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by

J. S Metcalfe

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Max Planck Institute for
Research into Economic Systems
Evolutionary Economics Group
Kahlaische Str. 10
07745 Jena, Germany
Fax: ++49-3641-686868

ACCOUNTING FOR EVOLUTION: AN ASSESSMENT OF THE POPULATION METHOD

J.S METCALFE
ESRC CENTRE FOR RESEARCH ON INNOVATION AND COMPETITION
THE UNIVERSITY OF MANCHESTER

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Introduction

The theme of these notes, in general, is the population dynamics of evolutionary processes, and, in particular, a number of accounting concepts that are central to any understanding of processes of evolution of the variation and selective retention kind. The accounting concepts I use are naturally true by the meaning attached to the terms employed but this does not make them any less useful as devices for sorting out different ideas in relation to evolutionary dynamics. Indeed, once the accounting concepts are clear it is a more straightforward matter to give an explanation of the evolutionary process in terms of cause and effect. The three sets of concepts I describe have in common a concern with 'population thinking', to use the phrase coined by Ernst Mayr (1959), which is one of the central methods of evolutionary analysis. My claim is that a proper evolutionary accounting is helpful to any understanding of the economics of creative destruction and the ongoing process of self transformation that is the distinctive feature of modern capitalism. More fundamentally the relationships explored here are essential elements in the study of economic development interpreted as the transformation of initial populations of activities into new kinds of populations. Processes of structural change of the creation and demise of activities are at the core of development as a process of "becoming something different". Moreover development can be uncovered at many levels in an economic system. A population perspective, for example, turns out to be crucial to the study of the competitive process in economic systems defined at the level of industries, sectors and markets. Business rivalry, underpinned by differential innovative activity, is the basis of the differential survival and growth of competing economic activities and the strategies deployed to create sustainable differences in competitive selection characteristics are at the core of the capitalist dynamic interpreted as an adaptive, evolutionary process. This kind of evolutionary argument is necessarily concerned with growth rate dynamics and the explanation of the diversity of growth rates across entities in a population. Growth dynamics and structural change are the two central features of variation/selection processes within populations and I explore them in terms of three themes, or sets of accounts, namely Logistic Growth Accounting, Competition Accounting and the Price Theorem. Before doing so some preliminary remarks on the troublesome concept of fitness are appropriate.

Fitness and Growth

What fitness means in evolutionary terms has for long been disputed territory (Michod, 1999; Brandon, 1991) and the sense that it is a tautology remains alive and well, especially outside of evolutionary theory. Yet tautologies, relations true by the meaning of the terms they describe and relate to, are frequently very helpful in unpacking the content of multi level theories of which evolutionary theory is one. They can act as filing systems to place different concepts in the proper relation one with another. There is a tautological way of defining fitness and indeed the accounting which follows is, if it is correct, tautological. But this does not mean that fitness is intrinsically a tautology far from it, it only means that we have to distinguish the expression of fitness, the differential growth rates of competing entities, for example, from the causes of those differential growth rates. First we note that fitness is a concept that arises in the context of the population approach to evolution. Here we consider a set of entities that differ individually and are deemed to be members of a population by virtue of being subjected to common selective pressures within that population[1]. Fitness is not a natural attribute of any entity: in most population based theories it is a derived consequence of the selective characteristics of that entity, the selective characteristics of all the other entities in the relevant population, and of the attributes of the selection environment. Jointly these three elements define a transmission process connecting the intra-population distribution of entity characteristics and the corresponding distribution of entity growth rates. If the characteristics of other, rival entities are changed or if the selection environment should "value" the entity characteristics differently then the distribution of individual fitness will change. To this extent fitness is a contingent property distributed across a population, it is caused not causal. An evolutionary theory does not begin with fitness values it deduces them from an underlying theoretical structure, and this dispenses with the tautology claim. It is useful here to dwell on the distinction between sorting processes and selection processes. (Vrba and Gould, 1986). In a sorting process, the entity growth rates are determined independently of one another even though they may vary individually over time. Structure then evolves so that the

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[1] Thus a population is not any arbitrary collection of entities but an ensemble unified by the experience of a common environment. The thorny questions of the units of selection is covered up too hastily in this definition but space precludes further discussion. See Knudsen and Hodgson, 2005 for further elaboration.

fastest growing members of the population increase in relative importance over time. Fitness is then an internal property of the entities in question and does not reflect interaction between the entities in the environment. It is this process of interaction that defines a selection process; the entity growth rates are mutually determining and reflect the constellation of selective forces defining that population. Fitness in this case is attached to an entity in the same way that 'profit' is attached to a firm.

Secondly, we should recall that the fitness of population members has many possible interpretations. Fitness as brute survival must be distinguished from fitness as differential growth, and from fitness in terms of ability to adapt through innovation. Each involves different fitness criteria, criteria that will also depend on the time frame over which fitness is to be assessed. Thus, for example, a firm may exhibit high short run fitness as a result of its present strategies but low long run fitness if it fails to adapt to innovations produced by rivals. Thirdly, if fitness values differ, the immediate consequence is that the structure of the population changes as measured in terms of the relative importance of the constituent members, it is the population that evolves, even if the members do not. Consequently, much of the attention of a population dynamic theory is focused on summary measures of the rate and direction of population change and we explore this in more detail below. Thus the population concept is an ordering device to explain how the relative importance of the different entities in the population will vary over time. Fourthly, it follows that the fitness of any member of a population is also an emergent property of the selection process; it is a result of the interaction within the population environment of the different entities such that their differential growth rates or survival are mutually determined and interdependent. To repeat fitness is not an intrinsic property of any single member of the population it is a predictable outcome of the interaction between the characteristics of the entities within the environment acting on the population.

