Population thinking and evolutionary economic analysis

Draft of Postscript for the Japanese edition of Andersen's *Evolutionary Economics: Post-Schumpeterian Contributions*

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INTRODUCTION

Although evolutionary economics have deep roots in the history of economic thought, its modern forms did not start to emerge before about 30 years ago (Witt, 1993). Even from this start, modern evolutionary economics has encompassed different approaches. They range from very general analyses of evolutionary games to specific studies of industrial dynamics, and the diversity has significantly increased over the years (Nelson, 1995; Dopfer, 2001; Foster and Metcalfe, 2001). So we are forces to ask what—if anything—is common for all these diverse studies of economic evolution. If we anticipate the answer that there only is a small common denominator, then we may also ask the additional question of whether and how to promote the unity of evolutionary economics.

These questions may be confronted in different ways. We may, for instance, look for a deep unity with respect to the nature of economic evolution and the methodology with which we obtain knowledge about it (Potts, 2000; Witt, 2001). But this is a difficult strategy for answering the questions, and the answers might be hard to grasp for the practitioners of evolutionary economics. Furthermore, ontology and methodology are notorious sources of controversy, so they are not likely candidates for promoting unity. Thus, it seems relevant to apply a complementary and simpler strategy for answering the questions of the present and future unity of evolutionary economics.

The present paper suggests that an important part of the actual and potential unity is found in the basic ways we think about economic evolution and in the analytic tools we apply to sharpen this thinking. Since evolutionary thinking and its analytic tools have not yet reached maturity, a simple survey does little to find and promote unity. Instead, we have to reconstruct and systematise evolutionary thought and the related tools, so the required effort in evolutionary economics may be compared with what Samuelson (1983) did for neoclassical economics in his *Foundations of Economic Analysis*. Like Samuelson, we need to find common denominators beneath the highly diverse surface of the literature. We may even find some room for a comparative static analysis of evolution. Otherwise, our study will lead to results that are different from those of Samuelson. The reason is that while his neoclassical analysis is based on substantively rational agents and tends to be performed in terms of representative agents, evolutionary economic analysis is based on boundedly rational agents and takes the form of population thinking.

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 population thinking. 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 properties. Since Plato, there has 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.

The switch from typological thinking to population thinking is not an easy one. Therefore, researchers trained in typological thinking would like to have a population with well-defined boundaries before they start to consider the variety among the individuals within the population. They would also like to have a definition of the maximum degree of variance that can exist within such a population. In the case of industries and firms (or, rather, plants), they would like to have a fixed definition of the boundaries of the industry and a general criterion to check whether we are really facing an industry and not a collection of industries. But a major point of population thinking is that those wishes cannot be fulfilled. Instead, we have to do with more flexible definitions of populations—especially that the interaction between their members includes a significant competitive element. This means e.g. that we may just as well consider a localised subpopulation as the overall population of an industry. The fruitfulness of the concrete demarcation of the population under study is largely an empirical matter that cannot be solved *a priori*.

Population thinking means that we deal with heterogeneous populations and that we consider this heterogeneity as a fundamental issue. This becomes especially important for behavioural characteristics that change over time, like the strategy in an evolutionary game or the productivity in a study of industrial evolution. In these cases, heterogeneity is upheld by the behavioural inertia that characterises boundedly rational agents. Such agents also have a tendency to copy behaviour of other agents. If we study the distribution of behaviour (like strategy or productivity) in the population, we normally observe that this distribution evolve over time. We also recognise that this evolution may be ascribed to two different forces. Selection is the force that implies that firms with different versions of the property have differential growth rates. Selection presupposes variance with respect to a particular property, and this property must be important in each member’s environment (including the other members of the population). Selection means that the average property of the population will change. But this average may also change because of innovations and random drift in the mean of the properties of the population. For instance, innovation means that agents may obtain behavioural characteristics that were not previously present in the population.

Even from this short account, it is obvious that population 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 our thinking' ground level, where we define what to look for. The problem here is that few are accustomed to this kind of statistical thinking—partly because has poor support from common analytic tools. To promote the unity of evolutionary economics there is thus a need for providing basic tools for basic population thinking.

Basic population thinking may bring us a long way in our analysis of economic evolution. But it supports some aspects of this analysis much better than other aspects. This becomes clear as soon as we realise that basic population thinking is largely a single-level version of intra-population thinking. Thus, we focus on the evolution that takes place in a population like the firms of an industry. But firms are not normally homogenous units of selection. Instead, they define an internal selection environment, where the units of selection are plants, groups or individual employees. So there is an obvious need to move from basic population thinking to multi-level population thinking. Furthermore, basic intra-population thinking does not treat the selection process that takes place at the super-population level. Here one core issue is to promote the thinking about the interaction and co-evolution of two or more populations. For instance, we may like to understand how a new core industry co-evolves with other industries. Experience shows that such an analysis is quite difficult, so there is a tendency to drop real inter-population thinking and instead study the interaction of populations that are assumed to be homogenous. Even worse problems are encountered when we turn to the core issue of how new populations emerge from old ones. For instance, there is an obvious need for an analysis of the branching of the computer industry into a number of more or less independent industries. For this purpose, we need intra-to-inter-population thinking, which may also be called tree thinking. The reason is that if we apply this thinking recursively, we see the evolving branching of populations like the branching of a tree. If we want to study the emergence of complex economic systems, we have to apply tree thinking.

The fact that there are multiple forms of population thinking clearly suggests one of the reasons for the lacking unity of evolutionary economics: different researchers are engaged in different kinds of population thinking. Quite many evolutionary researchers lean to the fairly well-defined intra-population thinking and a few try to extent its formalisms to multi-level population thinking. But large groups of researchers are engaged in less formalised studies based on multi-level population thinking, inter-population thinking and intra-to-inter-population thinking. Hitherto, communication between the different groups of researchers has apparently been relatively limited. But it is not difficult to recognise that there is a common ground for the researchers. All evolutionary researchers are well advised to grasp the basic forms of population thinking. The main reason is that they all have to cope with the evolution that takes place in single population—even if it is not their main focus. Furthermore, the concepts and tools of intra-population thinking may give some guidance for other kinds of thinking. Finally, the development of specially adapted concepts and tools for the more difficult kinds of thinking will often start from the well explored area of intra-population thinking. So intra-population thinking is a necessary condition for a viable evolutionary economics. But it is not a sufficient condition. As long as more complex forms of population thinking are poorly supported by analytic tools, the whole study of economic evolution is difficult to handle—even for those who tend to specialise in basic forms of evolutionary analysis.

