

ECONOMICS, ECOLOGY AND THE ENVIRONMENT

Working Paper No. 62

**Competition, Evolution and Optimisation:
Comparisons of Models in Economics and Ecology**

by

Clem Tisdell

October 2001



THE UNIVERSITY OF QUEENSLAND

Working Paper No. 62

**Competition, Evolution and Optimisation:
Comparisons of Models in Economics and Ecology[†]**

by

Clem Tisdell*

October 2001

© All rights reserved

[†] A revised version of a paper presented 2001 in the session “Biology and Economics (CEP)” at the 76th Western Economic Association International Conference held in San Francisco, 4-8 July. Revision of this paper has benefited from comments received in the Workshop on “Content, Meaning and Consequences of the Concept of Competition in Economics and Ecology” held at the Institute of Environmental Sciences, The University of Zurich, and from comments at the WEAI session. An earlier version of this article was produced as Working Paper No.6 in the *Economic Theory, Applications and Issues* series.

* School of Economics, The University of Queensland, Brisbane 4072 Australia.
Email: c.tisdell@economics.uq.edu.au

WORKING PAPERS IN THE SERIES, *Economics, Ecology and the Environment* are published by the School of Economics, University of Queensland, 4072, Australia, as follow up to the Australian Centre for International Agricultural Research Project 40 of which Professor Clem Tisdell was the Project Leader. Views expressed in these working papers are those of their authors and not necessarily of any of the organisations associated with the Project. They should not be reproduced in whole or in part without the written permission of the Project Leader. It is planned to publish contributions to this series over the next few years.

Research for ACIAR project 40, *Economic impact and rural adjustments to nature conservation (biodiversity) programmes: A case study of Xishuangbanna Dai Autonomous Prefecture, Yunnan, China* was sponsored by the Australian Centre for International Agricultural Research (ACIAR), GPO Box 1571, Canberra, ACT, 2601, Australia.

The research for ACIAR project 40 has led in part, to the research being carried out in this current series.

For more information write to Professor Clem Tisdell, School of Economics, University of Queensland, Brisbane 4072, Australia. Email c.tisdell@economics.uq.edu.au

Abstract

Competition, Evolution and Optimisation: Comparisons of Models in Economics and Ecology

Clem Tisdell

Discusses concepts of competition in economics and ecology and the relevance of evolution to both subjects. It is suggested that although speciation or increasing biodiversity tends to occur in undisturbed ecological systems, the opposite trend may occur in economic systems. Competition based on optimisation plays a significant role in theories of the evolution of species and some theories of the evolution of business or industrial structures. But evolution does not result in optimal selection of species or businesses for the future, and there is scope for doubt about what is being optimised by survivors in the evolutionary process. Ecological or biological theories of intra-specific competition involving scramble and contest competition are outlined and economic analogies are identified. It is argued that heterogeneity or diversity of individuals within a population of competing members has important implications for the sustainability or stability of populations involved in these types of competition. Comparisons are made between the survival of new industries and the probability of survival of populations of species.

Keywords: Biology, competition, evolution, market development, optimisation.

Competition, Evolution and Optimisation: Comparisons of Models in Economics and Ecology

1. Introduction

Both economics and ecology make considerable use of concepts of competition and of evolution (Eldredge, 1997; Hodgson, 1997). The purpose of this article is to compare these uses, and to consider the extent to which their application in ecology provides insights into economic phenomena and vice versa.

The concepts of competition and of evolution are first discussed in turn followed by consideration of links between competitive processes, optimisation and the evolution of systems. Then the nature of evolution of biological/ecological systems and links between optimisation, competition and evolution are compared and contrasted with that of economic systems. It is suggested that some areas of biological research into competitive processes, such as intra-species competition, could have a fertile research counterpart in economics, for instance in relation to the success or failure of firms in emerging industries.