Interpreted in this way fitness theories typically have a number of attributes. First, the characteristics of the entities that are selected for are typically multi-dimensional, so the direction and rate of evolutionary change depends on the environmentally dependent correlation between these characteristics. Consequently, selection for some characteristics may entail selection against other characteristics reflecting the nature of the trade offs that the environment imposes, including trade offs with characteristics that are selectively neutral. Change the environment and the relevant trade offs and patterns of correlation will change. Thus what the fitness notion does is to reduce the selection process to a common currency, fitness values are 'like commensurable quantities' although the causal explanation of those values may, and usually will, depend on attributes of the entities that are fundamentally different. Secondly, fitness theories are naturally statistical in that they provide explanations of the variation over time in the moments and other summary statements of the state of a population (Horan, 1995). Thirdly, the very process of selection may change the characteristics of the different entities whenever selection is associated with positive or negative feedback or density dependent effects. If there is negative feedback selection will tend to a stationary state in which several entities may coexist because the differences in their selection characteristics have been eliminated as a consequence of selection. If there is positive feedback or even no feedback at all then selection will almost certainly concentrate the population on a single 'winning' entity (Witt, 2003). Thus the famous idea that selection destroys its own fuel (Lewontin, 1974) and the corollary that evolution, if it is to continue, must be a three stage process – variation, selection and on going development of new variation (Foster and Metcalfe, 2000). Economists would recognise the states of feedback in terms of decreasing, constant and increasing returns with the possibility that the last may lock the population in to a state that is protected by barriers to invasion. Nothing in this account requires fitness to be a deterministic property of the entities or the population but stochastic effects only matter when we have positive and thus irreversible feedback in the selection process, for then history matters and small chance events may have lasting effects on the evolutionary outcome. No wonder fitness is such a difficult concept.

Before moving to the substance of these notes one final point is worth stating. It is that variation selection models open up the possibility of different kinds of dynamic explanation based on population analysis. In a typical, economic model, for example, the transient motion of the system will be described in terms of an approach to some invariant long run attractor, what we might term the distance from equilibrium method. Usually, in economics at least, the explanation of the equilibrium position is quite separate from the explanation of the transitional dynamics so giving the theory a dual nature in which the dynamics are typically *ad hoc* and do not draw on the same explanatory factors as does the explanation of the equilibrium attractors. This type of dynamic argument faces a number of difficulties not least in conditions where the equilibrium is changing faster than the transitional adjustment dynamics can converge to it. This is particularly so if we abandon the restrictive assumption that the processes of transition have no effects on the postulated equilibria. In a proper evolutionary process this is not tenable[2]. By contrast population thinking provides a different dynamic method, the distance from mean dynamic, in which the distribution of fitness values around the population average is causally related to the joint distribution of selective characteristics around their population means. In this method, the dynamics of the population system depend entirely on the variety that is contained within it and this variety is reflected in the evolution of the population structure.

With these preliminary remarks in hand we turn to the first of our three exercises in fitness accounting.

A) Logistic Growth Accounting.

Many of the dynamic problems that interest scholars of technical, organisational and institutional change fall within the ambit of a population analysis. A new entity is introduced into an environment that always contains some existing practice, however vaguely that alternative is articulated, for which the novelty is a potential alternative course of action or basis for activity. In much of the relevant literature the time profile of this absorption and displacement process is articulated in terms of a sigmoid curve of which the logistic is the most well known example. In the field of economics, for example, the ubiquitous logistic has a long and distinguished history in the study of innovation diffusion and technological substitution as well as in theories of economic growth that focus on the structure of an economy. Although the emphasis is typically on the focal innovation, in fact the analysis is always a population based analysis for in the background there is always the practice or device that is being displaced[3]. It is the basis

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[2] I have explored this idea in some detail in relation to the idea of restless capitalism in which it is the internal, ongoing generation of knowledge that denies the possibility of equilibrium. See Metcalfe 2001 and Metcalfe and Ramlogan 2005b for further elaboration of the link between the evolution of knowledge and economic evolution.

[3] It is a weakness of diffusion analysis (but not technology substitution analysis) not to recognise this population dimension. This is particularly so since neither the innovation nor its rivals will normally remain unchanged during the diffusion process and unless their comparative rates of improvement are held in view one risks misunderstanding the factors behind diffusion.

for any ecology minded theory of growth that sees that process in terms of the successive creation and destruction of economic niches and thus of the transformation of an economy through innovation, imitation and the growth of knowledge[4].

I shall suggest that the logistic process is a deep signature of an evolutionary process within populations that are governed by a variation and selection dynamic. Moreover, it is the connection with the evolution of populations which helps explain the empirical ubiquity of the logistic curve because all processes of structural change are population phenomena. However, a logistic process need not generate the familiar 'S' shaped logistic curve expressed as a function of time, indeed it may be associated with non monotonic time profiles, quite non logistic profiles, for the changing relative importance of many of the entities in a population. The logistic process has, therefore, a degree of generality that the logistic curve does not possess. For example, Marchetti and Nakicenovic (1979) in a study of the evolution of populations of rival energy technologies recognised that in the substitution process the logistic phase of growth and saturation is normally followed by a phase of decline such that a logistic time trend only captures part of the evolutionary process[5]. That growth may be followed by decline is unexceptional but that both aspects of evolution are captured in the same general logistic process is perhaps worthy of further investigation. Moreover, this logistic process depends on the distance from mean dynamic and its close relatives that we have alluded to already.

