

# **ECONOMIC THEORY, APPLICATIONS AND ISSUES**

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# **Economic Competition and Evolution: Are There Lessons from Ecology?**

## **ABSTRACT**

After discussing generally models in ecology and economics that combine competition, optimization and evolution, this article concentrates on models of intraspecific competition. It demonstrates the importance of diversity/inequalities within populations of species and other environments for the sustainability of their populations, given the occurrence of environmental change. This is demonstrated both for scramble (open-access) and contest competition. Implications are drawn for human populations and for industrial organization. The possibility is raised that within industry competition may not always exist between firms in all stages of the development of a new industry. Policy implications are considered. For example, it is argued that policies designed to encourage intense business competition and maximum economic efficiency have the drawback of eventually making industries highly vulnerable to exogenous economic changes.

**Keywords:** competition policy, ecology, economic efficiency, evolution, intraspecific competition, market development

**JEL Classification:** L100, J100, Q150

# **Economic Competition and Evolution: Are There Lessons from Ecology?**

## **1. Introduction**

Concepts of competition are central to most economic and ecological modelling (Eldredge, 1997; Hodgson 1997) and in the case of ecology, competition, optimization and evolution are closely linked. While there is less emphasis on these combined aspects in economics, they are central to economic survival types of models of market development (Shepherd, 1967; Scherer, 1980, pp.38-39,93) and related models.

This centrality is clear from the observations of Nelson and Winter (2002). They point out that ‘many neoclassical economists seem to hold to the view that, an evolutionary theory of the firm and industry behavior really amount to the same thing (Nelson and Winter, 2002, pp.25). This belief stems from Milton Friedman’s view that competition will select for the survival of those firms that maximize their profit (Friedman, 1953, pp.24). Furthermore, Winter (1964, 1971), Nelson and Winter (1982) and Hodgson (1994) lent support to this idea by using models to show that (given particular theoretical conditions) a close correspondence exists between survival of businesses and their maximization of profit. But that correspondence relies on a static or stationary world (Nelson and Winter, 2002, pp.26). Clearly, as in ecology, important theoretical links are made in economics between competition, optimization and evolution even though evolution has been less central to economic thought than ecological thought. This article is based on the view that by further exploring the common threads of ecological and economic theory it is possible to improve our understanding of economic processes.

Both in economics and ecology, a common thread is that competition between entities arises from their demands for limited resources. In addition, in economics, unlike in ecology, competition usually exists in market economic systems between businesses for their market access. Competition within groups of entities (intraspecific competition) and between groups of entities (interspecific competition) occurs both in economic and ecological systems. It is, therefore, not surprising that considerable cross-fertilization of ideas has occurred between economics and ecology as far as competition and its consequences are concerned, but there is room for further progress.

The purpose of this article is to assess this cross-fertilization of ideas and then pay particular attention to intraspecific competition. In relation to intraspecific competition, particular consideration is given to the importance of diversity of individuals and environments for the sustainability of economic and biological groups of entities or populations. In addition, the consequence of the size of populations for whether their members are involved in mutualism or competition is explored, and implications for policy are highlighted.

## **2. Competition**

Economic thought has significantly influenced the development of ecological theory (Rapport and Turner, 1977; Hirshleifer, 1977; Worster, 1994). Worster (1994) suggests that Darwin's (1882) development of the theory of evolution of species owes much to the views of T. R. Malthus (1798). In the opposite direction, Alfred Marshall (1898) was convinced that economic thought could obtain more inspiration from biological analogy than from physics. However, physics probably exerted a greater influence on economic thought than ecology or biology in the 20<sup>th</sup> century, notwithstanding increasing interest in evolutionary economics in the second half of that century.

Consequently, scope still exists for obtaining further valuable insights, especially in economics, by additional consideration of analogies between economics and ecology, as this paper is intended to demonstrate. Consider now some general analogies between ecological and economic competition, evolution and their interconnections before concentrating on intraspecific competition.

Concepts of competition are fundamental to both economics and ecology (Hirshleifer, 1977; cf. Nelson and Winter, 2002). To various degrees, living things (including human beings) compete for the means (or, at least, some of the means) necessary for their sustenance and their survival. The populations of all living things are subject to some resource availability constraints and all eventually experience resource-scarcity and competition for scarce resources (cf. Grover, 1997). Nevertheless, not all resources needed for survival are in short supply in every situation. For instance, in most terrestrial situations the availability of ordinary air is not a constraint to populations of living things because other resource constraints prevent this constraint from becoming operative.

Economics emphasises competition between individuals for scarce resources and the general processes involved in that competition, particularly via market mechanisms. It focuses mainly on competition by individuals or individual entities. The nature of competition envisaged in ecology is more complex and based to a lesser extent on individual entities than in economics. While competition of individuals within species and between species is considered to be important, the significance of mutualism (and in some cases commensalism<sup>1</sup>) within these processes is also recognized.<sup>2</sup> In addition, ecology links biological competition closely to the evolution of species, and in most cases this involves competition for reproductive partners. Thus, for sexually reproducing animals, competition is usually not entirely individualistic in nature but involves a degree of mutualism with partners, and often offspring. Furthermore, members of a species sometimes cooperate in competing with other species, and in addition, mutualism sometimes exists between species, and these in turn may be competing with other species. Consequently, processes of competition and of mutualism or co-operation between living organisms can be quite complex.

These types of processes are given comparatively little attention in economics. Nevertheless, mutualism can be important in the economic sphere. For example, family members are usually involved in mutualistic, as well as competitive relationships. Mutualism or complementarity exists between some industries. Mutualism is sometimes present between firms in the same industry eg. Marks and Spencer and its suppliers (Tisdell, 1996, Ch.13; Tse, 1985), and between Japanese car manufacturers and their suppliers of parts in Japan. Examples of economic mutualism between firms are also mentioned, for example, by Haughland and Grønhaug (1996), Cole (1998) and Yamamoto (2000). Several other business relationships exist where sharing of information (networking) can be mutually beneficial to those involved in this sharing.

The traditional economic view of economic interdependence stresses rivalry. This view of competition was promoted by Stigler (1987) who described competition as “a rivalry between individuals (or groups or nations) and it arises whenever two or more parties strive for something that all cannot obtain”. While there can be mutualism within a group or nation, this aspect is not highlighted by Stigler.

