a high level of cooperative behaviour (Gifford, 2000; Boyd, Gintis, Bowles and Richerson, 2003). But the narrowly defined issues normally studied by evolutionary game theory may imply that the full generality of Price's approach is not recognised (Price, 1995; Knudsen, 2002; 2004). Here the empirically oriented evolutionary economics of the Nelson–Winter tradition may be more helpful. At the same time, the connection to relatively complex empirical studies makes clear a core characteristic of Price's equations for both simple and multi-level analysis: they are designed for the analysis of relatively short-term studies (as emphasised by Frank, 1998, Ch. 1). The short-term approach is necessary for keeping the selection pressures constant, and this cannot be assumed for long-term evolutionary processes.

There are two major reasons for the long-term change of selection pressures. First, selection pressures change with the changing size of the population. As long as the population is small compared to the carrying capacity of its environment, selection favours units that are quick in exploiting the possibilities. But as the population grows, the selection changes to favour units that are finely tuned to survive in a crowded environment. Second, the environment is to a large extent composed of other populations. In the long-term there is a co-evolution between the different populations, and this co-evolution obviously changes selection pressures. For instance, an industry is competing and collaborating with other industries, and this interaction is changing over time. To handle both forms of density-dependent evolution, we need *inter-population thinking*. But this form of thinking is not directly supported by Price's approach. The delimitation of this approach should, however, be considered a useful feature and not a failure of the approach since it separates clearly the study of sort-term issues from the study of long-term issues. Thereby it serves to emphasise the urgent need for developing complementary tools for the study of longterm evolutionary change.

2. Intra-population analysis

The breakthrough in the general analysis of evolution came with the *Genetical Theory of Natural Selection* by the geneticist and statistician R. A. Fisher (1999), who may be called the founding father of the statistical analysis of intra-population evolution (and of much of modern statistics!). His starting point was a precise analysis of the process of selection, which he analysed in a way that was inspired by statistical thermodynamics. He called his main result 'the fundamental theorem of natural selection'. This theorem is summarised in Fisher's (1999, p. 46) statement that '[t]he rate of increase of fitness of any species is equal to the genetic variance in fitness.' If we study a step-wise evolutionary process, we may reformulate his theorem in discrete terms. Let w_i be the fitness of an individual unit (organism), w the mean fitness of the population and Δw the change in mean fitness. Furthermore, let $\mathrm{Var}(w_i)$ be the population's variance of fitness (the reason for the non-standard subscript will become clear in section 3). Then the Fisher theorem says that

$$\Delta w = \mathrm{Var}(w_i)\,. \tag{1}$$

This theorem describes a distance-from-mean dynamics, where the representation of a unit at the end of the period (its offspring) is determined by its relative fitness. Units with above-average fitness will increase their weight in the population, while units with below-average fitness have decreasing weight. The change in mean fitness is thus determined by the variance of unit-level fitness in the beginning of the period under study. Apparently, Fisher's theorem (1) is only about biological evolution, but his general formulation of selection and his inspiration from thermodynamics secured its general applicability. This general applicability may be emphasised by talking about the Fisher Principle (Metcalfe, 1994; 1998, Ch. 2), which serves as a starting point for the formalisation of population thinking. Especially, it helps us to recognise the enormous importance of statistical concepts — both in evolutionary theory and in the empirical study of evolution.

Fisher's work started — like the work of e.g. Nelson and Winter (1982) — from statistics of populations and their change. Beneath his concept of unit-level fitness is the fact that if selection favours the degree to which a particular characteristic/trait is present in the individuals, then the rate of change of the mean value of this characteristic is proportional to the variance of the characteristic within the population. Thus, we have to define the characteristics that are selected for, measure their variance, study the strength of the selective forces, and follow the consequences at the aggregate population level. It is, however, important not to make this analysis in terms of a pure selection process. By doing so we ignore that the change in the characteristic is not only due to selection but also to other causes of improvement and deterioration. This problem was mentioned by Fisher, but since it was not included in his formal analysis, it has much too often been forgotten. Metcalfe (1998) suggests that we should emphasise the Fisher principle (which includes the broader issues) rather than the narrow Fisher theorem. This task is, however, solved elegantly by George R. Price, who was also the co-founder of evolutionary game theory (Maynard and Price, 1973).