The postscript covers the different kinds of population thinking that have just been presented. It starts with basic intra-population analysis for single populations, and this is followed up by a short treatment of how this analysis can be extended to structured populations, where selection takes place at several levels. Then we turn to the issues of co-evolution of populations and the emergence of new populations. Finally some conclusions are drawn. Thus, the ambition is to give a broad coverage of the forms of evolutionary thinking and the related tools. The drawback is obviously that the coverage becomes rather sketchy. To focus the contents of the postscript, an emphasis is put on a simple and basic tool for intra-population thinking an its relevance for more complex forms of population thinking. This little known but surprisingly powerful tool is a formula for the decomposition of short-term evolutionary change. This formula was developed by George R. Price (1972), and it has recently started to spread into evolutionary economics from its stronghold in the analysis of social evolution in evolutionary biology. The application of Price's formula helps us to think clearly about the selection processes that form the backbone of economic evolution, but it also elucidates innovation processes and their consequences. Furthermore, it eases the move from single-level population thinking to multi-level thinking. The emphasis on this tool might help to make the postscript interesting. But it should be remarked that the postscript could just as well have been written in terms of a more well known—and closely related—tool: the replicator dynamic equation.

INTRA-POPULATION THINKING

Winter (1991, pp. 186–187) has pointed out that 'Evolutionary Economics relates to Armen Alchian's classic paper, "Uncertainty, Evolution and Economic Theory", in much the same way that transaction cost economics relates to Coase and "The Nature of the Firm".' In both cases, we have papers that serve as core points of reference for the subsequent discussion. Alchian's (1950) paper function as a standard reference to intra-population thinking. It is, however, easy to find predecessors. For instance, a group of Oxford economists dealt during the 1930 rules of thumb and other routines that determine firm behaviour, and their work was summarised by Harrod (1939). At the end of his paper Harrod turns to the background of such behavioural rules with the remark that 'It may be that certain procedures ... are thrown up purely by chance in the first instance and survive by a process akin to natural selection in biology.' He immediately extends this thought in the following way:

> New business procedures would then be analogous to new mutations in nature. Of a number of procedures, none of which can be shown either at the time or subsequently to be truly rational, some may supplant others because they do in fact lead to better results. Thus while they may have originated by accident, it would not be by accident that they are still used. For this reason, if an economist finds a procedure widely established in fact, he ought to regard it with more respect than he would be inclined to give in the light of his own analytic method. (Harrod, 1939, p. 7)

These formulations are closely related to Alchian paper, which actually sounds like an extension of Harrod's ideas into an approach that 'embodies the principles of biological evolution and natural selection by interpreting the economic system as an adoptive mechanism which chooses among exploratory actions generated by the adaptive pursuit of "success" and "profits"' (Alchian, 1950, p. 211). But Harrod's ideas are also close to those of Marshall. Even a quick analysis of Marshall's work in terms of modern population thinking demonstrates that it has nearly all the necessary components. However, Marshall had to give up his attempts to formalise population thinking, and therefore the planned second, evolutionarily oriented volume of his *Principles of Economics* was never written (Thomas, 1991; Niman, 1991). But Marshall's published first volume was filled with evolutionary thinking and remarks about its difficulties. For instance, he pointed out that the theory of survival in natural selection 'is not yet completely thought out either in its biological or its economic relations' (Marshall, 1949, p. 201). Here he might have thought about the genetic consequences of economic evolution, but he reached the same conclusion for proper economic evolution.

Evolutionary thinking is found even in Marshall's core chapters on the formal modelling of partial market equilibrium. This is considered analogous to the steady state of a population of trees in a forest. In the market, there is a selection against firms with low productivity, but even strong firms undergo a life cycle that ultimately makes them weak performers (Marshall, 1949, 263 ff., 305 ff.). Marshall's notion of the representative firm is an attempt to abstract from this population thinking. This abstraction is made with regret, but he is simply not able to formalise his population thinking at the level of firms. The use of the *ceteris paribus* clause of partial equilibrium analysis is similarly due to the fact that Marshall is even less able to perform multi-level population thinking for the case where the population of firms at the level of the whole economy is structured into many subpopulations.

Today the question is whether we are able to overcome the difficulties that a skilled economist and mathematician like Marshall could not handle. The short answer is that other researchers have done much of the job for us. The breakthrough 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!). Among his results, we shall concentrate on what may be called the Fisher principle (Metcalfe, 1998, Ch. 2). It is a generalised version of 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'. In the generalised form this principle is very important for learning about population thinking, but it is normally taken in a truncated form that delimit its usefulness. We shall stick to the general principle and explore how it can be used in a general and flexible manner. As a side effect, we shall recognise the enormous importance of statistical concepts—both in evolutionary economic theory and in the empirical study of economic evolution.

Fisher's work started—like the work of e.g. Nelson and Winter (1982)—from statistics of populations and their change. The Fisher theorem states that if selection favours the degree to which a particular property/trait is present in the individuals, then the rate of change of the mean value of this property is proportional to the variance of the property within the population. Thus, we have to define the properties 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 property 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 G. R. Price, who was also the co-founder of evolutionary game theory (Maynard Smith 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 is 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.

To illustrate the functioning of Price's form of intra-population thinking, it is easiest to deal with an evolutionary process that moves in discrete steps—like agricultural production, where a new generation of output is brought to the market every year. Most evolutionary games and most neo-Schumpeterian models are of this type. For such cases, it is possible to make a simple analysis of evolutionary change from one period to another period. The same analysis can actually be applied to any discrete-step evolutionary process in biology, economics, and elsewhere. This analysis appears very different from the widespread approach of replicator equations (Silverberg, 1988; Hofbauer and Sigmund, 1998), where we study the change of population shares of (groups of) agents with different properties, but the two approaches are actually complementary (Page and Nowak, 2002). However, the present discussion follows Fisher and Price in concentrating on the change of the mean of a property of the population.

In the case of the simplest evolutionary version of the Prisoner's Dilemma game the obvious property is the strategy. Here we study the frequency of players with the cooperative strategy in the two periods and find the change in this frequency. Similarly, we may take the Nelson–Winter model in which we measure the mean productivity in the population of firms in the two periods and calculate the change in this mean productivity. Price's equation may also be used on data collected from a real population of firms or households. Presently we, however, shall work with simple models.

When we try to explain the evolution of a mean property, we have the problem that it might be caused by many forces. It is, nevertheless, possible to decompose the change in the mean property into two effects of which at least the first is easy to understand. This decomposition is possible for any evolutionary change, so it may e.g. be applied to change in an evolutionary game or the Nelson–Winter model. In any case

Total change = Selection effect + 'Innovation' effect.

In this expression it is generally only the selection effect that has an immediate meaning. But as soon as we operate within a particular model or with well-defined empirical evidence, we shall often be able to give meaning to the ‘innovation’ effect. To simplify the discussion, we shall in the following concentrate our examples on a version of the standard Nelson–Winter model. Here the latter effect is largely an innovation and imitation effect, but we shall later see that it also includes the ‘deterioration of the environment’ (Fisher, 1999, pp. 41–42).

Such an analysis of evolutionary change has obvious advantages, but it cannot be understood without a little formal analysis. Even the impatient reader will need to hold on during this section, which will be used directly or indirectly in much of the postscript. To decompose evolutionary change we study the members of a population in two periods, 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. In the Nelson–Winter model the individual members of the population are best interpreted as the capital stock of firms. To perform the analysis, we need information on several variables for both these members and the aggregate population.