2. Concepts of Competition

Economic thought has to have had some significant influence on the development of ecological theory (Rapport and Turner, 1977; Hirshleifer, 1977; Worster, 1985). Worster (1985) suggests that Darwin (1882) was influenced in his development of the theory of evolution of species by the views of T. R. Malthus (1798). In the opposite direction, Alfred Marshall (1898) was convinced that economic thought would obtain more inspiration from biological analogy than from physics, physics probably exerted a greater influence in the 20th century on economic thought than ecology or biology, notwithstanding increasing interest in evolutionary economics in the second half of that century.

Concepts of competition are fundamental to both economics and ecology (Hirshleifer, 1977). 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. Its focus is mainly on competition by individuals or individual entities. Thus, its focus is mainly atomistic and individualistic.

The nature of competition envisaged in ecology is more complex and based to a lesser extent on individual entities. While competition of individuals within species and between species is considered to be important, the importance of mutualism (and in some cases commensalism) within these processes is also recognised. In addition, ecology links biological competition closely to the evolution of species, and in many 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, it is clear that processes of competition and of mutualism or cooperation can be quite complex.

There are analogies to these ecological processes in economics but economists have given these comparatively little attention. Nevertheless, it is clear that 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 may also be present between some firms in the same industry e.g. Marks and Spencer and its suppliers (Tisdell, 1996, Ch.13; Tse, 1985), and between Japanese car manufacturers and their suppliers of parts in Japan. Several other business relationships exist where sharing of information may be mutually beneficial to those involved in this sharing. Comparatively little attention has been given by economists to such mutualism and the ways in which it evolves.

The traditional economic view of economic interdependence involves rivalry. This view of competition is summarised by Stigler (1987) who describes 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 could be mutualism within a group or nation, this is not an aspect highlighted by Stigler.

The preoccupation of economists with competitive or rival economic relationships has been criticised by Kaldor (1977). By contrast, Kaldor 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 which are essentially parasitic in nature (usually involving some criminal activity such as protection rackets), and those entailing commensalism (cf. Svizzero and Tisdell, 2001)

3. Evolution

Evolutionary processes are central to a large body of ecological thought but on the whole have had less emphasis in economic theory, even though they are not entirely neglected, as is evident from the publication of the specialised journal *Evolutionary Economics*. A reason for the comparatively slight attention of economists to evolutionary processes may be the fact that there are significant limits to analogies between biological 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 its survival usually is and in some cases its growth. 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 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, it does not follow that no analogies are possible between economic and ecological processes, but undoubtedly caution is 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 and so on. While that might be a reasonable parallel, the cause of the economic phenomenon may be endogenous rather than exogenous. The latter may be assumed in some models of biological evolution, but not necessarily in all. Furthermore, economic processes may 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 if 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 utilising 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, p.1114).

It follows that 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. 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 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 globalisation 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 it 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 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. There are strong tendencies towards product standardisation in economic systems, and that economic evolution may be in the opposite direction to that in ecology (cf. Tisdell and Seidl, 2001).

4. Optimisation, Competition and Evolution

Optimisation, competition, and evolution 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. 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), it is likely the evolutionary paths are not unique and the actual long-run paths pursued may be influenced to a considerable extent by chance or chaotic events.

Consequently, 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.

The view has gained ground amongst some evolutionary economists that in economic competition the firms that survive 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 tend to remain. Thus a form of economic selection analogous to natural selection in biology takes place.

It should, however, be noted that the analogy is a very incomplete one. 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 the economics case 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. For instance, does optimisation 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 optimising some sub-goal or sub-goals? Dawkins (1986, p.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 optimise 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, p.21).

As Dawkins (1986, p.2) 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 have encouraged the emphasis of ecology on optimality, either indirectly, or directly, such as by Tullock (1971). The widespread use of such models in ecology is clear from the review by Rapport and Turner (1977).

A major problem, as envisaged by Dawkins (1986) is that optimising a particular sub-goal can be inconsistent with individuals maximising 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 maximising 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 minimising the net amount of energy expended in a certain amount of time, optimal foraging, does not maximise 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, p.21).