To overcome some of the ambiguities of Fisher's formulation of his theorem, Price (1970; 1972) made a decomposition of the evolutionary change that included not only the effect of selection but also the effect of causes that increase variation. Price's equation (or formula) is not easy to understand, so even though it resolves many of Fisher's problems, it is often used in a delimited version of less importance. Frank (1995; 1997; 1998) has been a major contributor to the development and diffusion of the full version of Price's decomposition of evolutionary change. His contributions demonstrate that a large number of evolutionary problems can be clarified by means of Price's equation. They also make clear that many researchers have been moving in the same direction as Price without noticing the full generality of their results and their relationship to Price. This fact is emphasised by Metcalfe (2002, p. 90): 'For some years now evolutionary economists have been using the Price equation without realising it.' This statement holds for Metcalfe's (1998; 2001) own important contributions to theoretical evolutionary economics, but it has also some truth for Nelson and Winter's (1982) pioneering contributions to evolutionary economics.

When we try to explain the evolution of a mean characteristic, we have the problem that it might be caused by many forces. It is, nevertheless, possible to decompose the change in the mean characteristic into two effects of which at least the first (the selection effect) is easy to understand. The second (which in this paper is called the innovation effect) is more difficult to grasp since its meaning depends on the type of evolution under study. However, a partitioning into these two effects is possible for any evolutionary change, so it may e.g. be applied to change in an evolutionary game or in the Nelson–Winter model. For these and any other evolutionary process, Price's equation states that

$$\text{Total evolutionary change} = \text{Selection effect} + \text{Innovation effect}. \tag{2}$$

This verbal description of Price's equation gives a first impression of the elements of evolutionary change, but it cannot be fully understood without a little formal analysis. To decompose evolutionary change we need a study of the individual members of a population at two points of time, where we denote variable values for the first period with their ordinary names and variable values for the second period by adding primes. The members that we study can either be individuals or groups of individuals. To perform the analysis, we need to operate in terms of several variables for both these members and the aggregate population (see Table 1). Let us gradually move through these variables before we restate the verbal equation (2) in formal terms.

Table 1. Notation.

Variable	Description	Definition
X, X'	variables for initial population and end population	
x_i	size of entity i	
x	size of population	$\sum x_i$
s_i	population share of i	x_i / x
z_i	value of characteristic of i	
Δz_i	change in value of characteristic of i	$z_i' - z_i$
z	mean value of characteristic	$\sum s_i z_i$
Δz	change in the mean characteristic	$z' - z$
$\mathrm{Var}(z_i)$	variance of characteristics	$\sum s_i (z_i - z)^2$
w_i	reproduction coefficient (fitness) of i	x_i' / x
w	mean reproduction coefficient	$\sum s_i w_i$
$\mathrm{Cov}(w_i, z_i)$	covariance of reproduction coefficients and characteristics	$\sum s_i (w_i - w)(z_i - z)$
$\beta(w_i, z_i)$	regression of reproduction coefficients on characteristics	$\mathrm{Cov}(w_i, z_i) / \mathrm{Var}(z_i)$
$\mathrm{E}(w_i \Delta z_i)$	expected value of change in characteristics in the end population	$\sum s_i w_i \Delta z_i$

For each member of the population we need to obtain information on four variables. The first is the characteristic value z_i. In the simple Nelson–Winter model z_i is the productivity of a firm's capital stock. The second variable is the change of this productivity between the two periods Δz_i. The third variable is the population share s_i. In the Nelson–Winter model — where the underlying population may be said to consist of machines — this variable is a firm's capital share s_i. The fourth variable is the reproduction coefficient w_i, which is simply one plus the growth rate. If we multiply the first-period size of a member by its reproduction coefficient, we obtain the size in the next period. Given this information about the members of the population, we study additional population-level information in order to explain the change of the mean productivity Δz.