For each member of the population we need to obtain information on four variables. The first is the property value A_i. In the simple Nelson–Winter model A_i is the productivity of a firm’s capital stock. The second variable is the change of this productivity between the two periods $\Delta A_i = A_i' - A_i$. The third variable is the population share s_i. In the Nelson–Winter model—where the underlying ‘population’ consists of machines—this variable is a firm’s capital share $s_i = K_i / K$, where K_i is the capital of a firm and $K = \sum K_i$ is aggregate capital. The fourth variable is the reproduction coefficient ω_i. If we multiply the first-period size of a member by its reproduction coefficient, we obtain the size in the next period. In the Nelson–Winter model we may talk about the reproduction coefficient of capital. Here the new capital stock $K_i' = \omega_i K_i$.

Given this information about the members of the population, we calculate additional population-level information. The core variable is the mean productivity $\overline{A} = \sum s_i A_i$. This variable can be used in two ways. Often it is used in an explicit study of the change of the population shares by means of the replicator equation, which in the simplest form is

$$\Delta s_i = s_i \left(\frac{A_i - \overline{A}}{\overline{A}} \right)$$

Presently, we shall not follow this replicator approach directly. Instead we shall dig deeper into the evolutionary process by decomposing mean productivity change $\Delta \overline{A} = \overline{A}' - \overline{A}$.

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 $\square_{\square,A}$. 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

$$\square_i = \square + \square_{\square,A} A_i + \text{error}.$$

The next population variable is the variance of the productivities $\mathrm{Var}(A) = \square\,(A_i \square \bar{A})^2$. The variance describes the differences on which selection operates. If $\mathrm{Var}(A) = 0$, 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

$$\mathrm{Cov}(\square, A) = \square\, s_i (\square_i \square \square)(A_i \square \bar{A}) = \square_{\square,A}\mathrm{Var}(A).$$

This study of the innovation effect starts from firm-level change in productivity $\square A_i = A\square\square A_i$. The effect of this change on mean productivity is dependent on the firms' employment shares in the second period, so we need to introduce the reproduction coefficients (since $s\square = s_i \square_i$). The total size of the effect is the mean or the expected value of all the firm-level contributions to the innovation effect

$$\overline{\square\square A} = \mathrm{E}(\square\square A) = \square\, s_i \square_i \square A_i.$$

Given the specifications of the selection effect and the innovation effect, we can readily understand to different versions of Price's decomposition of evolutionary change a Nelson–Winter model. Price's equation states that mean productivity change

$$\square\bar{A} = \frac{\mathrm{Cov}(\square, A)}{\square} + \frac{\mathrm{E}(\square\square A)}{\square} = \frac{\square_{\square,\mathrm{A}}\mathrm{Var}(A)}{\square} + \frac{\mathrm{E}(\square\square A)}{\square}. \tag{1}$$

This is the general version of Price's equation that may be used for the decomposition of any kind of evolutionary change. The equation shows that short-term change in productivity is determined by two effects. The first is the selection effect that exploits the (market-share 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 model. For an evolutionary process to take place, this parameter has to change more slowly than the individual variables.

In the Nelson–Winter model the second component is the innovation effect, but this is not generally correct (unless we e.g. accept the notion of negative 'innovations' and effects of environmental change). To see why this name is appropriate in the present context, we have to consider the meaning of $\mathrm{E}(\square\square A)$. 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 innovations 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 models Price's equation (1) may be significantly simplified. In a simplified Nelson–Winter growth model developed by Andersen (2003), where all capital is replaced in each period. Here the equation becomes

$$\Delta\bar{A} = \frac{\mathrm{Var}(A)}{\bar{A}} + \frac{\mathrm{E}(A\Delta A)}{\bar{A}}. \tag{2}$$

If we in this equation switch off the innovation effect by setting all firm-level productivity changes to zero, we see the pure selection dynamics of a simple Nelson–Winter model. Thereby, we quickly and elegantly reach a result that Nelson and Winter (1982, 243) obtained in a roundabout manner. They developed a growth model from which innovation was excluded. For this model of pure selection they proved several results. In a footnote they remarked that an

> ... analogue for Fisher's theorem in the present model is the proposition that the rate of reduction in industry average unit costs is equal to the share-weighted cross-sectional unit cost. This proposition is indeed a theorem under the assumptions of the present model, a fact we were led to verify by the parallel with Fisher's result.

We have obtained the same result in terms of productivities rather than costs. Still we have that the change of a property than influences fitness is proportional to the variance of that property.

Furthermore, the selection process means that the variance taken in the first period is less than the variance we found 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. If the regression coefficient is constant, then we will see a decrease in productivity change between the two periods. To avoid the 'retardation 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.

An obvious application of Price's equation is to follow what happens in the evolution of the somewhat more complex Nelson–Winter model of Schumpeterian competition. If we start with many equal-sized firms, and if different productivities have already emerged, then there is a rather strong selection effect. This selection effect is, however, influenced by the rate of depreciation of capital. It reaches a maximum with a depreciation rate of unity, where all production in the next period is made by new capital. As the industry becomes more concentrated, the selection effect becomes weaker. The reason is that firms with large market shares show monopolistic investment restraint. For such firms a large productivity gain may even lead to negative investment. The reason is that these firms maximise their profits in this way, but this also mean that they some of the productivity differentials are not used to increase mean productivity of the industry. In these and other ways, Price's equation allows a quick analysis of the aggregate behaviour of Schumpeterian competition.

MULTI-LEVEL POPULATION THINKING

Although the presentation of Price's formula has primarily related to the evolution of industrial populations, this formula is an identity that can be used for the study of any kind of change in which selection has a role to play. The decomposition may also deal with more structured populations than an industry in which every firm competes directly against any other firm. Actually, Price's formula has found a primary area of use for the study of structured populations. The reason is that both in studies of biological and cultural evolution it has become obvious that the formula suggests an easy and general way to handle populations that have both a group level and an individual level. Thus it functions as a major tool for the study of social evolution—no matter whether 'social' relates to ants of humans and whether social behaviour is influences by genes, culture or economic institutions (cf. Frank, 1998).

In the first 15 years of its existence, Price's formula found few applications (Grafen, 1985, p. 38), but after that time it has won fairly widespread applications among evolutionary biologists and, more recently, among some evolutionary game theorists in economics (Gintis, 2000, Ch. 11). It is especially Frank (1998) that has demonstrated the broad applicability and the unifying power of Price's formula. For instance, it has in biology served to obtain a certain degree of reconciliation between the majority view of individual-level selection and the minority view that emphasises group-level selection (Sober and Wilson, 1998; Gould, 2002, Ch. 8). Hitherto, group-level selection has largely been used to explain the biological and cultural evolution of 'altruistic' behaviour that seems to be a necessity for the functioning of human societies. However, given that 'altruism' is a potential of *Homo sapiens* in small to medium-sized groups, then the group-level analysis may also help to explain several aspects of business organisation and the functioning of localised groups of firms.