This idea has implications for the hypothesis of some evolutionary economists that the survivors in business competition are those firms, which maximise 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 maximisation. Furthermore, the concept of profit maximisation is not straightforward. For example, is short-term profit maximisation suggested or instead long-term profit maximisation in the Hicksian sense (Hicks, 1939) of maximising the capitalised value of the business? If it is the latter, what is the time-horizon for optimisation and how are the considerable uncertainties about future economic and technological variables allowed for? Is, in fact, the hypothesis of profit-maximisation, so vague as to be hardly operational?

In any case, pursuit of maximum capitalised 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 maximise the capitalised value of their firm, to do so may require loans and credits. 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 maximisation of its profit, however that is defined. Indeed, attempts to maximise the capitalised value of a firm can be inconsistent with its survival.

While economic argument about the appropriate concept of profit maximisation is an ‘old chestnut’, the concept is central to the contention that business competition favours the survival of firms that maximise 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-maximisers are survivors. Business survival depends on complex phenomena, and both design and chance play a part in it.

To recapitulate: while individuals that optimise are often considered to have the best chance of survival and where relevant, of reproducing, the goal or objective function being optimised or which should be optimised is unclear both in ecology and in economics. It seems that survival may depend on a balance between goals necessary for survival and living rather than the optimisation of a single objective. In line with this view, there is reason to doubt that profit-maximisation as an appropriate goal on its own for maximising 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. Furthermore, 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. Economic Hypotheses Suggested by the Study of Intra-specific Competition

Both competition between firms within industries and between industries is a key subject of microeconomic enquiry. Similarly, according to Fujii and Toquenaga (1998, p.178), “competition (both intra- and inter-specific) has been one of the most studied subjects in ecological research”. Arguably, despite the similar focus of economic and ecology, ecological research has paid much more attention to the *processes* involved in competition than has been so in economics research.

Ecological studies of intra-specific competition sometimes concentrate on resource competition and the extent to which members of an initial population survive. In studying the survival of initial populations of a species, ecologists give particular attention to the processes of contest competition and ‘scramble’ competition. See, for instance, Begon and Mortimer (1986).

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_1 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

$$\begin{aligned} P(x) &= 1 && \text{for } x \leq x_1 \\ &= 0 && \text{for } x > x_1 \end{aligned}$$

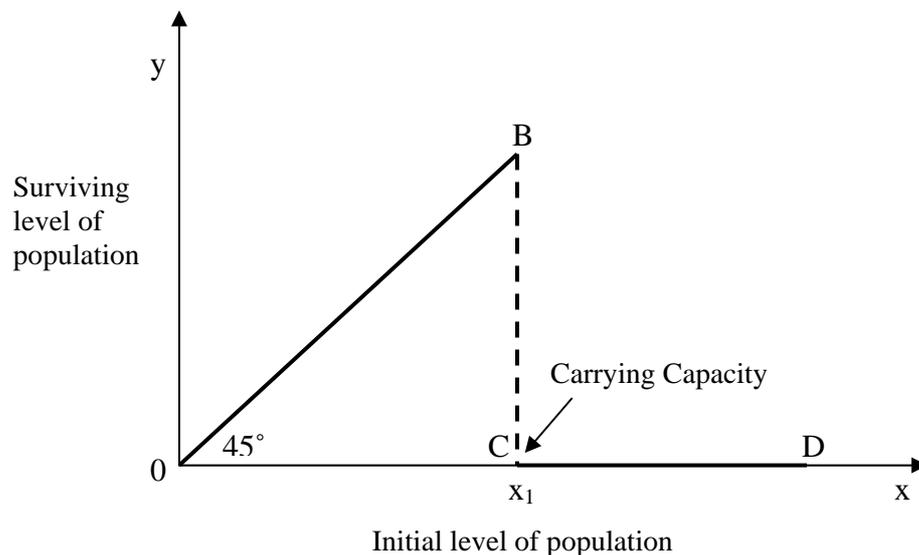


Figure 1. Population survival consequences of ‘scramble’ competition.