To fix ideas, consider a population of distinct entities. The measure of the scale of each entity at date *t* is $x(t)$[6]. By the fitness of each entity we mean its exponential growth rate of scale defined over the interval to time *t* defined by $g(t)$ such that

$$g(t) = \frac{1}{t}\log\left[\frac{x(t)}{x(0)}\right]$$

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[4] On the innovation diffusion literature see Metcalfe 2005a. On the ecological connection with the logistic, the classic reference is Lotka (1925/1956) while Kingsland (1985) provides an excellent history of the concept.

[5] For useful references to the technology substitution literature see, Fisher and Pry (1971), Kwasnicki and Kwasnicki (1996) and Mahajan and Petersen (1985). On the use of the logistic in relation to economic development see in particular, Nelson, 1968 and Nelson and Pack, (1999)

[6] In a biological model $x(t)$may represent the number of individuals said to be of the same kind. In an economic model it may represent the scale of activity of different producing units.

The relative importance of each member of the population is defined by its population share

$$s_i(t) = x_i(t)/\sum x_i(t)$$

These relative measures of population structure are the central focus of any variation selection approach to evolution and we shall show how their evolution obeys a logistic law like property. It follows as a matter of the definition of '$s(t)$' and '$g(t)$' that the dynamic process of selection for each entity in the population will obey the following relation

$$\frac{ds_i}{dt} = s_i(t)[g_i(t) - g_s(t)] \qquad (1)$$

with the mean fitness value defined by $g_s(t) = \sum s_i(t) g_i(t) \quad ; \quad \sum s_i(t) = 1$

Equation (1) is the familiar equation of a replicator dynamic process and it exactly embodies the distance from mean dynamic principle alluded to above. Whatever may determine the evolution of the individual growth rates, equation (1) is a complete description of the dynamics of the population and it holds exactly whatever the nature of the population. As explanied above, if the fitness values $g_i(t)$ are independently determined then we have a sorting process. If the individual growth rates are interdependent and simultaneously determined then we have a selection process proper within this population. In both cases, as long as the individual growth rates differ the average value $g_s(t)$ will not be constant[7].

On integrating (1) for each of the members of the population we have

$$s_i(t) = s_i(0)\exp\left\{\int_0^t [g_i(t) - g_s(t)]dt\right\}$$

subject to the constraint $\sum \int_0^t [g_i(t) - g_s(t)]dt = 0$

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[7] As explained below the evolution of this average obeys the Price equation and its particular instantiation in Fisher's principle.

The important point about this expression is that each population share evolves according to the history of its fitness relative to average fitness in the population as a whole. The evolutionary dynamic is precisely a distance from mean dynamic. However, this way of describing the population dynamic can be expressed differently to expose the logistic process contained within it. Take each $s_i(t)$ then we can write for that entity the relation

$$g_s(t) = s_i g_i + (1 - s_i) g'_{s_i}$$

where the quantity $g'_{si} = \sum_{j \neq i} s_j g_j$ is a weighted sum of fitness values across all the remaining elements in the population, it is not a weighted average, and it is different for each entity.

Then we can rewrite (1) as

$$\frac{ds_i}{dt} = s_i (1 - s_i) [g_i - g'_{si}] \tag{2}$$

In this expression $s_i(t)$ is a logistic function of the distance function $(g_i - g'_{si}) = G_i(t)$ and we can see this by integrating relation (2) to give

$$s_i(t) = \frac{1}{1 + A_i \exp - D_i(t)} = L_i(t)$$

with $A_i = \frac{1 - s_i(0)}{s_i(0)}$ determined as an initial condition. The integral function

$$D_i(t) = \int_0^t [g_i(t) - g'_{si}(t)] dt$$

I call the transfer function, after the economist Jack Downie who explored this dynamic process in his pioneering exposition of competitive dynamics in an industry (Downie, 1958). Thus the logistic process does not generate the conventional logistic curve over time but rather leads to a logistic mapping of the transfer function that captures the distributed nature of the evolutionary dynamics and the growth rate variety within the population.

This relation applies to all the entities in the population and it follows that each of them must evolve along their own specific logistic curve as a function of their individual transfer functions as shown in Figure 1. The curves have an upper asymptote of unity and two such curves are shown relative to initial date $t = 0$ remembering that the inflection point for each logistic curve always occurs when $s(t) = 0.5$.