The pre-occupation of economists with competitive or rival economic relationships has been criticized by Kaldor (1977). He emphasises the importance of complementarity rather than competitive relationships between industries and factors of production. While competitive and rival economic relationships are important, economics would be enriched by taking greater account of mutualistic economic relationships, as well as identifying situations of economic interdependence that are essentially parasitic in nature (usually involving some criminal activity, such as protection rackets), and those entailing commensalism (cf. Svizzero and Tisdell, 2001).

### **3. Mechanisms of Evolutionary Change**

Evolutionary processes are central to much ecological thought but have been given less attention in economic theory, even though not entirely neglected, as is evident from the publication of the specialised journal *Evolutionary Economics*. The comparatively slight attention of economists to evolutionary processes may be the consequence of significant limits to analogies between biological mechanisms of evolution and economic processes.

If, for example, a firm is considered by analogy to be the individual of a species and the industry the species, the replication of the firm corresponding to the reproduction of biological individuals does not appear to be a part of its agenda, although firms might want to survive and in some cases, grow. Furthermore, today's firms (companies) do not have the same degree of finiteness of their lives as biological individuals. So it is difficult to argue that, like biological species, firms have a desire to reproduce themselves, or in some way ensure the survival of their species or their industry unless the latter confers some particular advantage on them for their own survival.

In addition, in biology, genetic 'information' transferred to descendants plays a major role in selective evolutionary processes, along with mutations of such information. Again, it is difficult to find an exact analogy in economics. This is so despite the fact that Nelson (1987), in his theory of evolutionary economics, sees relevant fixed codes or customs of managerial behaviour within business as analogous to genes in biology. The degree of rigidity or inflexibility of such codes of conduct is likely to be much less than for genetic phenomena. Furthermore, ecological and biological evolution by genetic mutation and selection takes place on a much longer time-scale than does the unfolding of economic processes.



Nevertheless, while further analogies are possible between economic change and evolutionary ecological processes, caution is undoubtedly needed. For example, parallels have been drawn between the concept of 'punctuated' equilibrium in biological evolution (Grant, 1991, pp.340-341; Gould and Eldredge, 1977) and periodic innovatory cycles in economics involving widespread creative destruction of existing industries. While that might be a reasonable parallel, the cause of the economic phenomenon seems to be endogenous in this case rather than exogenous. The latter is assumed in some models of biological evolution. Furthermore, economic processes can evolve in the opposite direction to that suggested by ecological theory.

For example, given little change in external circumstances, many ecologists adopt the view that speciation tends to occur during a long passage of time. This means that the diversity and number of species tends to increase in the long term. However, the process of speciation is not necessarily a gradual process even in the absence of major exogenous events and significant human interference. Speciation is the rule over a very long time-period. The process of speciation appears to depend broadly on the variety of niches available and the extent to which mutation takes place. Suppose, for example, that a single species is utilizing two very similar niches. If evolution occurs that favours a new species in one of these niches, the pre-existing species in the end will be confined to the other niches since it is unable to compete effectively in the niche in which its use of resources conflicts with the new species (cf. Grover, 1997, pp.114). The extent to which genetic mutation occurs and the degree of variety or niches available heavily influences the extent to which speciation occurs; that is the extent of biodiversity is achieved in the biological system (Smith, 1998). Thus, if human activity reduces the variety of niches available to living things (as seems likely), then it could be expected to reduce biodiversity (cf. Tisdell, 1999a, Ch.4).

While the concept of an ecological niche is widely used in ecology (see for instance, Begon and Mortimer (1986) and Ricklefs (1993)), in practice definitions of it are not hard and fast, and to some extent the identification of such niches is subjective. The concept of a niche in biology is made more difficult to define because some niches are not physically determined but depend on the nature of the whole array of living species. Nevertheless, niches play a major role in the ecological theory of competition and evolution (Arthur, 1987).

Ecological niche-related theory has a counterpart in economics. The theory of spatial competition as, for example, investigated by Hotelling (1929) has similarities, and this can be extended to competition between differentiated products (Hartley and Tisdell, 1981, pp.234-238). In such cases, high-cost producers can only survive and compete with low-cost producers if they are located in a market niche sufficiently different to that of lower cost producers. If the situation happens to be relatively stable, this might lead to increasing variety of products with the passage of time. However, if the low-cost producers can reduce their costs of production at a sufficiently rapid rate, they may leave little or no room for specialist suppliers to survive. Consequently, no niches are left empty or exploitable other than by low-cost producers.

Whereas speciation may be the general pattern in biological systems not subject to exogenous forces (or massive human manipulation), it is not clear that economic processes evolve in the same manner. On a global scale, economic processes may result in reduced product variety, increased business concentration and reduced variety in business behaviour. Thus economic processes, mostly driven by market systems, may result in industrial systems evolving in the opposite direction to (largely) undisturbed ecological systems. Scitovsky (1976) has, for example, claimed that product variety has declined in the modern world. Authors such as Steindl (1965), Schumpeter (1942) and Marx (1954) foresee the possibility of increasing concentration of industry thereby indicating reductions in the variety of business structures. Tisdell (1999b) foresees the possibility that increasing globalization will foster business concentration and result in less diversity of businesses and ultimately slow technological progress (cf. Grabher and Stark, 1997, pp.535-536).

The question of product variety or diversity is complex. In recent times, although the variety of products globally may have declined, at the same time those available locally may have increased. Much depends upon how we envisage the geographical range in considering diversity of commodities i.e. for example, whether diversity is locally or globally defined. Furthermore, if we consider the time-dimension and measure the flow of commodities subject to product cycles, this flow may have increased in modern times. Furthermore, just as it can be difficult to quantify biodiversity, so it can be difficult to quantify business diversity because of multidimensional considerations. Nevertheless, the upshot of the discussion is that economic systems may not generate growing global diversity in business and greater diversity of commodities with the passage of time whereas speciation appears to be the

general rule in relatively undisturbed ecological systems.<sup>3</sup> There are strong tendencies towards product standardization in economic systems, and consequently diversity in economics may evolve in the opposite direction to that in ecology, as argued by (Tisdell and Seidl, in press).

#### **4. More on Links Between Optimization, Competition and Evolution**

Optimization, competition, and evolutionary change are closely linked in some expositions of economic and ecological theory (Hirshleifer, 1977). In ecology, this is partly a consequence of Charles Darwin's hypothesis that the fittest survive and reproduce (Darwin, 1882). On the whole, individuals of all species are in competition to survive and reproduce. The most competitive are favoured to leave behind survivors and so pass on their genes. By means of competition, natural selection takes place. The genes of those individuals showing the best ability to reproduce are passed on whereas those with less ability to do that are lost to the biological system (cf. Dawkins, 1982, 1989). In this way, evolution proceeds. Thus selected populations of species consist on the whole of individuals with the highest probability of reproducing and producing offspring also likely to reproduce effectively.