On the other hand, contest competition gives rise to a survival pattern of a different kind. Contest competition involves the exclusion of rivals by cannibalism or effective aggression, which may be combined with the staking out of exclusive territories. In fact, there are a variety of means in nature by which some members of a population obtain exclusive territories that provide them with enough resources to survive. Those members of a population in such cases unable to obtain territories usually perish. Exclusive territoriality in nature is akin to private property rights in economics.

Once again assuming that the carrying capacity of the resource-base is a population of x_1 , the population survival relationship for this case is theoretically of the type shown in Figure 2 by OBE. It differs from the scramble case because exclusion of competitors in this case enables the surviving population to survive up to the level corresponding to the carrying capacity of the environment.

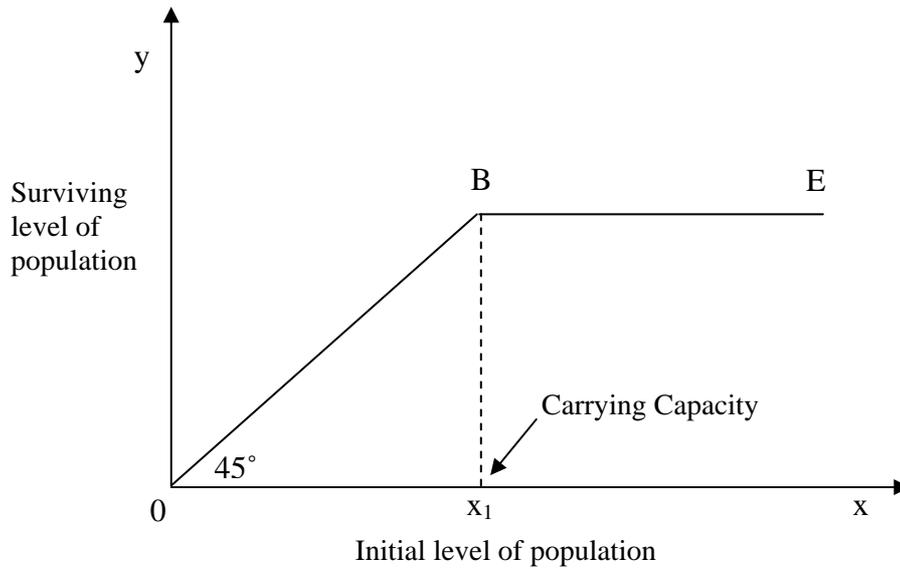


Figure 2. Theoretical relationships for survival of a population given contest competition.

However, these relationships do not allow for the deaths of members of the initial population that arise independently of intra-species competition. If such deaths occur naturally, the threshold initial population is in excess of x_1 . For instance, if the mortality rate is m , the initial population of the species only reaches the threshold for survival if it is equal to

$$x_2 = \frac{x_1}{(1-m)}.$$

This is illustrated in Figure 3. There $x_1 = y_1$ corresponds to the population carrying capacity of the resources available to support the population, but natural survival of the population even in the absence of resource limitations, is less than unity so line OBB' has a slope of less than 45° . Resource-constraints on population survival in this case are not encountered until $x > x_2$. Therefore, the scramble survival relationship is as shown by OB'C'D' and that for contest competition OB'E'.