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 j) that consist of firms (indexed by ji). 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. To emphasise that we are operating at this level, we add group subscripts to the variables at the right hand side of the equation. Furthermore, we multiply both sides of equation (1) by $\square$. Thus we have Price's equation for the group (district) level, where

$$\square\square\bar{A} = \mathrm{Cov}(\square_j, A_j) + \mathrm{E}(\square_j \square A_j). \tag{3}$$

This format of Price's equation might appear more mysterious than that of equation (1), but it has an advantage that is revealed by studying equation (3) under the new interpretation in terms of groups.

The left hand side is still dealing with means of the whole population, but on the right hand side we are also dealing with mean values. They are taken over the firms (indexed by ji) of each district. Thus

$$\rho_j = \bar{\rho}_j = \sum s_{ji}\rho_{ji},$$

$$A_j = \bar{A}_j = \sum s_{ji}A_{ji}, \text{ and}$$

$$\Delta A_j = \Delta\bar{A}_j = \sum s_{ji}\Delta A_{ji}.$$

Given this interpretation, we may return to equation (3) and observe that the left hand side ($\bar{\rho}\Delta\bar{A}$) says the same as the right hand side's product in the expectation term ($\rho_j\Delta\bar{A}_j$)—except for the group subscript. Since Price's formula is general, it can also be used to decompose this product. Thus, we have that

$$\rho_j\Delta A_j = \bar{\rho}_j\Delta\bar{A}_j = \mathrm{Cov}(\rho_{ji}, A_{ji}) + \mathrm{E}(\rho_{ji}\Delta A_{ji}).$$

Here we see how productivity change within a district (or any other group) can be decomposed into a selection effect and an innovation effect. By inserting this result into equation (3), we obtain the two-level Price equation

$$\bar{\rho}\Delta\bar{A} = \mathrm{Cov}(\rho_j, A_j) + \mathrm{E}\left[\mathrm{Cov}(\rho_{ji}, A_{ji}) + \mathrm{E}(\rho_{ji}\Delta A_{ji})\right]. \qquad (4)$$

According to this equation, we study change of mean productivity at the industry 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 important, 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. By means of district-level selection systems and externalities from firm-level innovative activities, we may try to give meaning to the last two effects. However, to explore more fully the multi-level process of evolution it is necessary to move beyond the limits of the simple forms of multi-level population thinking.

Until now, the grouping of firms has been attached to districts, and they may show up to have importance. But the grouping can be made in the most arbitrary way. For instance, we may apply Price's formula to groups defined by the first letter of the names of the firms. Thus, there must surely be many insignificant ways of grouping firms. The best is, of course, to use groupings to test theories. So the question is which kind of theory we should apply. Here the example of industrial districts points to Marshall's theory, but to cover broader issues we shall instead turn to theories of the evolution of cooperation. Such theories have not least 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, 1980). 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 handles by Price's equation, from which we for convenience exclude the innovation effect. To prepare for the Price decomposition we define A as the frequency of collaborators in the overall population. Thus $1 - A$ 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? Here we have

$$\bar{w}\Delta\bar{A} = \mathrm{Cov}(w_j, A_j) + \mathrm{E}\left[\mathrm{Cov}(w_{ji}, A_{ji})\right].$$

If we in this equation move $\bar{w}$ 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 this 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

$$\mathrm{Cov}(w_j, A_j) > -\mathrm{E}\left[\mathrm{Cov}(w_{ji}, A_{ji})\right].$$

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.

TOWARD INTER-POPULATION THINKING

In the preceding sections, we have explored formal intra-population thinking and stretched it to its multi-level limits. But the analysis of evolutionary processes also requires that we are able to handle the interaction between different industries by means of inter-population thinking. For instance, we would like to know how a population of firms co-evolve with its customer population and how the functioning is of broad networks of co-evolutionary relationships between populations Unfortunately, the requited form of thinking is more complex and less supported by formal tools than intra-population thinking. But this caveat should not lead to an abandonment of the study of crucial forms of economic evolution. Instead, we should confront these forms of evolution, and thereby we might even find that some of the more narrow tools are of great help. This has been demonstrated by e.g. Saviotti (1996; 2001) within the tradition of evolutionary replicator dynamic analysis. In relation to the present postscript, however, the complementary tradition based on Price's formula has also been able to exploit its generality to handle aspects of surprisingly difficult issues.

The first thing to note is that interactions between populations are handled by formal tools that have a family relationship with replicator dynamics: the Lotka–Volterra equations for interacting populations (Hofbauer and Sigmund, 1998, Part 1). But this tool was originally designed for dealing with the interaction between homogeneous populations. Thus, it was a non-evolutionary tool that has often been connected with typological thinking. This holds both for its economic and biological applications. Thereby the 'ecological' tradition was in sharp contrast with the intra-population tradition in both biology and economics, which has for a long time been based in evolutionary population thinking. This difference has, however, been bridged by evolutionary ecology (e.g. Pianka, 1999), which in the social sciences is e.g. covered by Hannan and Freeman (1989) and Carroll and Hannan (1999).

Even though the original differences have largely been overcome, there is still a serious difference between the two approaches. It concerns the assumptions about the density dependence of selection. Here the modern inter-population tradition is based on the assumption that the density of a population influences the selection among its members, just like the density of one population influences selection in other populations. In the evolutionary version of the famous predator–prey model, selection for many traits increases as an isolated population of prey grow toward its carrying capacity, while the density of predators represents a varying selection pressure on other traits. The intra-population tradition has traditionally abstracted from the density dependence of selection. The reason is partly that this tradition is engaged in analysing the selection for many properties within a single population. To simplify this analysis it is useful to hold selection pressure (e.g. in terms of predators) constant. The analysis of selection for many traits is also made easier if their relationships to selection are assumed to be additive. Therefore, this tradition tends to dislike complex interactions between properties. This is a useful strategy, but it tends to create the opinion that ‘it is a bad mistake to think that the Fundamental Theorem actually holds in the real world’ (Gintis, 2000, p. 197). This viewpoint is fully correct and founded in some of the deeper problems of the intra-population approach. But as it has been shown above there are several problems about the Fisher theorem that can be resolved.

However, with the help of the work of Frank (1998), Metcalfe (1998; 2001) and others, it is possible to avoid much of the controversy that relates to the Fisher theorem. First, it is easy to criticise Fisher’s emphasis on variance, but actually he emphasises factors that are now formalised in the second of Price’s effects. Second, the emphasis on selection and mutation with respect to a single property (here e.g. narrowly defined productivity) has led to the impression that evolutionary processes are relatively simple, but this is not the case. Actually, we ought to make Price decompositions for each of the huge number of properties that are selected for and that determine the (probabilistic) success of firms (and organisms). Third, the recursive expansion of Price’s equation demonstrates that selection can take place at different levels. Thus, a bridge is created between theorists that emphasise ‘individual selection’ and theorists that concentrate on ‘group selection’. This is done by emphasising that they cannot be taken as separate processes and that we can specify the conditions under which the inter-group selection is more important that the intra-group selection.