Note, however, that this process is the 'blind' result of past events and implicitly assumes that environments are relatively stationary. Consequently, the species and populations that evolve are not necessarily best suited to future environments if these environments differ substantially from those of the past. Thus, the processes involved are not forward-looking and they do not seem purposeful or teleological in nature. Furthermore, as pointed out by Gould (1989, 1990), evolutionary paths are not unique and the actual long-run paths pursued may be influenced to a considerable extent by chance or chaotic events. Therefore, the actual array of species which evolves may be less fit to survive than an alternative array which could have evolved had nature's dice been cast ever so slightly differently in the past.

Some evolutionary economists believe that those firms that survive economic competition are the most efficient available ones in providing economic benefits to society. The competitive process weeds out the less competitive firms and only the more competitive ones remain. Thus, a form of economic selection, analogous to natural selection in biology, takes place (cf. Friedman, 1953, pp.24).

However, the analogy is a very incomplete one and could be misleading. This is because in biology, evolution is closely linked to reproduction. As mentioned earlier, the analogy for reproduction of businesses is unclear, although it is likely that successful businesses will have would-be imitators and that such a business may grow in size. Furthermore, selection in economics may not result in the most efficient set of firms for current or emerging circumstances for similar reasons to those suggested by Gould (1989, 1990) in relation to biological evolution (cf. Tisdell, 1985). Actually, the problem of optimal selection is even more acute in economics than in biology because economic environments appear to change much more rapidly than biological ones.

The concept of evolution by natural selection is closely linked to the ability of individuals (in heterosexual cases, pairs of individuals) to reproduce. The question has arisen in biology of whether some identifiable types of inherited behaviour are likely to result in successful reproduction.<sup>4</sup> For instance, does optimization of any sub-goal necessary for living increase the likelihood of individuals surviving and successfully reproducing? Is the latter, that is the ultimate goal in much ecological thought, fostered by optimizing some sub-goal or sub-goals? Dawkins (1986, pp.21) refers to the “reproductive success of an animal over its entire life compared to rivals” as a measure of the long-term optimality of its behaviour. Pursuance of sub-goals appears to be concerned in her view with short-term optimality. For example, with whether an animal appears to optimize some function in its day-to-day life, “such as the amount of energy it is collecting in a certain amount of time” (Dawkins, 1986, pp.21).

As Dawkins (1986, p.p2) points out, “emphasis on animals as ‘optimisers’ has led to an extraordinary degree of confusion about what ‘optimal’ really means” in its application to adaptation and selection. Similar confusion also exists in economics. This is not surprising since to a large extent economists, for example Tullock (1971), have encouraged the emphasis of ecology on optimality, either indirectly, or directly. The widespread use of such models in ecology is apparent from the review by Rapport and Turner (1977). A major problem, as envisaged by Dawkins (1986), is that optimizing a particular sub-goal can be inconsistent with individuals maximizing their chances of survival and passing their genes on in the evolutionary process. In other words, the fittest in the evolutionary sense are likely to be those not maximizing any particular sub-goal (or short-term goal) but those maintaining an appropriate balance between sub-goals necessary for the maintenance of life.

For instance, obtaining food is necessary for life but minimizing the net amount of energy expended in a certain amount of time, optimal foraging, does not maximize the chance of individuals leaving offspring. “An animal that gathers food optimally might actually leave fewer offspring in its lifetime than an animal which gathers it less than optimally because it is so intent on feeding that it gets eaten by a predator. In other words, the long-term reproductive success kind of optimality and the short-term efficiency kind of optimality should be kept distinct” (Dawkins, 1986, pp.21).

This idea has implications for the hypothesis of some evolutionary economists that the survivors in business competition are those firms, which maximize profit (reviewed by Hirshleifer, 1997, pp.9-16), and that these are most efficient or fittest. It is probable that business survival does not depend, in an uncertain and changing world, purely on the pursuit of a single goal such as profit maximization. Furthermore, the concept of profit maximization is not straightforward. For example, is short-term profit maximization suggested or instead long-term profit maximization in the Hicksian sense (Hicks, 1939) of maximizing the capitalized value of the business? If it is the latter, what is the time-horizon for optimization and how are the considerable uncertainties about future economic and technological variables allowed for? Is, in fact, the hypothesis of profit-maximization, so vague as to be hardly operational?

In any case, pursuit of maximum capitalized value or long-term profit is likely to be constrained by liquidity considerations. While traditional microeconomics assumes perfect knowledge (Hicks, 1939) and a perfect capital market, this is far from the case in practice. Although the owners or managers of a business may wish to pursue a strategy, that in their view will maximize the capitalised value of their firm, to do so may require loans and credits. Not enough lenders, however, may not be confident of the success of such a strategy and may fail to finance it. Or if a company goes into the red in the short-term but has good prospects in fact for long-term profitability, its creditors may nevertheless be excessively influenced in their expectations about the profitability of the company by its short-term results, and the company may fail due to a shortage of credit. Thus, in reality the survival of a firm does not depend solely on the maximization of its profit, however that is defined. Indeed, attempts to maximize the capitalized value of a firm can be inconsistent with its survival.<sup>5</sup>

While economic argument about the appropriate concept of profit maximization is an ‘old chestnut’, the concept is central to the contention that business competition favours the survival of firms that maximize profit. While business competition can be expected to result in the elimination of firms that make persistent losses and have little prospect of future profit, it does not follow either that profit-maximizers are survivors. Business survival depends on complex phenomena, and both design and chance play a part in it.

To recapitulate: while individuals that optimize are often considered to have the best chance of survival and where relevant, of reproducing, the goal or objective function being optimized or which should be optimized is unclear both in ecology and in economics. Survival of individual entities may depend on a balance between goals necessary for survival and living rather than the optimization of a single objective. Consequently, the single goal of profit-maximization may not maximize the probability of survival of businesses.

Furthermore, just as species and individuals selected for survival are not necessarily the fittest for the future, for example because there is exogenous environmental change, or because chance factors of the type suggested by Gould (1998, 1990) apply, so the array of surviving firms in a competitive system is not necessarily the optimal set for the future. In addition, if industrial evolution reduces diversity of business organizations, the capacity for future beneficial evolution of the economic system may be reduced (cf. Tisdell, 1999b). In other words, the evolutionary dynamics of the system becomes impoverished.