To study the selection effect we need basic population-level statistics. Here it is useful to start from the regression coefficient of reproduction on productivity, which is denoted $\beta(w_i, z_i)$. This regression coefficient shows the degree to which selection exploits differential productivities. Normally we deal with partial regression coefficients, but in the present discussion we shall operate as if productivity is the only determinant of the reproduction coefficient. Thus its meaning can be caught by considering the linear relationship

$$w_i = \alpha + \beta(w_i, z_i) z_i + \text{error}.$$

The next population variable is the variance of the productivities $\mathrm{Var}(z_i)$. The variance describes the differences on which selection operates. If $\mathrm{Var}(z_i) = 0$, selection cannot produce any change of mean productivity. Given non-zero values of both the regression coefficient and the variance, we have a contribution to observed change of mean productivity. The information on the regression coefficient and the variance may be replaced by the covariance between reproduction coefficients and productivities $\mathrm{Cov}(w_i, z_i) = \beta(w_i, z_i)\mathrm{Var}(z_i)$. Following Price, we may simply define selection in terms of this covariance (see below).

The study of the innovation effect starts from firm-level change in productivity Δz_i. The effect of this change on mean productivity is dependent on the firms' capacity shares in the second period, so we need to introduce the reproduction coefficients (since $s_i' = s_i w_i / w$). The total size of the effect is the mean or the expected value of all the firm-level contributions to the innovation effect, i.e. $\mathrm{E}(w_i \Delta z_i)$. According to this definition of 'innovation', we are obviously dealing with change in productivity that may occur for a variety of reasons. Thus the innovation effect of evolutionary economics comprises innovation in the ordinary sense, imitation, learning, etc.

Given the above definitions, we can readily understand the two elements of Price's decomposition of evolutionary change with respect to a Nelson–Winter model. Price's equation states that mean productivity change

$$\Delta z = \frac{\mathrm{Cov}(w_i, z_i)}{w} + \frac{\mathrm{E}(w_i \Delta z_i)}{w} = \frac{\beta(w_i, z_i)\mathrm{Var}(z_i)}{w} + \frac{\mathrm{E}(w_i \Delta z_i)}{w}. \tag{3}$$

Equation (3) is an identity. Given some experience in elementary statistics, the derivation — which is given in the appendix — is fairly simple. The fact that Price's equation is an identity means that it holds for any change in a characteristic, and thus also for productivity change.

As we shall see in section 3, it is often convenient to formulate Price's equation in a slightly modified version, where

$$w\Delta z = \underbrace{\mathrm{Cov}(w_i, z_i)}_{\text{Selection effect}} + \underbrace{\mathrm{E}(w_i \Delta z_i)}_{\text{Innovation effect}} . \tag{4}$$

Here the left hand side describes the change in characteristic weighted by the mean reproduction coefficient of the population. In this case, the definition of the selection effect and the imitation effect is particularly simple. Furthermore, it should be noted that the left hand side is structurally similar to the contents of the expectation term ($w_i \Delta z_i$). This means that Price's equation can be used to expand itself (see below).

Equation (4) shows that short-term evolutionary change of e.g. productivity is determined by two effects. The first is the selection effect that exploits the weighted variance of the productivities. If this variance is large, then mean productivity may increase quickly. The effectiveness of this selection is influenced by the degree to which the relative reproduction coefficients of firms reflect their productivities, and this degree is measured by linear regression as we have already discussed. Thus, selection efficiency is an empirical question that we have to confront for each time step of the evolutionary process. The second effect is the innovation effect. To see why this name is appropriate in the Nelson–Winter context, we have to consider the meaning of $\mathrm{E}(w_i \Delta z_i)$. If there is no change in the productivity of any of the individual firms, then the sum is zero. Why should productivity change at the firm level be different from zero? There are, of course, many potential reasons for both negative and positive values, but in the present context we shall concentrate of the knowledge issue. Here productivity change may be positive because of innovation, imitation or learning processes. It might be negative because the firm does not have an effective system of reproduction of its knowledge. The expected aggregate effects of both learning and forgetting are, of course, influenced by the capacity shares of the firms.