This defence of Price’s version of the Fisher principle is not meant to say that it is well suited to handle all aspects of actual evolutionary processes. For instance, the introduction of density dependent selection may allow the coexistence of firms with different properties and different populations of firms. In the broad version Price’s equation does not exclude e.g. density-dependent changes in the regression coefficients, but is does little to help us to think about them. The reason is that its basic trick here is to emphasise short-term evolutionary change in a more or less equilibrated situation. This strategy means that we can remove all the interaction effects from our replicator equations. As soon as we turn to long-run evolution, this simplification is neither formally correct nor likely to capture the real process of economic evolution. This issue is forcefully developed by Frank (1998), but his conclusion is that we should try to avoid the complex issues. Instead, he argues for the use of comparative static tools, where the major requirement is that populations change more quickly than their parameters. This conclusion is, however, hardly transferable to evolutionary economics that is still engaged in exploring the basic mechanisms of economic evolution.

Let us consider the density dependence of the reproduction coefficients $\square_j$ more closely—first within a population and then with respect to interacting populations. 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 (1) tells us that there is no productivity change. Nevertheless, the reproduction coefficients may show change. 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 decomposition of the change of the average reproduction coefficient

$$\Delta\bar{\square}_j = \Delta\bar{\square}_j^{\text{select}} + \Delta\bar{\square}_j^{\text{inno}}.$$

To specify the two effects, we simply reapply equation (1), but now we include the subscript j to indicate that we are dealing with several populations. Thus,

$$\Delta\bar{\square}_j = \frac{\text{Cov}(\square_j, \square_j)}{\bar{\square}_j} + \frac{\text{E}(\square_j \Delta\square_j)}{\bar{\square}_j} = \frac{\text{Var}(\square_j)}{\bar{\square}_j} + \frac{\text{E}(\square_j \Delta\square_j)}{\bar{\square}_j}. \tag{5}$$

As earlier, the selection effect is straightforward. But since we have assumed that variance is zero, this effect also has to be 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 average reproduction coefficient $\Delta\bar{\square}_j$ is only due to density effects. So we should name it the 'environment effect' 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 j, 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 inter-population 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 j (N_j) and the aggregate number of machines in all populations (N) contribute to the selection pressure on the individual firm. Let us start by considering the situation where population j 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' average 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

$$\frac{dN_j}{dt} = r_j N_j - b_j N_j N_j = r_j N_j \left(1 - \frac{N_j}{K_j}\right) \tag{6}$$

where $K_j = r_j / b_j$. In this equation r_j is the maximum reproduction coefficient, which is found when N_j is very small. K_j is the steady state size of the population, which may be considered as the carrying capacity of the exploited resource with respect to population j. 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 (6), 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 ($N = \sum N_j$) 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 (6) only needs a minor modification to handle the multi-population case:

$$\frac{dN_j}{dt} = r_j N_j - b_j N_j N = r_j N_j \left(1 - \frac{N}{K_j}\right) \qquad (7)$$

Compared with equation (6), the only novelty of equation (7) is that N_j / K_j has been replaced by N / K_j. 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_j will survive.

This short description of density-dependent selection is based on the relative stability of the population parameters (r_j and K_j), while no such assumption was made in Price's equation (5). 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 (6) and the Lotka–Volterra equation (7) tend to consider the behavioural variance as absent or given. But in real evolution, the second term of Price's equation (5) 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_j. 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_j. 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 postscript’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_j and K_j 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 of 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 (7). 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 (7), 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_j and other core parts of inter-population thinking. So even when we perform ‘history-friendly modelling’ (Malerba et al., 1999), we are forced to make harsh simplifications.

INTRA-TO-INTER-POPULATION THINKING

In the previous section, we only considered a small subset of the issues of inter-population thinking. The reason is that the tools that we have considered give insufficient support for this kind of analysis. What is missing is not least an understanding of why the different populations exist. To handle this question we may turn to intra-to-inter-population thinking. Here we study how and why new populations emerge out of old populations. This is a difficult study, and we may avoid it by assuming the emergence of new populations by sudden jumps. Such jumps characterise Schumpeter’s (1934) theory of evolution based on radical innovations. In new growth theory, we find the same approach. Thus, Romer (1990) and Aghion and Howitt (1998) models novelty as new sectors in which monopolists produce intermediate goods. Such monopolists produce an increasing number of specialised inputs for the final goods sector. But the increasingly heterogeneous set of firms does not constitute a population. Instead there is one population in the final goods sector, where all firms are identical, and an increasing number of intermediate good producing ‘populations’, which each consists of one firm. So we are facing inter-population diversity but no intra-population variance. Furthermore, these firms have ‘rational expectations’ in the sense that they know the probability of obtaining an innovation and are able to calculate the optimal R&D effort (given that they are risk neutral).

Both the lack of population thinking in new growth theory and its assumption of substantive rationality exclude any analysis of the evolutionary process that in real economic life generates much of the observed economic growth. On this background it seems premature when Romer (1993, p. 559) suggests 'a natural division of labour in future research' between 'mainstream theorists and appreciative theorists' (p. 556). The former provide 'simple abstract models', while the latter provide 'aggregative statistical analysis and in-depth case studies' (p. 559). While Romer's diagnosis about the deficiencies of the formal tools of many theorists of economic evolution might be correct, his prescription has a big problem. It ignores the fact that the supposed suppliers of evidence—Romer mentions David, Fagerberg, Mokyr, Nelson (1993) and Rosenberg—are dealing with heterogeneous populations of boundedly rational agents that are not adequately formalised by the new growth theorists (cf. Andersen, 1999, pp. 34–37).

The activity that that Nelson and Winter (1982, pp. 45–48) call appreciative theorising is not least engaged in intra-to-inter-population thinking. Such theorising try to specify central facts about cases of economic evolution and then to modify or develop concepts and models that give an adequate account for these cases. The purpose is neither to prove the correctness of a given model nor to use the model for defining the relevant data. Thus, this approach might seem methodologically unsound. Appreciative theorising, however, has an obvious and important function: to bridge between abstract formal tools and the tasks and practices of empirically oriented industrial economists, economic historians, econometricians, etc. Recently, appreciative theorising has taken the form of relatively complex and 'history-friendly' models that bridge between empirically oriented studies and the more abstract models developed in or in relation to Nelson and Winter (1982). Malerba et al. (1999, pp. 3–6) argue that while the first generation of neo-Schumpeterian evolutionary economic models has largely been characterised by an attempt to understand the basic logic of evolutionary processes, the major challenge presently is to develop a second generation of history-friendly models that can be of major help for empirical research in economics. This second generation of evolutionary models intends to reflect major stylised facts obtained by empirical researchers and that ends up not only by 'history-replication' but also with 'history-divergent' simulations. The immediate results presented by Malerba et al. (1999) and Malerba and Orsenigo (2001) suggest the need of emphasising the role of the diversity of demand, the emergence of new technologies and markets, and the role of entry and venture capital. Thus, the history-friendly models move from intra-population thinking to the more complex forms of population thinking—with an emphasis on what we here call intra-to-inter-population thinking.