##### **5. Intraspecific Competition (Scramble and Contest); Population Sustainability Depends on Diversity or Inequality**

Two types of ecological models of intraspecific competition of population, one involving scramble competition and the other contest competition, highlight the importance of diversity or inequalities for the survival or sustainability of populations. It is argued that these relationships are also relevant to several economic and social situations.

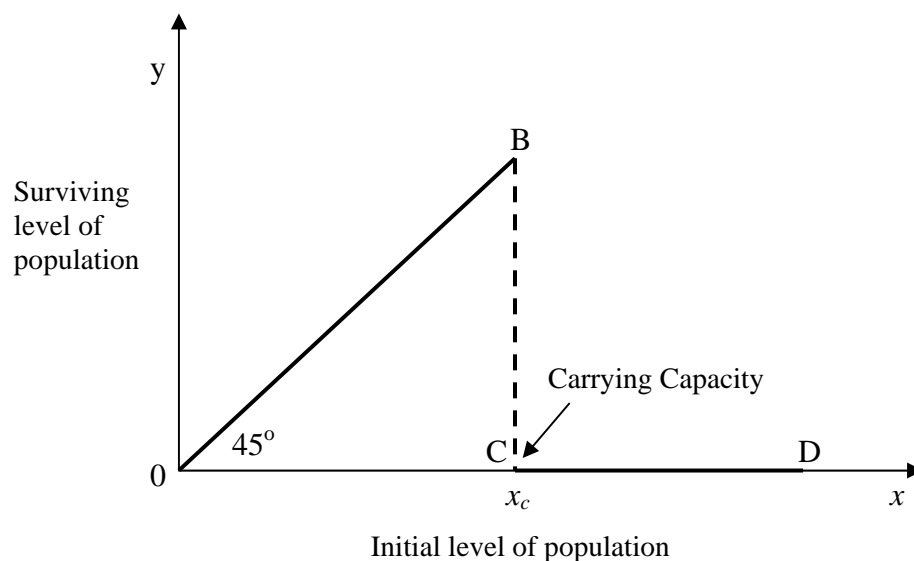
The basic ecological theories of these two types of resource competition as for example outlined by Begon and Mortimer (1988), will now be introduced, economic ‘analogs’ will be identified, and implications of inequalities will be outlined.

### A. Scramble Competition

Scramble competition involves simultaneous common exploitation of a limiting resource by the initial population of a species. In economics, it corresponds to open-access to natural resources. If scramble competition prevails, ecologists believe that no significant limit to the survival of the initial population of a species is reached until the limiting resource is used to its carrying capacity. Once the carrying capacity of the limiting resource is exceeded, the level of the surviving population crashes, in the extreme case to zero, because no individual obtains enough of the limiting resource to survive. Where  $x_c$  is the population carrying capacity of limiting resource, the relationship between the initial level of population and the surviving population level is like that shown in Figure 1 by OBCD. Or, the probability of any number of the initial population surviving  $P$ , is

$$P(x) = 1 \quad \text{for } x \leq x_c$$

$$= 0 \quad \text{for } x > x_c$$



**Figure 1:** Population survival consequences of ‘scramble’ competition

Alternatively, this scramble competition model can be specified as follows; if:

$R =$  total available quantity of the limiting resource per unit of time;

$x =$  the size of the initial population;

$r =$  the quantity of the limiting resource required by each individual in the population to survive;

the carrying capacity of the environment is:

$$x_c = R/t.$$

All of the initial population survive if  $x \leq x_c$  but all perish if  $x > x_c$ .

Ecologists have tested this model by using selected insects believed to practice scramble competition. They have done this experimentally by providing a particular quantity of a limiting resource (usually food), varying the initial level of the insect population and then determining the size of surviving population after a period of time (see for example, Fujii and Toquenaga, 1988).<sup>6</sup>

This model can also be extended (made dynamic) by incorporating endogenous population growth using the basic Malthusian hypotheses for population growth, normally that population increases as long as individuals obtain more than their minimum requirement of the limiting resources eg. food for survival, but that population growth ceases if all just obtain this minimum requirement. In those circumstances, the species employing scramble competition is vulnerable to extinction.

With the passage of time, the population of a species under those conditions increases to  $x_c$ , if it is initially less than  $x_c$ . At equilibrium, the whole homogenous population is vulnerable to extinction. If due to any disturbance the species population should temporarily exceed  $x_c$ , the whole population crashes. Furthermore, if for some reason the level of carrying capacity should temporarily fall, extinction of the whole population occurs. In this catastrophe-type model the population equilibrium is locally stable from the lower side but locally unstable on its upper side.

This theory can be 'grafted' into that of Malthus and Ricardo. In that case, total availability of the limiting resource to the species is a function of its population level. Letting  $x$  represent the population level of the species,  $R = f(x)$  where  $f' > 0$  the population of the species increases as long as  $R/x$  exceeds  $r$  and eventually reaches equilibrium when income fall to subsistence level, that is to the level where  $f(x)/x$  equals  $r$ . Given that  $r$  of the limiting resource is required by each member of species for survival, the population of the species is extremely vulnerable to extinction once it has achieved equilibrium. Extinction can be precipitated by a shift down in  $f(x)$  or by a random increase in population above  $x_c$ .