In specific cases, Price's equation (4) may be simplified. If we study pure selection processes, the innovation effect is zero. This is obviously what is assumed in Fisher's equation (1). To see the connection to Price's equation, we observe that the evolving characteristic is the reproduction coefficients themselves. Thus Fisher's theorem can be derived from the Price equation in the following way:

$$w\Delta w = \mathrm{Cov}(w_i, w_i) = \mathrm{Var}(w_i).$$

Hereby it is emphasised that Fisher is operating in relative terms, i.e. he works with $\mathrm{Var}(w_i/w)$.

Nelson and Winter made a similar study of a pure selection process — although they were explicitly working in terms of an evolving characteristic. On this background it is not surprising that they (Nelson and Winter, 1982, p. 243) obtained the same result — in a somewhat roundabout manner. By means of Price's equation the result is directly obtained. For all pure selection processes we find that the change of a characteristic than influences fitness is proportional to the variance of that characteristic. We also find that the selection process means that the variance in the first period is less than the variance we find for the second period. The reason is both due to the movement of mean productivity and changes in capacity shares: firms below the mean have become smaller while the mean has moved closer to the firms that increase their capacity share. To avoid the slowdown of change we need to switch on the innovation effect. This not only gives a short-term effect on mean productivity change. It also provides new variance with which the selection mechanism can work in future periods. The same problem emerges in productivity studies like those reviewed by Bartelsman and Doms (2000). To compare the increasing number of studies that are based on longitudinal microdata, the authors emphasise a partitioning of aggregate productivity that has great similarity with, and are easily rewritten to, Price's equation. The advantage of doing so is that the evaluation of the data becomes immediately connected to core results of evolutionary economics.

3. Multi-level population analysis

Simple intra-population analysis has serious limitations that becomes obvious when we study the evolution in populations that are partitioned in a nested way. Take, for instance, the productivity studies reviewed by Bartelsman and Doms (2000). Here the plant is often taken as the unit of selection, but plants are connected to firms, and firms are often connected to national economies within the global economy. Thus we have to deal with selection of plants within firms, selection of firms within national economics, and selection of national economies within the global economy. Since the national level is increasingly blurred due to transnational firms, we might have to make separate studies of the selection of plants within firms and the selection of plants within national economies. But irrespectively of our partitioning of the overall system, there is an obvious need to study the different kinds of selection that takes place at the different levels.

Let us start with Marshall's (1949, Part IV, Ch. 10) well-known theory of industrial districts. This theory was based in the commonplace observation that many English cities and geographical areas were highly specialised around the production of a small set of goods and that they upheld this specialisation over long time spans. It is possible to apply two-level population thinking to analyse this phenomenon. To simplify we consider only a single industry of a competitive economy. We assume that this population can be decomposed into sub-populations, each of which lives in an industrial district. Thus, we have an industry that is structured into districts (indexed by *i*) that consist of firms (indexed by *ij*). To explore the functioning of such industrial districts, we shall start by expressing Price's equation for the group level of the population — like the districts. Thus we now interpret equation (4) as dealing with industrial districts within a national economy. This means that

$$w_i = \sum s_{ij} w_{ij},\ z_i = \sum s_{ij} z_{ij} \text{ and } \Delta z_i = \sum s_{ij} \Delta z_{ij} \ .$$

Given this interpretation, it is obvious that we may apply Price's equation (4) to the evolution that takes place within the industrial districts. For each district we find that

$$w_i \Delta z_i = \underbrace{\mathrm{Cov}(w_{ij}, z_{ij})}_{\text{Intra-district selection effect}} + \underbrace{\mathrm{E}(w_{ij} \Delta z_{ij})}_{\text{Intra-firm innovation effect}} \ . \tag{5}$$

If we insert equation (5) into equation (4) and split the overall expectation term, we find that

$$w \Delta z = \underbrace{\mathrm{Cov}(w_i, z_i)}_{\text{Inter-district selection effect}} + \underbrace{\mathrm{E}(\mathrm{Cov}(w_{ij}, z_{ij})}_{\text{Intra-district selection effect}} + \underbrace{\mathrm{E}(\mathrm{E}(w_{ij} \Delta z_{ij}))}_{\text{Intra-firm innovation effect}} \ . \tag{6}$$

If we compare equation (6) with equation (4), we see that what was at the level of industrial districts considered an innovation effect is now partitioned into the expectation of the selection effects within the districts and the expectation of the more narrowly defined innovation effect within the firms. In other words, we study change of mean productivity at the national level in terms of three effects. First, there is selection between the districts of the industry. Here we can either directly use the covariance between district reproduction coefficients and district productivities or use the formulation with the regression coefficient and the variance of district productivities.