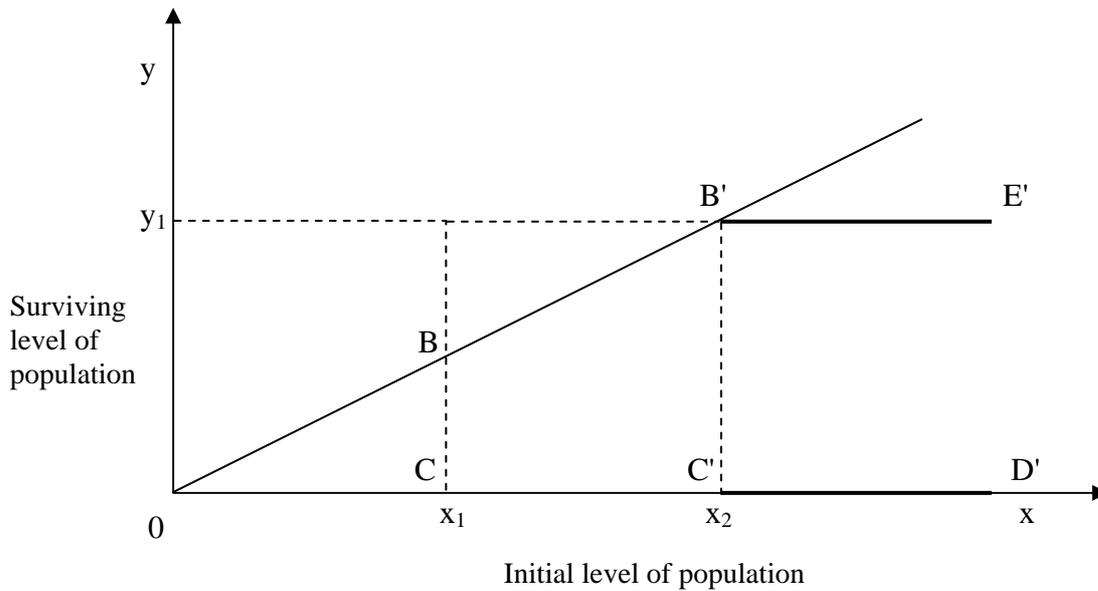


Figure 3. Adjustment of scramble and contest competition relationships to allow for mortality other than that due to competition for resources.

In reality, population survival curves will not, usually, accord exactly with the stark forms indicated above. They may, for example, show some degree of continuity and be curvilinear. For example, the relationship shown by curve OFG in Figure 4 may reflect essentially contest competition and that shown by curve OHJ in this figure scramble competition (cf. Fujii and Toquenaga, 1993). Furthermore, more complicated models can be constructed allowing, for example, for migration possibilities, if they exist, and for reproduction.

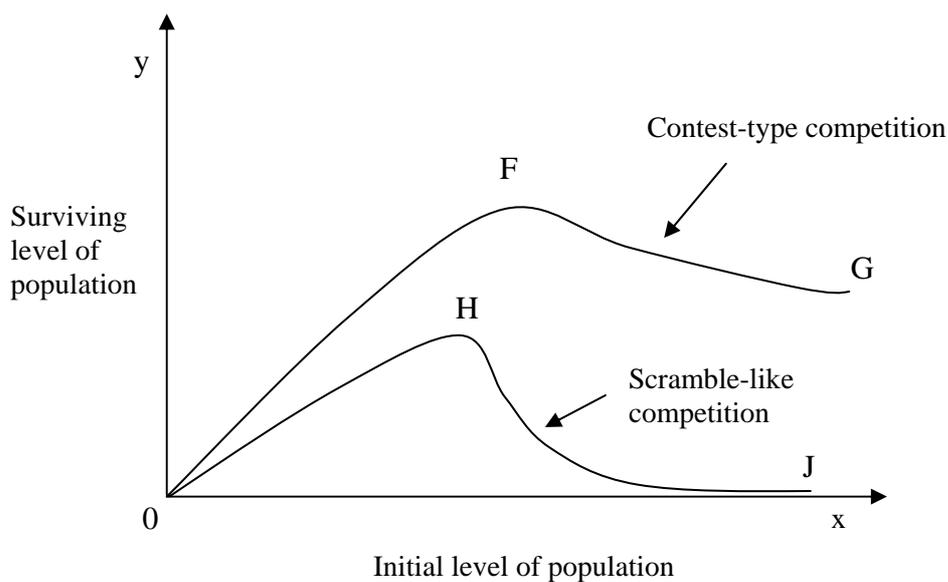


Figure 4. Modified population and survival curves to allow for other than extreme cases.

It may be useful to explain further the relationships shown in Figure 4. In the scramble case, the carrying capacity limit may not be so definite or unique because in the population of species usually some heterogeneity 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 4.