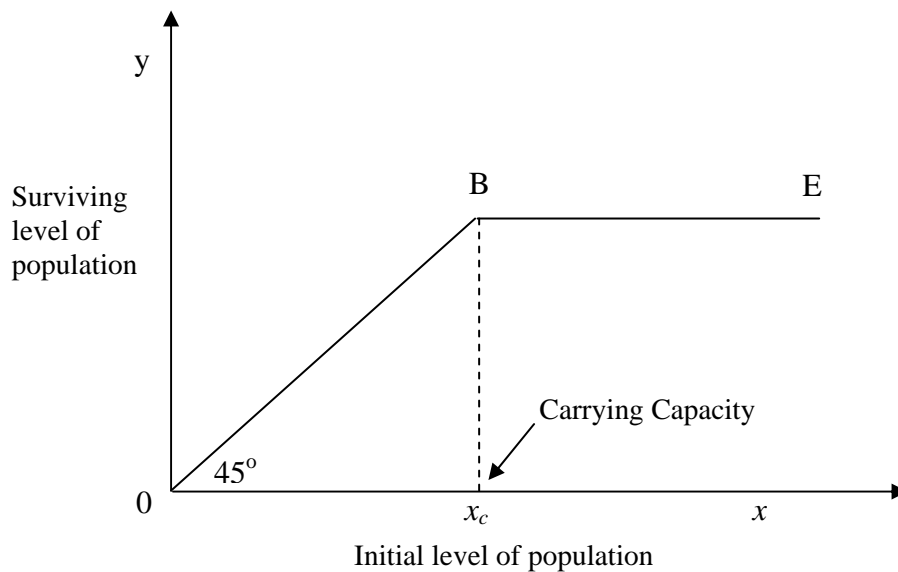
What makes species involved in scramble competition so vulnerable to extinction? First, they would be less vulnerable to extinction if Malthusian population dynamics did not apply and they could hold their population sufficiently below carrying capacity to provide a buffer against population disturbances or a reduction in carrying capacity, as some human populations have. Secondly, equality of access to and availability of the limiting resource to all creates a problem for the stability of the model. If some members of the population had privileged availability this would create greater stability provided the privileged group did not also increase its population up to the limits of its resource availability. By one means or another the privileged group would need to be restricted in size. Should the non-privileged perish, the surviving privileged group might, for example, exclude some of its members to create a new non-privileged group.

In biological laboratory experiments, it is found that species thought to engage in scramble competition do not as a rule exactly display the type of relationship illustrated in Figure 1 (see Fujii and Toquenaga, 1993). This is probably because there is less homogeneity present in reality than assumed in the basic model. Environments are not uniform and not all individuals in a population have exactly the same minimum requirements for limiting resource. Heterogeneity (diversity) of local environments (spatial diversity) and diversity of requirements for survival within the population of a species seem to increase the likelihood of a species surviving. Inequality adds to the stability of the population. By contrast the creation of ‘a level playing field’ in which all members of the population are competitive and equally very efficient in using the limiting resource may result in eventual collapse of populations. Some inefficiencies and irregularities in scramble-like competitive systems may be necessary to the survival of populations that practice such competition.

### ***B. Contest Competition***

In ecological theory, populations of species that rely on intraspecific contest competition are seen as having a better chance of survival than those relying on scramble competition. At least this so given the relevant theoretical models. Contest competition results in individuals staking out ‘rights’ to the limiting resource and defending those usually by aggression. In most cases, this involves creating exclusive territories and the incumbent has complete rights to the limiting resource within its territory.

Provided at least some members of the initial population are able to obtain territories of sufficient to provide them with the minimum requirement of the limiting resource, the total available quantity of which is  $R$ , then the type of short term population relationship shown in Figure 2 applies (cf. Begon and Mortimer, 1986). Here,  $x_c = R/r$ . This relationship contrasts with that in Figure 1, for in this case  $x_c$  of the population of species continues to survive if the initial population exceeds carrying capacity  $x_c$  whereas in the former case, the whole initial population perishes. But in reality the situation is probably much more complex.



**Figure 2:** Theoretical relationships for survival of a population given contest competition

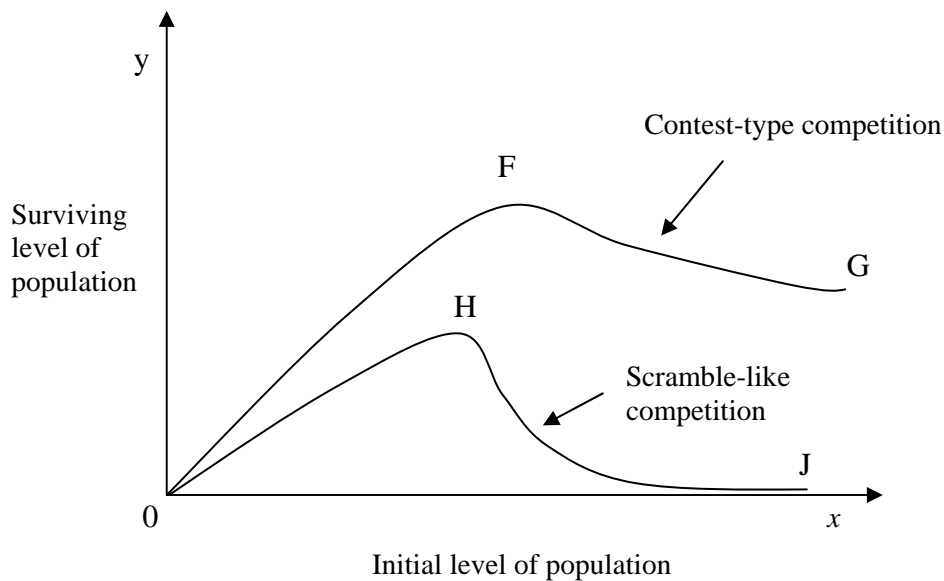
However, it would be coincidental if territories were so staked out by members of the initial population in a way that each territory-holder just had,  $x_c$  of the limiting resources. Furthermore, under changing environmental conditions, the whole initial population would be very vulnerable to extinction in such a case. For example, suppose that the aggregate availability of the limiting resource suddenly declined reducing its availability in all territories. All of the initial population would then perish unless some individuals could establish larger territories to provide themselves with enough of the resources for their survival.

If, in fact, organisms in some territories had a surplus of the limiting resource, this could add to the sustainability of the population. This surplus would act as a buffer against environmental variation.

Those occupying a territory may, in a dynamic situation, continue to have offspring provided, they have sufficient (or more than sufficient) resources for subsistence. Nevertheless, population within a territory may not increase up to the means of subsistence within the territory. This happens if an exclusion strategy is adopted for offspring. When this strategy is adopted offspring are excluded from the territory by dominant members (parents) when they reach a certain age (mostly maturity), and must find another territory if they are to survive. “Property rights” combined with the above exclusion mechanism tend to make such populations highly sustainable, mainly because resources are not fully utilized. Inequality of resource ‘entitlements’ arising from inequalities in dominance (a type of diversity), therefore, plays an important role in the sustainability of species involved in contest competition. The full impact of Malthus’s principle of population growth can be circumvented in such systems. It is also apparent that contest competition can take many different forms and that a fuller exposition of the dynamics requires these forms to be considered specifically because some forms result in highly sustainable populations of species whereas for other forms, populations are highly vulnerable to chance events or to environmental change, just as in the scramble case. Stable situations seem to be ones in which competition between members of a population is unequal. The playing fields for competition is not level.