Second, there is the expected value of the intra-district selection effects. If the mean of these effects is significant, it is due to the differences in the selection process in different districts. Third, there is the expected value of the innovation effects — first over firms and then over districts.

Another kind of theories that may be explored by multi-level population analysis have been developed in evolutionary game theory — both in its formal version and in its computer-simulation-oriented version. Let us think of the latter and start from Axelrod's (1990; 1997) work, which at an early point included collaboration with one of the most important researchers on social behaviour in biology (Axelrod and Hamilton, 1981; see also Hamilton, 1996). According to this approach, social life is seen as a series of Prisoner's Dilemma games. Here it is possible to collaborate and obtain a welfare gain, but the temptation to exploit a collaborator means that the dominant strategy is to defect. Since this holds for both players, the result is that no welfare gain is obtained. The apparent solution is to introduce repeated games, where each player remembers previous games and punish defectors (the tit-for-tat strategy). Unfortunately, this solution is fragile to errors and misunderstandings. Social life, furthermore, is hardly stable enough to make the tit-for-tat solution feasible in medium-sized or large populations. Instead the solution seems to be to consider social life as structured into groups that in some way or another exclude many defectors and where collaboration is so productive that the effects of the actions of the collaborators outweigh the negative influence of remaining defectors.

The analysis of this solution can be handled by Price's equation, from which we for convenience exclude the innovation effect. To prepare for the Price decomposition we define z as the frequency of collaborators in the overall population. Thus $1-z$ is the frequency of defectors. Furthermore, we define the reproduction coefficient of a player with a given strategy in the first period as the number of players (including himself) that have been persuaded to follow the strategy in the next period. This number is determined by the relative payoff of the strategy. In an unstructured population, the payoff of collaboration is defined to be below that of defectors, so it will die off. So what about a population structured in groups? Equation (6) holds for each group and the innovation effect is equal to zero. Thus we have that Inter-group selection effect Intra-group selection effect

$$w\Delta z = \underbrace{\mathrm{Cov}(w_{ij}, z_{ij})}_{\text{Inter-group selection effect}} + \underbrace{\mathrm{E}(\mathrm{Cov}(w_{ij}, z_{ij})}_{\text{Intra-group selection effect}} . \tag{7}$$

If we in equation (7) move w to the right hand side, we see that the equation is about change of frequency of collaborators in the overall population. This change is influenced by two effects. Take first the expectation term: the intra-group selection effect on the frequency of collaborators. This effect must be negative as long as there are mixed groups. To see this, remember that $\mathrm{Cov} = \beta \mathrm{Var}$. Consider the contributions to the variance group by group. In homogeneous groups (either collaborators or defectors), variance is zero. Given the assumptions of the Prisoner's Dilemma, the regression coefficient has to work against collaborators. So the intra-group selection effect is negative as long as there are mixed groups. Furthermore, any unprotected group of collaborators can be taken over by defectors.

In order to avoid that collaborators are driven out of the overall population, the inter-group selection effect must be positive, i.e. there must be a positive regression coefficient of reproduction on the frequency of collaborators at this level. Furthermore, the effect must be sufficient to outweigh the negative intra-group selection. Thus

$$\mathrm{Cov}(w_i, z_i) > -\mathrm{E}(\mathrm{Cov}(w_{ij}, z_{ij})).$$

The mechanism here is that a group's mean payoff increases as the number of collaborators increases. Thus, although the relative number of collaborators decreases in mixed groups, the absolute number of collaborators may increase because their groups increase significantly more than average.