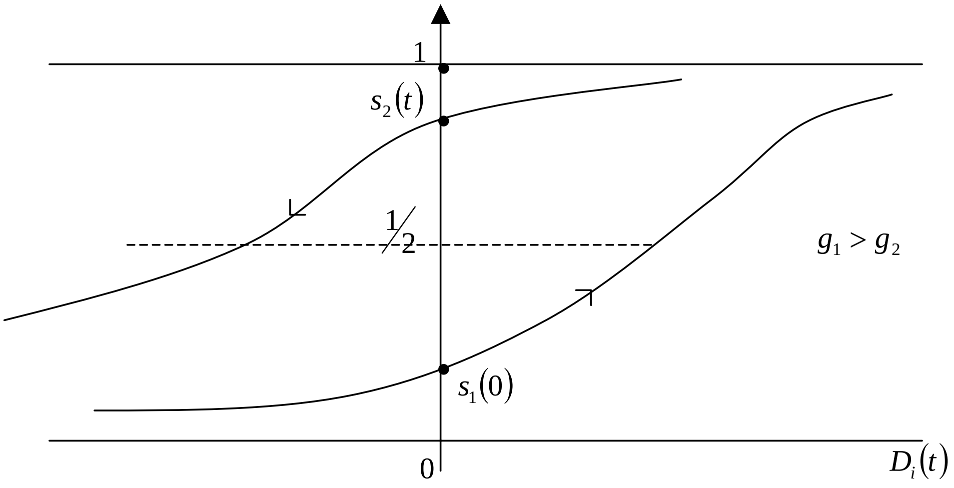
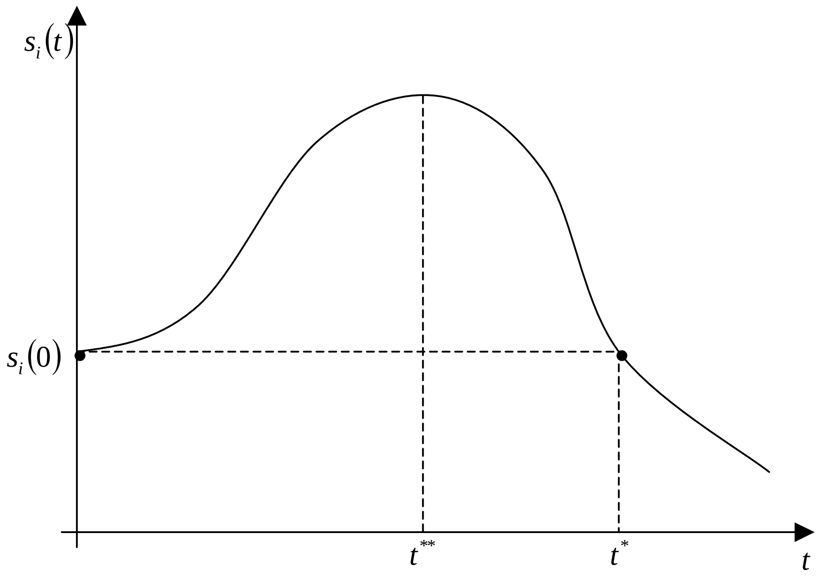


Figure 1

Now as long as $G_i(t) > 0$, that entity is fitter than ‘average’ and $s_i(t)$ increases over time and the relative importance of that entity is increasing in the population. But clearly this cannot be so for all the entities some must be less fit than ‘average’ and be declining in relative importance. Thus when $G_i(t) < 0$ the entity share moves down the logistic, and this will be so when $g_i(t)$has fallen below the population value of $g'_s(t)$- in figure 2 this occurs at time $t**$, while at time $t*$ the value of $D(t*) = 0$, and at this date the value of the relative share in the population has returned to its initial value.

This logistic relation appears to be one of great generality, as it applies to all evolutionary approaches to population dynamics and forms a signature of the distance from mean dynamics within the population.

However, the important lesson from this exercise is that the logistic process does not in general generate a logistic curve measured against time *simpliciter*. In empirical terms this means that we cannot interpret the absence of the simple logistic trend curve as evidence of the non operation of the logistic process. What is the condition for a logistic process to support a logistic curve in the traditional sense? It is that we can express the Downie function in the form $D_i(t) = \alpha_i \cdot t$, so that it is linear in time. Clearly this can only be true if there are no more than two competing members of the population and if their respective growth rates are independent constants[8]. Thus while the logistic process is general; the instantiation of it in a simple logistic curve is very special. Figure 2 shows the more general relation of a population share plotted over time, with growth followed by decline and intermediated by momentary 'saturation'. In part, this time profile this helps explain why other non logistic 'S' curves, such as the Gompertz of log normal find frequent empirical representation and it also helps explain the decline phase of an entity in the population which has often been observed in technological substitution studies[9].



At t^{**}, $G_i(t) = 0$, at t^{*}, $D_i(t) = 0$.

Figure 2

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[8] The Fisher Pry model (1971) is precisely a binary substitution model leading to the simple logistic curve.

[9] See references cited in footnote above.

Of course this is no more than an accounting for evolution. The dynamic relations must hold for every population when we define the notions of population share and growth rate in the way that we have. It only becomes the basis for a refutable theory of evolutionary change when we impose a particular theory of why the individual growth rates differ and vary over time. In many evolutionary accounts these causal explanations will be based on some theory of a competitive process and it is to an accounting for competition that we turn to next. Before doing so some additional brief remarks on the logistic process are in order.