While it is correct that intra-population thinking does not sufficiently support empirical studies of economic evolution, history-friendly modelling has to apply analytic tools that are adapted for intra-to-inter-population thinking. The same was the case in evolutionary biology, where the Fisher approach needs a complementary approach. Fisher's approach assumes that evolution takes place in huge populations and that sufficient time is available to select out individuals with subnormal fitness. Since not even Darwin had such a strong assumptions, Fisher may be characterised as a hyper-Darwinian. But his assumptions make it difficult to grasp intra-to-inter-population events. In this respect the formal modelling of Sewall Wright is much more flexible (Provine, 1986). Wright assumes that a population is placed in a fitness landscape that allows subpopulations with different properties emerge, and this assumption makes his approach relevant for empirical studies of subpopulations and the emergence of new species, like the ones performed by the pioneers of the neo-Darwinian synthesis (Mayr and Provine, 1980; Mayr, 1982). Here the properties of new species are not only determined by natural selection but also by random drift in small populations and by the random properties present in the subpopulations that found new species.

Underlying these results is the presence of a persistent amount of inheritable variance in natural populations, and this heterogeneity has shown to be present in empirical studies. Wright's emphasis on persistent heterogeneity is, however, contrary to Fisher's assumptions, and a Wright–Fisher controversy has been important for the development of evolutionary biology. This controversy sharpened by Kimura's theory of neutral evolution, but the study of molecular evolution has demonstrated that both sides of the neutralist–selectionist controversy have their part of the truth (Page and Homes, 1998, Ch. 7). In economic evolution there seems even less ground for a one-sided application of Fisher's assumptions. So Price's cautious development of the Fisher tradition might be of particular importance here.

An abstract study of the segmentation of the resources underlying the emergence of new populations and the continued existence of multiple populations is hardly satisfactory for empirical studies of economic evolution. So there is an urgent need to proceed to an economic evolutionary analysis of the most obvious source of segmentation in economic life: the division of labour and division of knowledge. Here there are two major strategies. The first strategy is to turn directly to the diversity of the market environment. The second strategy is to start from the inner diversity of the firms and/or households. We shall apply the second strategy by starting from multi-activity firms, so the task is to explain why and how individual activities become outsourced and coordinated by more-or-less clear-cut market mechanisms. Here we relate to the traditions in industrial economics and growth theory that trace back to the Smith-inspired ideas of Marshall (1949) and Young (1928). In this tradition, there is an intense interest in the close relationship between the internal economies of firms and the external economies that arises from inter-firm specialisation with respect to production and knowledge creation. To obtain a quick and concrete picture of these relationships, it is helpful to quote Young's (1928) description of his favourite example: the disintegration of the printing trade.

> The successors of the early printers, it has often been observed, are not only the printers of today, with their own specialized establishments, but also the producers of wood pulp, of various kinds of paper, of inks and their different ingredients, of typemetal and of type, the group of industries concerned with the technical parts of the producing of illustrations and the manufacturers of specialized tools and machines for use in printing and in these various auxiliary industries. The list could be extended, both by enumerating other industries which are directly ancillary to the present printing trades and by going back to industries which, while supplying the industries which supply the printing trades, also supply other industries, concerned with preliminary stages in the making of final products other than printed books and newspapers.

This story is Young's answer to the monopoly paradox that arose from Marshall's (1949) allowance into his system of economies of scale. There is no real paradox as long as we allow into our models the indefinite divisibility of production activities. This divisibility often makes a small well-focussed firm more productive than a large firm with a broad scope of activities. Although concentration is a real process, the trend is broken by the evolution of markets for gradually more intermediate goods that slowly undermine many of the industrial giants. Even in relation to such models one might, however, ask whether the limits of divisibility will be met 'at the end of the road'. In a Smithian context Richardson's (1975, p. 357) answer is 'that the end of the road may never be reached. ... For just as one set of activities was separable into a number of components, so each of these in turn become the field for a further division of labour.' The opening up of these possibilities is part of the evolutionary process itself: 'the very process of adaption, by increasing productivity and therefore market size, ensures that the adaptation is no longer appropriate to the opportunities it has itself created.' (Richardson, 1975, p. 358)

Let us reconsider Price's equation (1). Now we are dealing with mean productivity change with respect to the jth intermediate goods sector. Before exchange has emerged in this sector, all producers of final output are engaged in this area of production. Thus, the reproduction coefficients are only weakly related to the productivities in this sector. This situation changes drastically with the emergence of a market for the intermediate good. Now the reproduction coefficients of the specialised firms become narrowly connected to their productivities in their speciality. Therefore, they tend to focus their research, and thus the innovation effect increases significantly. The consequence of their focus for the selection effect is more ambivalent. During a transition period, an increased variance emerges, so the increased regression coefficient has fuel on which to work. This transition period may, however, be rather short. Low productivity firms quickly shift from make to buy, and competition among specialised suppliers means yet another decrease of variance. It is, however, obvious that Price's formula gives us the discipline to analyse clearly all the stages.

The two-level Price equation (4) may provide further help in structuring the problems. Thus, we may distinguish between the group of firms that that produces the intermediate good for its own use and the group of specialised suppliers. But this equation also forces us to define precisely the selection levels of the economic system. As long as there is only a well-developed market for final goods, each firm is selected according to the mean of its activity-specific productivities. Thus, inter-firm selection concerns the firm as a whole, while intra-firm selection deals with individual activities. As soon as intermediate goods markets emerge, market selection works on (some of) the intra-firm activities, but this is also an area for intra-firm selection. So conflicts may emerge. When exchange has emerged, the generalist strategy implies relatively small productivity changes with respect to intermediate good j, while the specialist strategy secures a larger innovation effect because research is focussed.

DISCUSSION AND CONCLUSIONS

This postscript has dealt with the emergence and differentiation of 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 thinking 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.' But although the old evolutionary economics from Adam Smith, Malthus and Marx via Menger and Marshall to Veblen and Schumpeter obviously lacked an adequate 'apparatus', its attempts to grasp economic evolution represent important sources for present-day evolutionary economics. The importance of these sources springs largely from the fact that even without adequate tools it is possible to understand important aspects of economic evolution and to have grand visions of its functioning. Furthermore, the contributors to old evolutionary economics often applied difficult forms of population thinking and they suggested bridging concepts that even today have much relevance. But the representatives of the 'old evolutionary economics' (Andersen, 1994, Ch. 1) developed complex mixes of population thinking and typological thinking, so a cautions approach is required. Such a caution does not characterise Hodgson's (1993, pp. 39–46) taxonomy of modes of thinking in old evolutionary economics largely ignores the mixed forms of thinking. According to him, real population thinking ('phylogenetics') is a property of a quite small club of economists (Malthus and Veblen). Adam Smith and Marshall are excluded from membership because of an ('ontogenetic') form of typological thinking. Later Hodgson (2001, pp. 27–32) has made modifications in modified taxonomies and some reclassifications. However, the problem of the mixed forms of thinking has not been confronted, and Smith and Marshall have kept their original place.