Our simple analysis based on Price's equation does not allow a broader study of the problems involved in upholding a high frequency of collaborators in a population that interact according to the Prisoner's Dilemma. It is, however, obvious that the situation can be improved significantly of collaborators have the possibility of largely playing with other collaborators. One strategy for securing this is 'altruistic punishment' (Gintis, 2000, pp. 271–278). This strategy implies that altruists punish defectors at a personal cost, while the benefit is gained by the group as a whole. Such punishment may imply that it does not pay to be a defector. But how can it pay to be such a kind of altruist? Price's equation tells us so — if we reinterpret A as the frequency of this kind of altruists. Computer simulations appear to demonstrate that this mechanism might have been working for the altruistic propensities of humans (Boyd et al., 2003), but in the present context, it is more interesting to know whether we have an evolutionary mechanism that explains many of the phenomena of economic organisation. This seems indeed to be the case.

4. Toward inter-population analysis

The analytical tools for both simple intra-population thinking and multi-level population thinking have deliberately emphasised short-run evolutionary change. Here 'short run' is defined as a period in which the population variables change significantly faster than the environmental variables and the related selection pressures. But in evolutionary studies we often have to move to toward longer-run change, and here we cannot realistically assume environmental constancy and thus a constancy of the 'ecological' interactions between different populations. Instead we have to confront the difficult problems inter-population thinking — including the coevolution between different populations. Although Price's equation is not designed for such issues, it is fully compatible with analytical tools for long-term analysis (Page and Nowak, 2002) and it may even promote such an analysis.

Let us consider the density dependence of the reproduction coefficients w_i — first within a population and then with respect to interacting populations. As before populations are denoted by subscript i and the members of the populations by ij. For concreteness, we shall relate to the Nelson–Winter model. To get started, we shall initially switch off innovation and give all firms the same productivity. Given these assumptions, there is neither a selection effect nor a real innovation effect. Thus, Price's equation (4) tells us that there is no productivity change. Nevertheless, the reproduction coefficients may show change from one period to the next. To see why, let us measure the size of the population by its capacity — e.g. the number of machines. Then we make a Price partitioning of the change of the mean reproduction coefficient of population i. The total change and the individual effects may be denoted

$$\Delta w_i = \Delta w_i^{\text{selection}} + \Delta w_i^{\text{innovation}}.$$

To specify the two effects, we simply reapply equation (4), but now we include the subscript i to indicate that we are dealing with several populations. Thus,

$$w_i \Delta w_i = \mathrm{Cov}(w_i, w_i) + \mathrm{E}(w_i \Delta w_i) = \mathrm{Var}(w_i) + \mathrm{E}(w_i \Delta w_i). \tag{8}$$

As earlier, the selection effect of equation (8) is straightforward. But since we have assumed that variance is zero, the selection effect is also zero. However, due to the explicit treatment of density dependence, we have to reconsider the meaning of the second effect. Since by assumption no innovation takes place, the change in the population's mean reproduction coefficient Δw_i is only due to density effects. So we may name it the 'environment effect' rather than the 'innovation effect'. But since the focus of the present postscript is on innovation, we shall stick to the name that is presently so confusing.

Seen from the viewpoint of a firm in industry i, its environment consists of other firms of the same industry, firms of other industries, and the resources that it exploits. To simplify the analysis, we assume that both intra-population competition and interpopulation competition concern the exploitation of the same resource (e.g. a population of customers). This assumption implies that both the number of machines in population i (x_i) and the aggregate number of machines in all populations (x) contribute to the selection pressure on the individual firm. Let us start by considering the situation where population i is alone. In this case, we may apply the logistic equation to describe the situation. According to this equation, the level of crowding with respect to resource exploitation determines the populations' mean reproduction coefficient. As a small population of machines grows larger, crowding reduces the reproduction coefficient until the population reaches unity at the 'carrying capacity' of the resource. This is the density effect or interaction effect — determined by the squared number of population members. But the reproduction coefficient is also influenced by each member's intrinsic capability to grow.