Further Implications

In many cases we are interested not only in the relative importance of an entity in its population but also in some absolute value of the measure of its importance and how this varies over time. Since the absolute and relative measures are related by

$$x_i(t) = s_i(t) \cdot X(t) \qquad \text{; with} \quad X(t) = \sum x_i(t) \text{ and}$$

$$g_s(t) = g_X(t)$$

it follows that the absolute growth rate is governed by

$$\begin{aligned} \frac{d}{dt}\log x_i(t) &= \frac{d}{dt}\log s_i(t) + g_X(t) \\ &= L_i(t) + g_X(t) \end{aligned}$$

Thus the absolute value $x_i(t)$ can only follow a logistic curve if $g_X(t) = 0$, and if $L_i(t)$ also generates a logistic curve. In a stationary environment with *X(t)* a constant this is possible but not more generally. Thus to consider a familiar economics example, it is often assumed that the relevant population environment grows exponentially in absolute scale, in which case $g_X(t)$ is constant and $x_i(t)$ for all surviving entities will approach a path of exponential growth.

Next consider the problem of hierarchical selection. In some situations we are interested in the presence of populations nested within broader populations such that population j may be one of several sub populations within population k. Different selective forces may operate within and between these populations and the changing relative importance of an entity at the different levels will reflect the hierarchical nature of selection. A firm, for example, will have one measure of importance in its primary industry and another measure in the national economy and the way these measures evolve over time will reflect the interaction of selective forces at the different levels. Thus if entity *i* is a member of population *j* which in turn is a member of, entity in, population *k* it would follow as a matter of accounting that

$$s_{ik} = s_{jk} \cdot s_{ij}$$

and that the rates of relative growth are related by

$$\frac{d}{dt}\log s_{ik} = \frac{d}{dt}\log s_{jk} + \frac{d}{dt}\log s_{ij}$$

Expressed in terms of the logistic processes at each level it follows that they are related by

$$\hat{L}_{ik} = \hat{L}_{jk} + \hat{L}_{ij}$$

whence, $$L_{ik}(t) = CL_{jk}(t) \cdot L_{ij}(t)$$

where C is a constant of integration reflecting the initial conditions. Thus in terms of hierarchical selection the logistic accounting leads to a chain rule within and across the sub populations.

Finally, consider the so-called retardation principle. It is a well known feature of the logistic process that when the growth rate of the entity is positive it is also declining in value, and when it is negative it is accelerating. This is otherwise known as the principle of retardation and it has played an important role in evolutionary growth theorising and in empirical work. Indeed, Abramovitz (1989) in his famous survey of growth theory made it one of the eight characteristics of a growing capitalist economy and in so doing drew attention to a powerful body of empirical work on the retardation hypothesis carried out by among others Kuznets (1929, 1954) and Burns (1934).

To explore the generality of this idea consider the definition of the population average growth rate $g_s(t) = \sum s_i(t) g_i(t)$,

whence it follows that the instantaneous rate of change of this average has two components

$$\frac{dg_s}{dt} = \sum g_i(t)\frac{ds_i}{dt} + \sum s_i(t)\frac{dg_i(t)}{dt}$$

Or, making use of the relation between the growth rates and the dynamics of population shares, we can write this as

$$\frac{dg_s}{dt} = V_s(g_i(t)) + R_s(t)$$

The first term on the right, the variance of the growth rates across the population reflects Fisher's fundamental theorem of natural selection, and we say more on this in section C below. The second term is the average rate of change in the individual growth rates, the average rate of retardation. The condition for retardation on average is that

$$\frac{dg_s}{dt} - V_s(g) < 0$$

So if $g_s(t)$ is constant we must find retardation on average and this would be entirely consistent with acceleration of the growth rates for some components in the population. Retardation is a population phenomenon in 'slowly' expanding, stationary or declining populations. Only if the average growth rate g_s is increasing fast enough can retardation be translated into acceleration. It follows that, as a general rule the higher the level of aggregation across a hierarchy of populations, the less the observed variation in the growth rate average which in turn predisposes the average pattern of growth rates towards retardation.

This retardation principle has a further consequence. Consider a population for which the growth rates of the component entities are constant. Then it follows immediately that the aggregate population growth rate cannot be constant unless all the individual growth rates are the same. But then there is no variety in fitness and no basis for the population to evolve. Conversely, if the aggregate growth rate is constant this is only consistent with constant growth rates of the components if all the growth rates are the same. Thus the well known model of a semi stationary economy that forms the backbone of much theorising in growth economics poses a dilemma. Steady growth either at the individual or aggregate level is only possible if there is no possibility of evolution in that population. A semi stationary economy cannot accommodate structural change contrary to the record of history; it does not appear to be a good basis for the comprehension of growth dynamics in innovation driven economies.

B) Accounting for the Competitive Process

We now turn to a second example of evolutionary accounting that focused on the processes of competition in a population. The population method is a remarkably general tool of analysis in that it provides an exhaustive way to account for all the changes that occur in a population of economic activities over some time interval of length, Δt. In particular, it is a framework for understanding the developmental significance of differential growth of activities and causally linking those growth rate differences to the competitive characteristics of the members of a population, usually firms in an economic model of competition. To fix our ideas more precisely, let the population consist of a group of firms who are the members of this population by virtue of being subject to the same selective process. Each firm is associated with its unique set of selective characteristics that are evaluated by a common market environment. To begin let each firm be a single plant firm producing an identical product so that selection of production activities and selection of firms are one and the same[10]. Four processes exhaust the possibilities of population change:

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[10] See Metcalfe 1998 for a joint analysis of product and process differentiation.