### ***C. More Discussion of Scramble and Contest Competition***

In reality, population survival curves derived from experiments do not, usually, accord exactly with the stark forms indicated in Figures 1 and 2. They may, for example, show some degree of continuity and may be curvilinear. For example, the relationship shown by curve OFG in Figure 3 may reflect essentially contest competition and that shown by curve OHJ in this figure scramble competition (cf. Fujii and Toquenaga, 1993). Those forms seem to arise from diversity.



**Figure 3:** Modified population and survival curves to allow for other than extreme cases

In the scramble case, the carrying capacity limit may not be so definite or unique because in the population of species some diversity or heterogeneity usually exists in the resource requirements of individuals. This results in some individuals perishing before others do as resource limits are approached thereby reducing pressures on the remaining members of the population. Thus this can explain the curve OFG in Figure 3. Furthermore, equal access to resources may not occur in practice.

In the contest-case, exclusion of competitors may become more difficult as the competing population increases. As the population increases, extra energy may need to be expended by those possessing resources (territory) to defend these and the intensity of the competition for gaining territories may increase. This can depress the level of the surviving population, once population levels become high. In the extreme case such competition could even result in population collapse. If open-access occurs in establishing resource possession, at high initial population levels territories may become too small for the survival of the population or the cost of acquiring and holding a territory may become so high that all perish. Therefore, the outcome could be the same as in the scramble case, depending upon the nature of the mechanism governing possession of the limiting resource.

Nevertheless, in the contest competition case, if a sufficient gradient of (social) dominance exists in the population competing for ‘territories’, this can contribute to sustainability of the

population of the species. This is because when a steep (social) dominance gradient exists the less dominant are quickly and easily eliminated by the more dominant in the competition for territories. So diversity or heterogeneity in social dominance can contribute to sustainability or stability of populations of species. The distribution of dominance behavioural characteristics in a population may be a consequence of inheritance, or the distribution may arise from experience, or the distribution may evolve from experience and self-organization as suggested by Hemelrijk (1999), or both.

Both the case of scramble competition and contest competition, a degree of sustainability or stability is imparted to the modified population-survival curves (see Figure 3) if population heterogeneity or diversity exists. Assuming that the limiting resource is homogeneous, variations in the requirements of members of the competing population of species for the limiting resource can, as explained above, impart a degree of sustainability to the level of the surviving population if either scramble or contest competition occurs.

The above 'pure' theories of scramble and contest competition assume resource homogeneity. In reality, the limiting resource may not be homogeneous, and this can affect the nature of the population-survival curves and the dynamics of competition between members of a population. Usually diversity of resources is favourable to the survival of species. Nevertheless, diversity of heterogeneity of individuals in the population also remains important for ensuring the sustainability of the population, given resource-constraints on population growth. Presumably these considerations also are, or have been, relevant to the survival of some human populations subject to natural resource-constraints. For example, human societies with steep social dominance gradients relying on contest competition may show greater population resilience when the availability of natural resources are reduced than those without such gradients

The importance of diversity accords with the following observation of Begon and Mortimer (1986, p.28):

Typically, intraspecific competition affects not only the quantity, but their quality as well, which becomes more and more effected as [population] density increases. This combined with the variability of both environment and individuals, means that there is usually no

sudden threshold for competition in nature. Rather it increases generally over an extended range.

#### *D. Parallels in Economics*

Diversity plays an important role in helping to sustain populations where intraspecific competition exists. Even within Ricardo's model of long-term steady-state equilibrium of a human population (Ricardo, 1817), the human population must exhibit diversity (in access or need for food) if it is not to be wiped out by a temporary disturbance which reduces the per capita income level temporarily below subsistence levels. This is necessary to make the system stable.

These models have parallels to human competition for use of natural or environmental resources.<sup>7</sup> For instance, scramble competition underlies several global environmental catastrophe theories that predict eventual environmental collapse due to human over exploitation of natural resources to which there is open-access eg. the use of the atmosphere for greenhouse gas emissions. In general, open access to natural resources of economic value involves a type of scramble competition. In some cases (but not all) scramble competition can be transformed into contest competition by the assignment of private property rights to natural resources and this can avert the eventual unsustainable use of these resource by humans (cf. Coase, 1980).

It was stated above that there are significant limitations to applying ecological evolutionary theory to the economics of industrial organization because firms do not reproduce in a manner similar to living organisms. However, the following may be an acceptable analogy involving intraspecific competition. Industries in which entry of firms is very easy, such as those that operate under pure (a perfect competition) or under monopolistic competition exhibit open-access to the markets involved. In such industries in long-run equilibrium all firms are just able to earn normal profits. In effect, as long as above normal profits occur in those industries entry occurs and the market 'territories' of existing firms are reduced. Consequently, in equilibrium each firm just holds a territory large enough for it to survive by obtaining normal profit. A sudden decline in market demand will result in all firms making below normal profit and will threaten the survival of all, if all are equally placed. The situation is analogous to the contest case in which in equilibrium each individual has just

enough of the limiting resource to survive. The population is very vulnerable if the incumbents are equally matched.

This suggests that industries that are less perfectly competitive (do not have easy entry) and in which participants are not equally matched in their economic performance will be more sustainable if exogenous economic changes occur (eg. a collapse in industry demand), than those industries where entry is easy and all firms are equally matched, for instance, where all firms have adopted the most efficient economic practices. Hence, there can be a conflict between greater economic competition, economic efficiency and relative stability of economic systems.

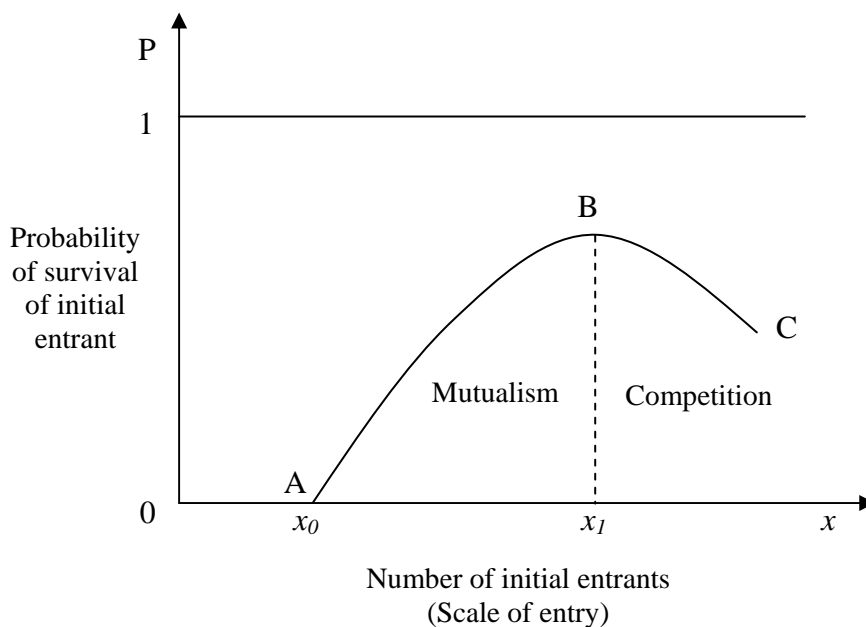
## **6. Evolution of a New Industry and Changes from Mutualism to Competition Between Firms**