The logistic equation applies change rates rather than reproduction coefficients. It is also most conveniently expressed in continuous time. It states that the change rate of the size of the population

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = r_i x_i - b_i x_i x_i = r_i x_i \left(1 - \frac{x_i}{K_i}\right), \tag{9}$$

where $K_i = r_i / b_i$. In this equation r_i is the maximum reproduction coefficient, which is found when N_i is very small. K_i is the steady state size of the population, which may be considered as the carrying capacity of the exploited resource with respect to population i. When this population size is reached, the change rate is zero and the reproduction coefficient is unity.

To give evolutionary meaning to the logistic equation (9), we have to remember that we are dealing with potentially heterogeneous firms. Thus, differential traits may imply that some firms show above-average reproduction coefficients in particular situations. When the population of machines is very small, individual firms that are organised in a way that allows them to expand quickly will have the highest reproduction coefficients. Thus, the frequency of such traits will increase, while other traits will be selected out of the industry. This is the r-selection of MacArthur and Wilson (2001). This selection regime becomes permanent if the population of machines is often reduced in size, and the industry thus has to restart its expansion. Otherwise, the population will move toward the carrying capacity of the resource, and here K-selection among the firms is predominant. This kind of selection favours firms with traits that increase their efficiency in exploiting the resource — like firms with quality products or complicated game strategies.

The simplest way of moving from the analysis of density dependence within a single population to the multi-population case is to assume that the total number of members of all populations ($x=\sum x_i$) influences the rate of change of each individual population. This assumption means that the capacity of all firms from all the industries have an equally negative influence on the reproduction coefficient of a particular firm. Thus, we may apply a simplified version of the Lotka–Volterra equations. In our simple competitive case, equation (9) only needs a minor modification to handle the multi-population case:

$$\frac{\mathrm{d}x_i}{\mathrm{d}t}=r_i x_i - b_i x_i x = r_i x_i\left(1-\frac{x}{K_i}\right). \tag{10}$$

Compared with equation (9), the only novelty of equation (10) is that x_i/K_i has been replaced by x/K_i. But the consequence is significant. Now whole industries may have an average behaviour that gives them relatively high reproduction coefficients when the overall population density is small. But such r-strategy industries tend to do gradually more badly as the aggregate population density increases. If this expanding exploitation of the resource is not stopped by set-backs, then it is the relative sizes of the carrying capacities of the industries that determines their destiny. If industry A is adapted to r-selection and industry B is adapted to K-selection, then $K_B > K_A$. This means that when industry A has reached a zero change rate, industry B is still expanding. Thus, industry A will start to decrease and ultimately it will vanish. If the exploitation of the resource allows sufficiently stable populations, only the industry with the highest K_i will survive.

This short description of density-dependent selection is based on the relative stability of the population parameters (r_i and K_i), while no such assumption was made in Price's equation (8). Instead, this equation formally presupposes that we stick to short-term evolutionary change. In this way, it becomes a universal tool. When we move to density dependence and inter-population thinking, we need additional and less universal tools. But even here Price's equation may help to clarify the details of the evolutionary process.

For instance, studies in terms of the logistic equation (9) and the Lotka–Volterra equation (10) tend to consider the behavioural variance as absent or given. But in real evolution, the second term of Price's equation (8) is including both an environment effect and an innovation effect. Thereby it suggests that the important thing when a set of populations starts to reach the individual carrying capacities is not only their given abilities to handle this situation. It is probably more important how they innovate. The effect of innovation on the change in mean reproduction coefficients will also have an effect on their saturation sizes K_i. Thus, it is important to remember that these 'parameters' are really variables. Therefore, we should include into our study the changes of the carrying capacities ΔK_i. It appears plausible that the industry that has the best innovative performance under K-selection will be the one that survive. To fixate this issue, it is convenient to call the adaptation to a crowded situation *K*-innovation.