This form of taxonomy is not very helpful for a study of the difficult emergence of population thinking about economic evolution. A more detailed consideration about Smith's analysis of competitive processes and the evolution of the social division of labour, it appear to include much population thinking—although his emphasis on long-term productivity gains from the division of labour means that it is less harsh than Malthus's work on the reproductive struggle in human populations. When we turn to Marshall's work, the picture becomes misleading—as we have already seen.

While the different types of population thinking show continuity in relation to the tradition from Smith via Marshall to Young and modern theorists, they show an obvious contrast to the Schumpeterian vision. However, Schumpeter has nevertheless inspired the development of population thinking. To understand this inspiration it is helpful to consider the Schumpeterian pattern of evolution through disruptive entrepreneurs as a complement rather than an alternative to the Marshallian pattern of the knowledge-based branching of economic activities—both in industrial districts and in the economy as a whole (Andersen, 1996). This complementarily becomes clear when we recognise that Schumpeter often placed the Marshallian pattern in the so-called circular flow of economic life. Thus, his circular flow is far more than a Walrasian system that has been transformed into routine behaviour. It is rather a way of removing all more-or-less automatically functioning economic processes from attention in order to focus on a kind of innovative economic behaviour that is not at all automatic. To the extent that economic evolution is such an automatic process, it is thus not a part of the core of Schumpeterian analysis. But here two comments are important. First, such automatic evolution is still—even according to Schumpeter—a part of economic life. Second, there are important parts of the division-of-labour-like economic evolution that is not at all automatic and which includes difficult innovative interventions.

The postscript has demonstrated that population thinking is more multiform than normally recognised. Thus, evolutionary economists not only need the fairly well established intra-population thinking. In addition, we need intra-to-inter-population thinking as well as co-evolutionary inter-population thinking. All these types of thinking been dealt with, but it is obvious that both the discussion and the formal tools have largely supported intra-population thinking. However, an important theme of the paper was Price's formula for the decomposition of evolutionary change is surprisingly powerful in supporting manifold tasks of evolutionary analysis. So although it apparently is a natural extension of the statistically oriented intra-population thinking in the tradition of R. A. Fisher, it may also help to transcend this tradition. The reason is partly that Price's formula avoids making strong assumptions about the kind of evolutionary processes that may be covered. This means that the formula 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 formula 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.

After this cautious conclusion, it might be relevant to have a look into a hypothetical future where the tooling of evolutionary economics is highly improved. The empiricists of this hypothetical future will analyse the facts of economic life by means of a given toolkit that includes both evolutionary theory and methods for the empirical study of evolution. One of their tasks will be to explain relatively stable properties of the structure of markets and industries by means of one or more standard processes of evolution. Thus, they consider the observed stability as the outcome of past evolutionary change. As a side effect, they might also be able to find some of the conditions for the stability of these structures. Another task will be to study aspects of economic life that still undergo evolution. They will study both 'Marshallian' gradual evolution and 'Schumpeterian' bursts of evolutionary change. But they will probably largely explain economic growth and development by the former type of evolution. However, their toolkit will allow them to recognise that rapid emergence and change of new subpopulations at the disaggregate level is the precondition for relatively stable growth and development at more aggregate levels of the economy. They might also be able to give predictions about these processes and advise on how to control them.

The evolutionary theorists of the hypothetical future will be engaged in the improvement of the toolkit for evolutionary economics. Their tasks might be defined in two ways. First, the empiricists will meet evolutionary processes and evolved behaviour that cannot be adequately handled by the existing toolkit and they will obtain results that apparently contradict established theory. Even in a distant future, some theoretical tasks are likely to be defined in this way. The reason is that the processes of economic evolution are very complex and subject to change. Second, theorists will set tasks for themselves. These tasks will often concern the consistency and structure if the evolutionary theories and the descriptive tools. This activity may be fuelled by a continuous stream of additional concepts that are needed for particular applications but that also should be fitted into larger theoretical structures. Tasks will also continue to emerge from the teaching of evolutionary economics. The reason is partly that evolutionary processes are very tricky to handle and that it is probably impossible to describe them formally in a fully axiomatic way.

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REFERENCES

Aghion, P. and Howitt. P. (1998), *Endogenous Growth Theory*, Cambridge, Mass. and London: MIT Press.

Alchian, A. A. (1950), 'Uncertainty, Evolution and Economic Theory', *Journal of Political Economy*, **58**, 211–221.

Andersen, E. S. (1994), *Evolutionary Economics: Post-Schumpeterian Contributions*, London: Pinter.

Andersen, E. S. (1996), 'The Evolution of Economic Complexity: A Division-and-Coordination-of-Labour Approach', in E. Helmstädter and M. Perlman (eds.), *Behavioral Norms, Technological Progress, and Economic Dynamics: Studies in Schumpeterian Economics*, Ann Arbor, Mich., University of Michigan Press, pp. 97--119.

Andersen, E. S. (1999), 'Multisectoral growth and national innovation systems', *Nordic Journal of Political Economy*, **25**, 33–52.

Andersen, E. S. (2002), 'Railroadization as Schumpeter's standard example of capitalist evolution: An evolutionary–ecological interpretation', *Industry and Innovation*, **9**, 41–78.

Andersen, E. S. (f2003), 'Knowledges, specialisation and economic evolution: Modelling the evolving division of human time', in J. Foster and J. S. Metcalfe (eds.), *Frontiers of Evolutionary Economics*, Vol. 2, Cheltenham and Northampton, Mass., Elgar (forthcoming).

Axelrod, R. (1990), *The Evolution of Cooperation*, reprint edn., London: Penguin.

Axelrod, R. (1997), *The Complexity of Cooperation*, Princeton, N.J.: Princeton University Press.

Axelrod, R., and Hamilton, W. D. (1981), 'The evolution of cooperation', *Science*, **211**, 1390–1396.

Boyd, R., Gintis, H., Bowles, S., and Richerson, P. J. (2003), 'The evolution of altruistic punishment', *Proceedings of the National Academy of Sciences*, **100**, 3531–3535.

Carroll, G. R., and Hannan, M. T. (1999), *The Demography of Corporations and Industries*, Princeton, N.J.: Princeton University Press.

Dopfer, K. (ed.) (2001), *Evolutionary Economics: Program and Scope*, Vol. Boston, Mass., Kluwer.

Fisher, R. A. (1999), *The Genetical Theory of Natural Selection: A Complete Variorum Edition*. Oxford: Oxford University Press.

Foster, J. and Metcalfe, J. S. (eds) (2001), *Frontiers of Evolutionary Economics: Competition, Self-Organization and Innovation Policy*, Cheltenham and Northampton, Mass.: Elgar.

Frank, S. A. (1995), 'George Price's contributions to evolutionary genetics', *Journal of Theoretical Biology*, **175**, 373–388.