- Pure replication of the activities of the continuing (surviving) firms that remain in the population over the interval, Δt, measured in terms of changes in the scale of output (activity) of each firm.
- The exit (death) of firms, alive in the population at the beginning of the interval Δt but departing the population within the interval
- The entry (birth) of new firms in that population within the time interval, Δt,
- Innovations (mutations) in the selection characteristics possessed by the continuing firms so that they vary individually between the initial and terminal dates defining the interval.

By partitioning the population of firms into survivors, entrants and exits we can perform a complete analysis of the change in the population between the two dates. An analysis of selection only in terms of the surviving firms, an important element in evolutionary analysis, is not entirely satisfactory for it loses sight of extremely important processes in relation to the birth and death of firms and indeed the birth and death of entire economic activities. Innovation too in the surviving firms is an essential element in economic evolution, for it corresponds to a change in the characteristics of the entities and thus a change in the distribution of selective advantage in the population (Foster and Metcalfe, 2000). As with all evolutionary arguments the focus of concern is upon the differential growth rates of the different activities in the population.

All of this can be stated more formally in the following competition accounting scheme. Let the first census date be at date t, and the second at date $t+\Delta t$. Let $X(t+\Delta t)$ and $X(t)$ be the aggregate output rates across the whole population at the two census dates. Define compound growth rates such that $g\Delta t$ is the growth rate of total activity, $g_c\Delta t$ is the growth rate of the activity of the continuing firms and $g_e\Delta t$ is the growth rate of the activity of the firms that exit during the interval. Thus, for example, $X_c(t+\Delta t)=X_c(t)(1+g_c\Delta t)$ defines the output profile of the surviving firms. Let $N(t+\Delta t)$ be the output contributed by those firms that enter the population in the interval Δt. Define the entry rate, $n\cdot\Delta t$, such that $N(t+\Delta t)=n\cdot\Delta t\cdot X(t+\Delta t)$. Similarly, define $e\cdot\Delta t$ is the fraction of output $X(t)$ accounted for by the firms that subsequently exit in the interval. Let $E(t+\Delta t)$ be the output contributed in the interval by the exiting firms while they remain alive, whence $E(t+\Delta t) = e\Delta t \cdot X(t)(1+g_e\Delta t)$.

It follows that

$$X(t+\Delta t) = X_c(t) + E(t+\Delta t) + N(t+\Delta t)$$

or

$$X(t+\Delta t) = X(t)\left\{\frac{(1-e\Delta t)(1+g_c\Delta t)+e\Delta t(1+g_e\Delta t)}{1-n\Delta t}\right\}$$

It is convenient to assume that all the exit events occur at the beginning of the interval, in which case, $g_e\Delta t = -1$, and we find that the growth rates, entry and exit rates are related by

$$\frac{(1+g\Delta t)}{(1+g_c\Delta t)} = \frac{(1-e\Delta t)}{(1-n\Delta t)} \tag{3}$$

Whenever the entry rate is the same as the exit rate then the growth rate of the surviving firms is the same as the growth rate in the population as a whole. More generally, as e is greater or smaller than n, then g is greater or smaller than g_c, which accords with common sense, provided we remember that the exit and entry rates are defined as proportions of aggregate activity not as numbers of firms.

We can now identify the dynamic of population change in respect of the surviving firms and the population as a whole. If we define $c_i(t)$ as $X_i(t)/X_c(t)$ the share of each surviving firm in the aggregate output of the survivors, it follows that

$$c_i(t+\Delta t) = c_i(t)\left\{\frac{1+g_i\Delta t}{1+g_c\Delta t}\right\}$$

and $$\frac{\Delta c_i}{\Delta t} = \frac{c_i(t+\Delta t)-c_i(t)}{\Delta t} = c_i(t)\left\{\frac{g_i-g_c}{1+g_c\Delta t}\right\} \tag{4}$$

with $$g_c(t) = \sum c_i(t)g_i$$

Equations (4) are primitive replicator dynamic relations that hold exactly for surviving entities, and they tie the rate of change of the structure of the sub-population to the diversity of growth rates contained within it. If the population is to evolve it must be a population defined by growth rate diversity, which is to say nothing more than the obvious statement that evolution is a dynamic process. If entity i is to increase its share of the activity of the surviving group it is necessary and sufficient that it grow more quickly than the average for its population, $g_i > g_c$, and conversely, if i is to decline in relative importance over the interval. Notice for completeness that since $\sum c_i(t) = 1$ it follows that $\sum \Delta c_i(t) = 0$, always a useful check on the internal consistency of the replicator process.

Now consider the total population and define $s_i(t)$ as $X_i(t)/X(t)$, the share of a continuing firm in the total output produced in the time interval, after taking account of entry and exit, and it follows that

$$\begin{aligned} s_i(t+\Delta t) &= s_i(t)\left\{\frac{1+g_i\Delta t}{1+g\Delta t}\right\} \\ &= s_i(t)\left\{\left(\frac{1+g_i\Delta t}{1+g_c\Delta t}\right)\left(\frac{1-n\Delta t}{1-e\Delta t}\right)\right\} \end{aligned} \tag{5}$$

whence, the two measures of population change are related by

$$\frac{s_i(t+\Delta t)}{s_i(t)} = \frac{c_i(t+\Delta t)}{c_i(t)}\left(\frac{1-e\Delta t}{1-n\Delta t}\right) \tag{6}$$

If the exit and entry rates coincide then the two measures of structural change coincide and $g = g_c$. In general they will not, and although a surviving firm may be increasing its share in that sub population ($g_i > g_c$) it may still be experiencing a declining share in the total output if n is sufficiently greater than e. Relations (4), (5) and (6) provide the elements of a replicator dynamic corrected for processes of entry and exit.