The short discussion of *r*-selection and *K*-selection is in line with the present paper's general preference for simple analytic tools. Such tools tend to clarify many discussions and they suggest empirical questions (e.g. the measurement of r_i and K_i in different industries, and the study of *K*-innovation). But it is, of course, important to know whether the simple tools can handle complex issues. Ultimately, we have to cope in some way or another with the evolutionary consequences of the whole range of inter-industrial relationships. For instance, Schumpeter (1939) challenges us to handle the multiple ways in which the so-called 'railroadization of the world' changed economic structure during the nineteenth century (cf. Andersen, 2002). Here we obviously cannot perform the analysis by means of the truncated version of the Lotka–Volterra equation (10). In principle, we have to include the interaction coefficients between a number of industries and study the resulting complex dynamics. The question is, however, whether the inclusion of the detailed effects of the density of each industry on the densities of all the other industries will help us much. For instance, we have to drop the idea of using a single density variable like in equation (9), but we have to find other simplifications to avoid the analytical problem to become unmanageable. Schumpeter's idea of radical innovations might be the beginning of such a tool, but it is hard to see how it can become analytically operational. In the more complex setting it also becomes very hard to define K_i and other core parts of inter-population thinking. So even when we perform 'history-friendly modelling' (Malerba, Nelson, Orsenigo and Winter, 1999), we are forced to make harsh simplifications.

5. Conclusions

This paper has dealt with population thinking from a particular viewpoint: the need of analytical tools. Although the situation is by far satisfactory, we have today significantly sharpened forms of population analysis to confront the problems of economic evolution in a more efficient manner than has hitherto been the case. To describe the new situation, we may apply Schumpeter's (1954, p. 39) formulation that 'a new apparatus poses and solves problems for which the older authors could hardly have found answers even if they had been aware of them.' The paper has demonstrated that population thinking is more multiform than normally recognised, and therefore it needs a complex analytical toolbox. However, an important theme of the paper was that Price's equation for the decomposition of evolutionary change is surprisingly powerful in supporting manifold tasks of evolutionary analysis. So although it apparently is a simple extension of the statistically oriented intra-population analysis in the tradition of R. A. Fisher, it may also help to transcend this tradition. The reason is partly that Price's equation avoids making strong assumptions about the kind of evolutionary processes that may be covered. This generality comes at a cost, namely that the equation is not sufficient to define a long-term path of evolutionary change. But this limitation should be seen as its strength rather than its weakness. For instance, it is far too easy to forget about the web of inter-population links when a system of replicator equations is projected into the long run. Price's equation helps us to be more modest by pointing to the many assumptions underlying such long-run dynamics. Presently, the major task for our understanding of economic evolution is, probably, to deepen our analysis of its shorter-term aspects.

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Appendix: Derivation of Price's equation

The derivation of Price's equation (3) is fairly simple. We simply exploit the definitions given in table 1 of the paper. Here are the first steps:

$$\begin{aligned}\Delta z = z' - z &= \sum s_i' z_i' - \sum s_i z_i \\ &= \sum (s_i + \Delta s_i)(z_i + \Delta z_i) - \sum s_i z_i \\ &= \sum \Delta s_i z_i + \sum (s_i + \Delta s_i)\Delta z_i .\end{aligned}$$

The task is to rewrite these two terms into the components of Price's equation. But before we do so, we note that $\sum \Delta s_i z = 0$ and that

$$s_i' = x_i'/x' = x_i w_i / xw = s_i w_i / w.$$

We are now ready to rewrite the first term:

$$\begin{aligned}\sum \Delta s_i z_i &= \sum \Delta s_i z_i - \sum \Delta s_i z \\ &= \sum \Delta s_i (z_i - z) \\ &= \sum (s_i' - s_i)(z_i - z) \\ &= \sum s_i (w_i / w - 1)(z_i - z) \\ &= 1/w \sum s_i (w_i - w)(z_i - z) \\ &= \frac{\mathrm{Cov}(w_i, z_i)}{w} .\end{aligned}$$

Similarly we rewrite of the second term:

$$\begin{aligned}\sum (s_i + \Delta s_i)\Delta z_i &= \sum s_i' \Delta z_i \\ &= \sum s_i (w_i / w)\Delta z_i \\ &= 1/w \sum s_i w_i \Delta z_i \\ &= \frac{\mathrm{E}(w_i \Delta z_i)}{w} .\end{aligned}$$

Thus we have derived Price's equation:

$$\Delta z = \frac{\mathrm{Cov}(w_i, z_i)}{w} + \frac{\mathrm{E}(w_i \Delta z_i)}{w} .$$