Frank, S. A. (1997), 'The Price equation, Fisher's fundamental theorem, kin selection, and causal analysis', *Evolution*, **51**, 1712–1729.

Frank, S. A. (1998), *Foundations of Social Evolution*, Princeton, N.J.: Princeton University Press.

Gintis, H. (2000), *Game Theory Evolving: A Problem-Centered Introduction to Modelling Strategic Behavior*, Princeton, N.J.: Princeton University Press.

Gould, S. J. (2002), *The Structure of Evolutionary Theory*, Cambridge, Mass. and London: Harvard University Press.

Grafen, Alan (1984), 'Natural selection, kin selection, and group selection', in J. R. Krebs and N. B. Davies (eds), *Behavioural Ecology: An Evolutionary Approach*, 2nd edn, Sunderland, Mass: Sinaur.

Hannan, M. T., and Freeman, J. (1989), *Organizational Ecology*, Cambridge, Mass. and London: Harvard University Press.

Harrod, R. F. (1939), 'Price and cost in entrepreneurs' policy', *Oxford Economic Papers*, **2**, 1–11.

Hodgson, G. M. (1993), *Economics and Evolution: Bringing Life Back into Economics*, Cambridge: Polity.

Hodgson, G. M. (2001), How can evolutionary economics evolve, in Y. Aruka (ed.) (2001), *Evolutionary Controvercies in Economics: A New Transdisciplinary Approach*, Tokyo, Springer.

Hofbauer, J. and Sigmund, K. (1998), *Evolutionary Games and Population Dynamics*, Cambridge: Cambridge University Press.

MacArthur, R. H., and Wilson, E. O. (2001), *The Theory of Island Biogeography*, reprint edn., Princeton, N.J. and Oxford: Princeton University Press.

Marshall, A. (1949), *Principles of Economics: An Introductory Volume*, reprint of the 8th edn, Basingstoke and London: Macmillan.

Maynard Smith, J., and Price, G. R. (1973), 'The logic of animal conflict', *Nature*, **245**, 15–18.

Mayr, E. (1976), *Evolution and the Diversity of Life: Selected Essays*, Cambridge, Mass. and London: Belknap/Harvard University Press.

Mayr, E., and Provine, W. B. (eds.) (1980), *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, Cambridge, Mass. and London, Harvard University Press.

Malerba, F., Nelson, R. R., Orsenigo, L., and Winter, S. G. (1999), '"History-friendly" models of industry evolution: The computer industry', *Industrial and Corporate Change*, **8**, 1–36.

Malerba, F., and Orsenigo, L. (2001), 'Innovation and market structure in the dynamics of the pharmaceutical industry and biotechnology: Towards a history friendly model', *Industrial and Corporate Change*, **11**, 667–703.

Metcalfe, J. S. (1998), *Evolutionary Economics and Creative Destruction*, London and New York: Routledge.

Metcalfe, J. S. (2001), Evolutionary approaches to population thinking and the problem of growth and development, in Dopfer (2001).

Metcalfe, J. S. (2002), 'Book review: Steven A. Frank. 1998. Foundations of Social Evolution', *Journal of Bioeconomics*, **4**, 89–91.

Nelson, R. R. (1995), 'Recent evolutionary theorizing about economic change', *Journal of*

Economic Literature, **33**, 48–90.

Nelson, R. R. (ed.) (1993), *National Innovation Systems: A Comparative Analysis*, New York and Oxford: Oxford University Press.

Nelson, R. R. and Winter, S. G. (1982), *An Evolutionary Theory of Economic Change*, Cambridge, Mass. and London: Belknap/Harvard University Press.

Niman, N. B. (1991), 'Biological analogies in Marshall's work', *Journal of the History of Economic Thought*, **13**, 19–36.

Page, K. M., and Nowak, M. A. (2002), 'Unifying evolutionary dynamics', *Journal of Theoretical Biology*, **219**, 93–98.

Page, R. D. M., and Holmes, E. (1998), *Molecular Evolution: A Phylogenetic Approach*, Cambridge, Mass.: Blackwell.

Pianka, E. R. (1999), *Evolutionary Ecology*, 6th edn., New York: Harper & Row.

Potts, J. (2000), *The New Evolutionary Microeconomics: Complexity, Competence and Adaptive Behaviour*, Cheltenham: Elgar.

Price, G. R. (1970), 'Selection and covariance', *Nature*, **227**, 520–521.

Price, G. R. (1972), 'Fisher's "fundamental theorem" made clear', *Annals of Human Genetics*, **36**, 129–140.

Provine, W. B. (1986), *Sewall Wright and Evolutionary Biology*, Chicago: University of Chicago Press.

Richardson, G. B. (1975), 'Adam Smith on competition and increasing returns', in A. S. Skinner and T. Wilson (eds), *Essays on Adam Smith*, Oxford: Clarendon.

Romer, P. M. (1990), 'Endogenous technological change', *Journal of Political Economy*, **98**, S71–S102.

Romer, P. M. (1993), 'Idea gaps and object gaps in economic development', *Journal of Monetary Economics*, **32**, 543–573.

Samuelson, P. A. (1983), *Foundations of Economic Analysis*, enlarged edn., Cambridge, Mass. and London: Harvard Univesity Press.

Saviotti, P. P. (1996), *Technological Evolution, Variety and the Economy*, Aldershot: Elgar.

Saviotti, P. P. (2001), Considerations about a production system with qualitative change, in Foster and Metcalfe (2001).

Schumpeter, J. A. (1934), *The Theory of Economic Development: An Inquiry into Profits, Capital, Credit, Interest and the Business Cycle*, London: Oxford University Press.

Schumpeter, J. A. (1939), *Business Cycles: A Theoretical, Historical, and Statistical Analysis of the Capitalist Process,* 2 vols., New York and London: McGraw-Hill.

Schumpeter, J. A. (1954), *History of Economic Analysis*, ed. E. B. Schumpeter, London: Allen and Unwin.

Silverberg, G. (1988), Modelling economic dynamics and technical change: Mathematical approaches to self-organization and evolution, in G. Dosi, C. Freeman, R. R. Nelson, G. Silverberg and L. Soete (eds.) (1988), *Technical Change and Economic Theory*, London, Pinter.

Sober, E., and Wilson, D. S. (1998), *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Cambridge, Mass. and London: Harvard University Press.

Thomas, B. (1991), 'Alfred Marshall on economic biology', *Review of Political Economy*, **3**, 1–14.

Winter, S. G. (1991), 'On Coase, competence, and the corporation', in Williamson, O. E., and Winter, S. G. (eds.), *The Nature of the Firm: Origins, Evolution, and Development*, New York and Oxford, Oxford University Press, pp. 179–195.

Witt, U. (ed.) (1993), *Evolutionary Economics*, Aldershot, Elgar.

Witt, U. (2001), 'Evolutionary economics: An interpretative survey', in Dopfer (2001).

Young, A. A. (1928), 'Increasing returns and economic progress', *Economic Journal*, **38**, 527–542.