As for 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. Because 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. This possibility is not mentioned by Fujii and Toquenaga (1993). In economics, this case corresponds to circumstances involving insecurity of property rights and governance by force rather than the law.

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 4) if population heterogeneity or diversity exists. Assuming that the limiting resource is homogeneous as the above models do, variations in the requirements of members of the competing population of a species for the limiting resource can, as explained above, impart a degree of sustainability to the level of the surviving population if scramble competition occurs.

In the contest competition case, if a sufficient gradient of social dominance exists in the population competing for 'territories', this competition is likely to depress the size of the surviving population once the carrying capacity of the limiting resource is reached by less than would be so in the absence of such a steep dominance gradient or its absence. 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 it is diversity or

heterogeneity in social dominance that contributes to sustainability or stability of surviving populations in this case. 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 arise from experience and self-organisation as suggested by Hemelrijk (1999), or both.

Note that the above 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. Nevertheless, diversity of heterogeneity of individuals in the population remains important for ensuring the sustainability of the population given resource-constraints on population growth. Presumably also these considerations 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 natural resources are limited than those without such gradient.

It is interesting to note 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 arrange”.

This also suggests that 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, 1887), the human population must exhibit diversity if it is not to be wiped out by a temporary disturbance which reduces the income level temporarily below the subsistence level. This is necessary to make the system stable.

These models have several other possible parallels to human competition for use of natural or environmental resources. 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 e.g. 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 eventual unsustainable use of these resource by humans. But it is not always economic or possible to assign private property rights to the use of natural resources.

Cases could also occur in which human population are involved in mixtures of scramble and contest competition but these will not be discussed here.

6. Survival of Businesses Supplying a New Product Mutualistic and Competitive Population-Survival Models

One of my main interest here in the above aspect of ecological thought is in relation to the emergence of new industries or products (Tisdell, 2001), especially the processes involved in the marketing of new products. Whereas ecological population-survival models seem mostly to suggest either neutral or competitive survival relationships in relation to initial populations, such assumptions seem inappropriate in economic modelling of the introduction of new products.

The theory of the processes involved in the introduction of new products is complex and as yet little explored in economics. The likelihood of survival of initial entrants supplying new products varies with a wide range of circumstances. Only a few of these circumstances can be allowed for and I shall expound some of the possible relationships involved by considering the probability of survival (in supplying the new product) of firms initially supplying the new products.

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 OABC in Figure 5. 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 between x_0 and x_1 . Subsequently, contest-like competition becomes dominant and the probability of survival of an initial entrant begins to fall. Situations in which such relationships are likely to arise are outlined in Tisdell (2001). 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*.

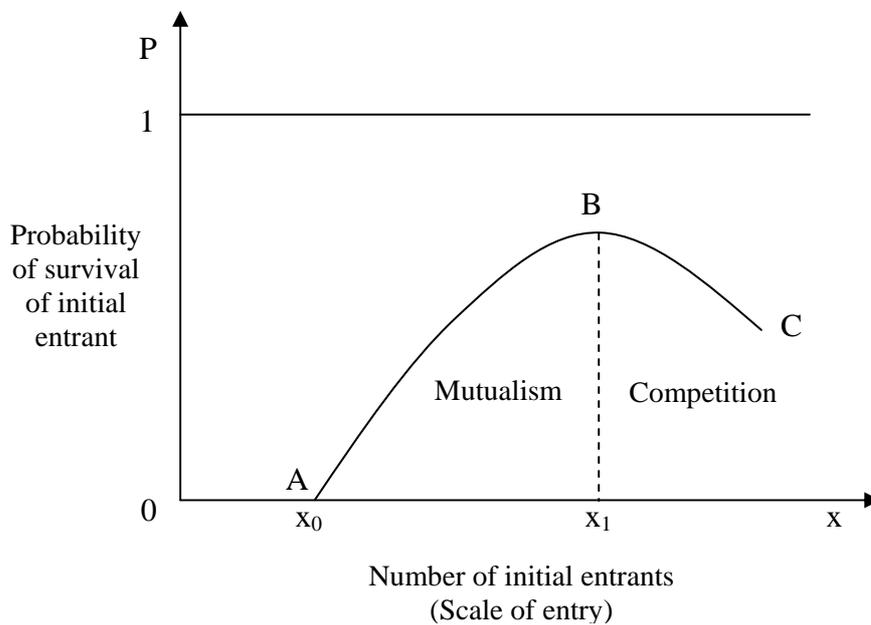


Figure 5. A survival curve for some types of new products and entrants supplying these.