Alfred Marshall (1898) was keenly aware that external economies between firms can significantly affect industry-wide costs, and alter economic conditions faced by individual firms in an industry as an industry expands or evolves. This idea has not been developed in economic analysis as much as it deserves to be. Fuller consideration of the processes involved can expand the range of useful analogies between ecology and economics. Consideration of the evolution of industries supplying a newer product provides an example. Here it is contended that initially mutualism is often dominant between firms in such an industry in establishing the market for such a product. However, when the market becomes well established, mutualism is replaced by (intraspecific) competition between firms in the industry in relation to the market.

This can be related to the product-cycle. In the earliest stages, all firms gain by establishing and expanding the market. External economies from market development often dominate. But as the market becomes well established and approaches saturation point, external economies from market development are exhausted. The basic underlying theory is outlined in Tisdell (2002) who also argues that the theory applies, for example, to the development of markets for new aquaculture fish products. Therefore, only the essence of the problem is stated here in order to draw parallels between economics and ecology.

It is argued here that in many new industries the probability of survival of a firm entering a new industry depends on how many other firms enter the industry 'initially' for example.

For novel products, the curve for probability of survival of an initial entrant (assuming that all entrants in aggregate are basically similar) might be as shown by relationship 0ABC in Figure 4. A minimum threshold exists in this case for survivability. Unless the initial population of entrants (or scale of entry) exceeds  $x_0$  an initial entrant has no hope of survival. Because of favourable market external economies (mutualism), the probability of survival of an initial entrant rises for initial scales of entry between  $x_0$  and  $x_1$ . Subsequently, contest-like competition becomes dominant and the probability of survival of an initial entrant begins to fall. Note that in the case shown, there is no circumstance under which all initial firms survive because some are assumed to always disappear for reasons other than competition per se.



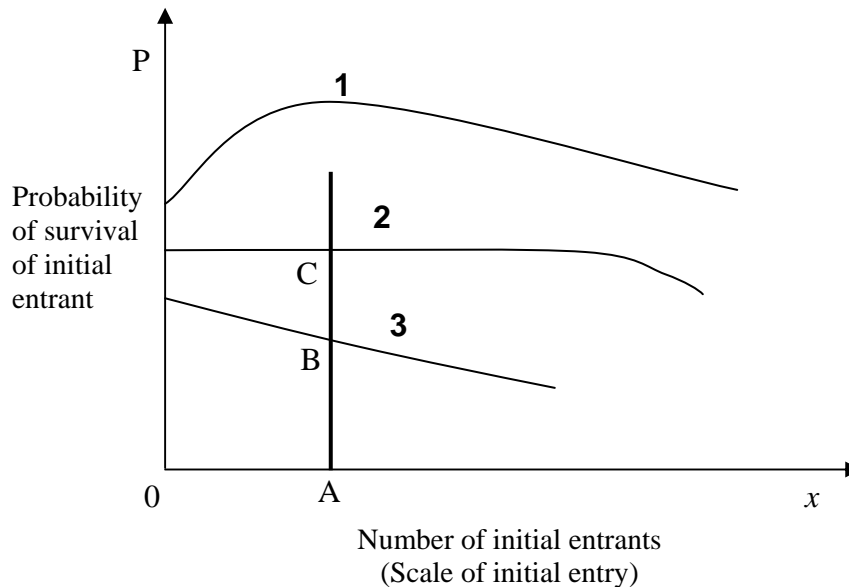
**Figure 4:** A survival curve for some types of new products and entrants supplying these

Given the relationship shown in Figure 4 mutualism (involving positive market externalities) is dominant for the initial number of entrants up to  $x_1$  and after that competition becomes dominant. Furthermore, unless entry is on a scale of more than  $x_0$  the whole industry or the new product fails to become established.

The relationship shown in Figure 4 applies to the introduction of some but not all new products. In some cases, the threshold OA may not exist and the mutualistic phase may not be marked. This may approximately be so, for example, where an aquacultured product (the 'new' product) is being introduced to a market where the wild caught product provides the



initial competition. In such a case, the probability of survival of an initial entrant in marketing the product might take the form indicated by the curve identified by 1 in Figure 5. No initial threshold of entrants is present for survivability.



**Figure 5:** Some alternative possible probability of survival curves as a function of the scale of initial entry to a new market

In Figure 5, the curves marked **2** and **3** indicate the form of a couple of other survivability relationships as a function of the scale of initial entry to a new market. Case **2** has similarities to both the contest and scramble cases because competition does not occur until the initial population reaches a sufficiently high level. In the economics case, this may be because initial entrants are selling in spatially separated markets. In case **3**, competition is present if there is more than one member of the initial population. It is also conceivable that in some economic circumstances, only portions of curves **2** and **3** apply because a minimum positive scale of entry is needed to ensure any prospect of establishing the market. In a very simple case, this might be imagined to be the scale OA, and so curve **3** is only applicable to the right of B and curve **2** to the right of C.

The above is an incomplete theory of the survival of groups of firms supplying new products or products to new markets. However, it provides suggestions about this topic in the light of ecological theory. In addition, the survival of many species may depend on some minimum initial population (threshold), and the survival of some is likely to be a mutualistic function

of their level of initial population up to a particular positive level of that population. Such possibilities call for some extension of the ecological theories of competition considered above. In fact, Allee (1931) suggested a similar group effect in population ecology mirroring the economic situation depicted in Figure 4.