In many cases it is more transparent to work with the replicator dynamic in continuous time, in which case, letting the time interval Δt tend to zero, we can replace (1) to (3) by

$$g = g_c + n - e \tag{3'}$$

$$\frac{dc_i}{dt} = c_i(t)(g_i - g_c) \tag{4'}$$

$$\frac{ds_i}{dt} = s_i(t)(g_i - g) = s_i(t)(g_i - g_c - n + e) \tag{5'}$$

These relations provide a complete description of the different sources of evolution that restructure any population as a result of the growth rate diversity contained within it. They are compatible with any theory of the underlying evolutionary processes whether deterministic or stochastic. Like any accounting scheme, they are a filing system in which to locate the various forces that jointly exhaust the competitive process, a filing system that serves to provide a complete partitioning of the processes that describe the development of a population at the most inclusive level. They tie together four kinds of competitive change which, in practice, we expect to give rise to causally effective explanations in relation to the development of the population, and they also provide a frame in which to place competition policy in its developmental context. What we see through this population method is the fundamental evolutionary theme that change is contingent on variety. The structures of the populations change because the growth rates of the survivors are distributed around a population average growth rate and because the entry and exit rates differ. In short, development is an evolutionary process of displacement and replacement, a process of self transformation in which the population in question is transformed into something different. It is in this sense that competition is a regulator of development a method of reallocating resources to different uses, a method for generating structural change. From this perspective an economy is a set of interdependent interacting populations of activities that utilize resources and the accounting method will apply at any level of disaggregation we choose. Developmental change is nested and we can focus the lens of population change according to the problem in hand[11].

An Example: Accounting for Competition and Productivity Growth

To illustrate this point consider a familiar index of the rate of technological change, the growth in resource productivity in an industry over some time interval. Using the accounting framework, we can group the factors at work in an evolutionary growth accounting into 'selection processes', defined in terms of the differential growth or decline of survivors and the elimination of exiting firms, and 'innovation processes', defined in terms of the entrants and the innovation induced changes in the characteristics of the surviving firms. Suppose that the characteristic in question is the average unit labour input (the inverse of labour productivity) in this population of firms, labelled z, and we want to know how the population average value, labelled $\bar{z}$, changes over our time interval.

It follows from the definitions above that in relation to the 'selection processes'

$$\bar{z}(t) = (1-e)\bar{z}_c(t) + e\bar{z}_e(t)$$

where $\bar{z}_c(t) = \sum c_i(t) z_i(t)$ and $\bar{z}_e(t)$ is the average value of $z(t)$ for those entities that will exit over the interval Δt. Similarly, in relation to the 'innovation processes'

$$\bar{z}(t+\Delta t) = (1-n)\bar{z}_c(t+\Delta t) + n\bar{z}_n(t+\Delta t)$$

where $\bar{z}_n$ is the average value of $z(t+\Delta t)$ for the entrants over the interval. The change in $\bar{z}$ follows as

$$\Delta\bar{z} = \bar{z}(t+\Delta t) - \bar{z}(t) = \Delta\bar{z}_c + n\Delta t\left(\bar{z}_n(t+\Delta t) - \bar{z}_c(t+\Delta t)\right) - e\Delta t\left(\bar{z}_e(t) - \bar{z}_c(t)\right) \qquad (7)$$

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[11] On the micro meso macro distinction in evolutionary analysis see Dopfer *et al,* 2004.

Expression (7) is a complete evolutionary accounting for the change in average population value of labour productivity. On the right hand side, the first term is the combined effect of selection and innovation operating on the surviving firms. The second and third terms reflect the productivity levels in entrants and exits, expressed as deviations from the average productivity value for the continuing entities at the appropriate dates[12]. Consideration of the innovation and selection term in this expression brings us to the third and final of our accounting topics.

C) The Price Equation

In this final section we consider the third of our accounting relations, the so called Price Equation for decomposing the change in some population average into component parts. This is by now a well known result in evolutionary population analysis (Price, 1970; Frank, 1998; Metcalfe, 1998; Andersen, 2004; Gintis, 2002; Knudsen, 2004). It is a general method for decomposing the change in average value of some population characteristic into two additive effects, one due to selection the other due to innovation. Thus, following a proper accounting of our productivity change example at the two dates, we find

$$\begin{aligned}
\Delta \bar{z}_c &= \sum c_i(t+\Delta t) z_i(t+\Delta t) - \sum c_i(t) z_i(t) \\
&= \sum \Delta c_i z_i(t) + \sum c_i(t+\Delta t) \Delta z_i \\
&= \frac{1}{1+g_c}\left\{\sum c_i(t)(g_i - g_c) z_i(t) + \sum c_i(t)(1+g_i)\Delta g_i\right\}
\end{aligned}$$