Given the relationship shown in Figure 5 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 5 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 say 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 6. No initial threshold of entrants is present for survivability.

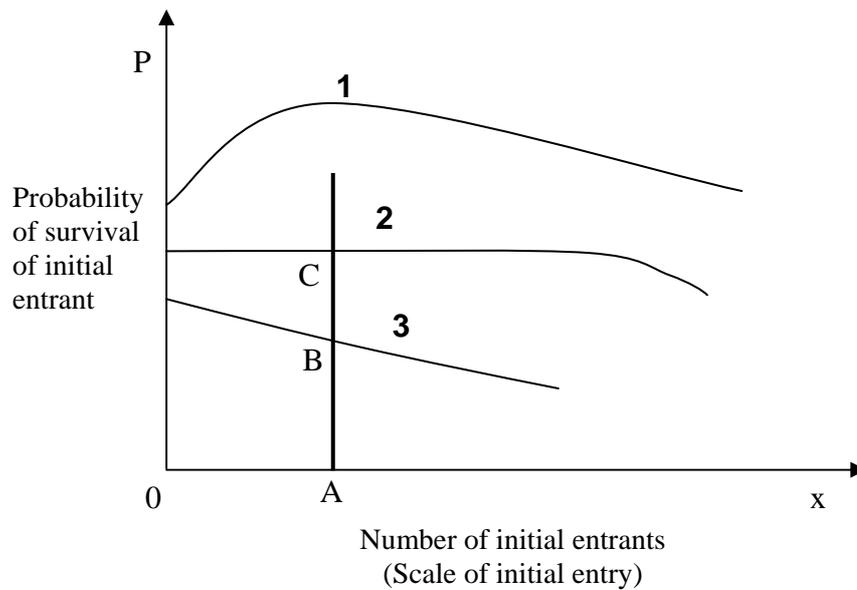


Figure 6. Some alternative possible probability of survival curves as a function of the scale of initial entry to a new market.

In Figure 6, 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 .

Note that 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 5. It may also be that the types of relationships

illustrated by Figure 6 apply to the population of some species and that their relevance varies with factors having parallels with those in economic models.

7. Conclusion

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 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. This lesson has yet to be learnt by some economists (cf. Grabher and Stark, 1997). Furthermore, the comparisons have highlighted the importance of diversity in population for sustainability or stability in both competition 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 it seems to be a relationship involving prospects for reproduction rather than for market or resource development.