## **7. Conclusions and Policy Consequences**

Given the major concern of both ecology and economics with competition and the growing interest of economists in evolutionary processes, or in processes generally rather than comparative statics, considerable scope continues to exist for fruitful interaction between ecological and economic thought (cf. Hannon, 1997). However, economic phenomena and ecological phenomena are not identical. Hence, considerable care must be taken in drawing analogies between ecology and economics. As mentioned, it is difficult to draw a direct link between biological reproduction, natural selection and evolutionary paths in ecology and similar possible paths in economics. Although businesses wish to survive as do most creatures, it is not apparent that they wish to reproduce. Ecology yields some interesting insights into the nature of survivors and the probability of survival of members of a population. For instance, modern ecology makes it clear that the survivors in a population are not necessarily the fittest for the future, and they may not even be the best selection for the present, a lesson not fully appreciated by some economists (cf. Grabher and Stark, 1997). Furthermore, the comparisons have highlighted the importance of diversity in populations for sustainability or stability in both competitive economic and ecological systems.

Ecological theories of population dynamics involving scramble and contest competition were seen to have analogies in economics. However, not all business situations involve economic rivalry. As shown, mutualism leading to business cooperation in the development of new markets may occur initially and this may subsequently be replaced by rivalry and competitiveness between businesses. A similar relationship is relevant for the pattern of survival of some species, as indicated by the group or Allee effect (Allee, 1931). However, this ecological relationship probably does not have the same basis as in the case of new market development because the Allee effect is a relationship involving prospects for reproduction of species rather than for market or resource development.

Consider some of the possible policy implications of this analysis.

First it is clear that private property rights can help to sustain human populations, if human populations tend to increase up to the means of subsistence. For instance inequality in land rights, possibly arising from contest competition in some human populations, can add to the sustainability of those populations. Each land-holding can be regarded as a territory of its incumbent(s). In this regard, the rules of change in territorial rights become important. In some developing societies, the adoption of a rule of equal division of property (land) between all offspring can result in all the offspring perishing as human population increases, although equal division or inheritance creates no problem for a time if properties are large initially. Napoleon I saw this as a problem and passed laws restricting land subdivision in France. Furthermore, if some families or territory-holders can have an economic surplus, this tends to make for greater sustainability of human populations where the bulk of the population is in dire poverty. Creating equality in such circumstances can jeopardize the sustainability of the whole population, In higher income societies, however, where population growth is not a major problem (it is often zero or negative) greater equality in availability of resources to the human population does not create a problem for the sustainability of human populations. The policy implication is that resource inequality in countries where population growth tends to press on the means of subsistence may be necessary for survival of their population given mechanisms of intraspecific competition. If, however, population growth can be halted or drastically reduced (as for example, achieved by China's one-child policy) population survival is possible with greater equality of access of individuals to resources.

Considerable scope exists for adapting ecological models of intraspecific competition and population dynamics to the economics and demographics of human communities, especially in developing countries. The role of property rights and of (social) dominance might be central to such studies.

Secondly, ecological scramble theory suggests that industries in which entry of firms is very easy are in the long run likely to become very vulnerable to exogenous economic change. In the long term there is a lack of economic resilience because firms may have little diversity and no profit reserves. They will have little diversity, for example, if all, as a result of competition, use the same most efficient techniques.

Thus policies that encourage great business competition, reduce all entry barriers to an industry and encourage firms to use the best available technique can add to industrial

vulnerability. Short-run static efficiency obtained by establishing a so called level playing field may be obtained at the expense of greater economic vulnerability. Moderation of competition policies to allow for this phenomenon seems appropriate.

Thirdly, governments may sometimes act as catalysts to develop mutually beneficial relationships between firms in an emerging industry. On the basis of the theory outlined above, scope exists for governments to encourage co-operation between businesses in establishing markets for an emerging industry. This has been recognized both in Japanese and French industrial policy. But in the case of emerging industries consisting of small firms, it may be difficult to obtain government recognition and support for their evolution given the nature of politics (cf. Tisdell, 2001).

Thus there are economic lessons to be learnt by cautiously considering analogies between economic situations and ecological theory. Furthermore, scope for fruitful interactions between economic and ecological ideas is far from exhausted.

## **8. Notes:**

- 1 Commensalism occurs when an animal or plant lives with, on, or in another to its own benefit but the relationship is neither parasitic nor mutualistic. The relationship has no impact on the host. For example, the relationship between some epiphytes and trees is of this nature.
- 2 The selfish gene theory of Dawkins (1982, 1989) is consistent with the view that in ecology individualistic competition is given less emphasis than in economics. In Dawkins' theory, the 'gene' is seen as the unit of natural selection rather than the individual. The passing on of genes may in some circumstances involve self-sacrifice, as is explained by Dawkins (1989, Ch 2). Furthermore, it sometimes requires mutualistic co-operation of partners or even with other species on occasions. See in particular Dawkins (1989, pp.233). See also Note 4.
- 3 As pointed out by Smith (1998, Ch 4, also pp.295) in the presence of stable natural environments, biodiversity tends to increase with the passage of time because changing (mutating) genetic material can take advantage of ever more specific niches. The mechanisms driving product diversity in economics are less clear but they are discussed in Tisdell and Seidel (in press).

- 4 Successful reproduction (involving the transmittal of genes to successors) is the linchpin of the ecological theory of R. Dawkins (1982, 1989) about biological evolution. But could this theory be circular and of limited predictive value? The genes that survive appear in retrospect to have maximized their chances of survival. Some might claim that they have acted ‘as if’ they have selfishly optimized their chances of survival and they have, therefore, proven to be the fittest to survive. But how scientifically useful is the ‘as if’ principle? These genes (at least some) might have survived by chance (cf. Gould (1989, 1990). Furthermore, what was optimized is difficult to determine, particularly since conscious actors do not seem to be involved. In these circumstances, it is not difficult to have an outlook similar to that of Dr Pangloss (Voltaire, 1947). Or a view similar to a reviewer of this paper who claims ‘we are always maximizing something in reality with a list of constraints’. But what is that something and what are the constraints? Authors, such as M. Dawkins (1985), try to address such matters directly.
- 5 For example, this would create liquidity problems for the firm and in certain cases, shake financial confidence in the business.
- 6 The period of the experiment can be so short that reproduction does not occur nor do natural deaths occur from other than a shortage of the limiting resource. The model can in principle be adjusted for births and deaths.
- 7 One reviewer suggested that other policy parallels might include the desire of local politicians to diversify or maintain a diversified local economy (to provide a buffer against industry downturns) or the desire of environmentalists to maintain local biodiversity, to provide a buffer against climatic change, for example.

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