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[12] In his survey of industry dynamics processes in LDCs, Tybout (2000) discusses some limited empirical evidence in favour of relatively high rates of turnover in plants and employment, the finding that efficiency, compared to survivors, is lower in exiting plants and in entrant plants, and that these categories rarely account for more than 5% of total output in any year. This suggests that some entrants fail to survive, and that those that do soon overcome the liability of newness and achieve at least average levels of productivity in the relevant populations. The same decomposition, or variants of it, has been used extensively in recent empirical work demonstrating the importance of selection for productivity growth (Carlin *et al*, 2001; Bailey *et al*, 1992; Bartelsman and Doms, 2000). This empirical literature provides striking empirical verification of the dynamic nature of competition and of the importance of distinguishing selection of activities in plants from selection of firms. Its conclusions are deeply dependent, of course, on access to finely disaggregated micro data, since aggregation always masks evolution.

or $$(1+g_c)\Delta\bar{z}_c = C_c(g_i z_i) + E_c((1+g_i)\cdot\Delta z_i) \tag{8}$$

Expression (8) is the Price equation; in which, $C_c(g_i z_i)$, the measure of the selection effect, is the (c_i weighted) covariance between fitness values (the growth rates g_i) and the values of z_i at the initial census date. This captures the idea that the change in the average value of the characteristic depends on how that characteristic co-varies with growth rates across the population; in short, that evolution is a matter of correlation. The second term, $E_c((1+g_i)\cdot\Delta z_i)$, the measure of the innovation effect, is the expected value (again c_i weighted) between the growth rates and the changes in the characteristic values at the level of each firm. Notice the recursive nature of this formulation; for if the entities are also defined as sub populations of further entities we can apply the Price equation successively to each sub population. For example, if entity i itself consists of a sub-population of j entities we can apply the Price method and write

$$(1+g_i)\Delta\bar{z}_i = C_{cj}(g_{ij}, z_{ij}) + E_{cj}((1+g_{ij})\Delta z_{ij})$$

and apply this to each of the i entities in the original population. As Anderson (2004) suggests, the Price equation “eats its own tail”, an attribute of considerable significance in the analysis of multi-level evolutionary processes. It means that we can decompose population change into change between any number of sub-populations and change within sub-populations in an identical fashion, so that at each level of aggregation we can reflect the forces of adaptation whether through selection or innovation. Since these relations are accounting relations they are compatible with any theory of evolutionary change that combines together the principles of variation, selection and innovation. Indeed, evolutionary economists have developed a rich set of explanations of competition that fit within this framework (Nelson and Winter 2002; Dosi, 2000; Metcalfe, 1998; Witt, 2003).

The force of this general approach can be summarised simply. Though selection is only one level of explanation for population change it cannot be separated from innovation. Innovation creates the variety (including entry) on which selection depends and the ensuing process reshapes the conditions for further innovation. It is an ensemble rather than an individual type of explanation but one that is based on the specifics of individual variation (Matthen and Ariew, 2002).

We have applied the accounting across two generations of a population of firms, and, of course, we can iterate the procedure indefinitely. As we do so the composition of the population of the firms will change and a date may be reached when not one of the original members of the population remains alive. In changing the members of the population we naturally change the distribution of capabilities and propensities to grow and to innovate so that the causal nature of the evolutionary process varies in the background. However, the activity continues and provided that the forces of selection remain the same and we can continue to speak of a given population.

A Special Case: Fisher's Fundamental Theorem

One special application of (8) is when the characteristic z_i is taken to be the growth rate g_i for; in this case we find that

$$(1+g_c)\Delta g_c = V_c(g_i) + E_c((1+g_c)\Delta g_i)$$

where $V_c(g_i)$ is the variance in the growth rates within the population of continuing entities. This form of the selection effect is known as Fisher's Fundamental Theorem, after its originator, the distinguished biologist and statistician R.A. Fisher (1930). We have already come across it in our discussion of retardation where we expressed the same idea in continuous rather than discrete time. If the growth rates are interpreted as fitness values then selection has the effect of increasing average fitness in the population. Too much should not be made of it in this specific context. It is a direct consequence of defining the growth rates as we have, and it captures only the selection part of the evolution of the average growth rate. However, its significance lies in its being a very special case of a much wider principle, Fisher's Principle (Metcalfe, 1998), namely that the statistical variability within the population accounts for the rate and direction of evolutionary change – the variation cum selection view of development[13].

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[13] In fact, there is a deeper interpretation of the selection effect in the Fisher/Price accounting. It is that the rate of change of the nth cumulant of the distribution of any characteristic is proportional to the magnitude of the (n+1)th cumulant. I call this the cumulant theorem (Metcalfe 1998).

We show below how this principle is one of considerable power in tracking the forces of evolution in economic populations.

Thus far we have developed an accounting scheme for any evolutionary process within some arbitrary population. To repeat, it is entirely neutral as to the explanation of the growth rates, innovation rates and entry and exit rates in any population, providing the framework into which more substantive theories can be located, compared and tested. What gives the scheme its content in any case is the particular explanation that causally links the characteristics of the entities to the differential growth of their scales of activity. These schemes may be deterministic, stochastic or combinations of both in their causal structure but they will all fall within the accounting net for population change.

Concluding Remarks

Accounting matters for a proper treatment of evolutionary processes and I have explored this claim in terms of the centrality of logistic processes, competition dynamics and the Price theorem to variation and selection models of evolution. The unifying theme that links all three is their relation to the population method in evolutionary theory. Economies, in particular are defined by interacting populations at multiple levels of definition and the propositions explored here should be useful in any attempt to model more formally the process of creative destruction. Indeed, we have said nothing of the appropriate way to link fitness to its underpinning economic causes only that any such theory needs to reflect a proper evolutionary accounting.

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