References

- Allee, W. C. (1931) *Animal Aggregations: A Study in General Sociology*, University of Chicago Press, Chicago.
- Arthur, W. (1987) *The Niche in Competition and Evolution*, John Wiley, Chichester, UK.
- Begon, M. and Mortimer, M. (1986) *Population Ecology: A Unified Study of Animals and Plants*, 2nd edition, Blackwell Science, Oxford.
- Darwin, C. (1882) *The Origin of Species by Means of Natural Selection*, Murray, London.
- Dawkins, M. S. (1986) *Unravelling Animal Behaviour*, Longman, London.
- Eldredge, N. (1997) "Evolution in the Marketplace", *Structural Change and Economic Dynamics*, **8**, 385-395.
- Fujii, K. and Toquenaga, Y. (1993) "Mode of Competition and Interspecific Competition Outcomes". Pp.178-198 in H. Kawanabe, J. E. Cohen and K. Iwasaki (1993) *Mutualism and Community Organization: Behavioural, Theoretical and Food-Web Approaches*, Oxford University Press, Oxford.
- Gould, S. J. (1989) *Wonderful Life: The Burgess Shale and the Nature of History*, Norton, New York.
- Gould, S. J. (1990) *The Individuals in Darwin's World*, Edinburgh University Press, Edinburgh.
- Gould, S. J. and Eldredge, N. (1977) "Punctuated Equilibrium: The Temper or the Mode of Evolution Reconsidered", *Palaeobiology*, **3**, 114-151.
- Grabher, G. and Stark, D. (1997) "Organizing Diversity's Evolutionary Theory, Network Analyses and Postsocialism", *Regional Studies*, **31**(5), 533-544.
- Grant, V. (1991) *The Evolutionary Process A Critical Study of Evolutionary Theory*, 2nd edition, Columbia University Press, New York.
- Grover, J. P. (1997) *Resource Competition*, Chapman and Hall, London.
- Hannon, B. (1997) "The Use of Analogy in Biology and Economics. From Biology to Economics, and Back", *Structural Change and Economic Dynamics*, **8**, 471-488.
- Hartley, K. and Tisdell, C. (1981) *Micro-Economic Policy*, John Wiley, Chichester, UK.
- Hemelrijk, C. R. (1999) "An Individual-oriented Model of the Emergence of Despotic and Egalitarian Societies", *Proceedings of the Royal Society London*, 266, 17, 361-369.
- Hicks, J. (1939) *Value and Capital*, 2nd edition, Clarendon Press, Oxford.
- Hirshleifer, J. (1977) "Economics from a Biological Viewpoint", *The Journal of Law and Economics*, **20**, 1-52.
- Hotelling, H. (1929) "Stability in Competition", *Economic Journal*, **39**, 41-57.

- Kaldor, N. (1977) “Equilibrium Theory and Growth Theory”. Pp.273-291 in M. J. Boskin (ed.) *Economics and Human Welfare*, Academic Press, New York.
- Malthus, T. R. (1798) *An Essay on the Principle of Population as it Effects the Future Improvement of Mankind*, J. Johnson, London.
- Marshall, A. (1898) *Principles of Economics*, 4th edition, Macmillan, London.
- Marx, K. (1954) *Capital*, Foreign Languages Publishing House, Moscow. Translation of the 3rd German edition.
- Nelson, R. (1987) *Understanding Technical Change as an Evolutionary Process*, North-Holland, Amsterdam.
- Rapport, D. J. and Turner, J. E. (1977) “Economic Models in Ecology”, *Science*, **195**, 367-373.
- Ricardo, D. (1817) *Principles of Political Economy and Taxation*, Murray, London.
- Ricklefs, R. E. (1993) *The Economy of Nature*, W. H. Freeman, New York.
- Schumpeter, J. (1942) *Capitalism, Socialism and Democracy*, 2nd edition, Harper Brothers, New York.
- Scitovsky, T. (1976) *The Joyless Economy*, Oxford University Press, Oxford.
- Steindl, J. (1965) *Random Processes and the Growth of Firms: A Study of the Pareto Law*, Griffin, London.
- Stigler, G. J. (1987) “Competition”. In J. Eatwell, M. Milgate and P. Newman (eds.) *The New Palgrave*, Macmillan, London.
- Svizzero, S. And Tisdell, C. (2001) “Concepts of Competition in Theory and Practice”. *Revista Internazionale di Scienze Economiche e Commerciali*, **48**(2), 145-162.
- Tisdell, C. A. (1985) “Conceptual Issues in the Measurement of Economic and Productive Efficiencies”, *South African Journal Economics*, **53**, 55-66.
- Tisdell, C. A. (1996) *Bounded Rationality and Economic Evolution*, Edward Elgar, Cheltenham, UK.
- Tisdell, C. A. (1999a) *Biodiversity, Conservation and Sustainable Development*, Edward Elgar, Cheltenham, UK.
- Tisdell, C. A. (1999b) “Diversity and Economic Evolution”, *Contemporary Economic Policy*, **17**, 156-165.
- Tisdell, C. A. (2001) “Externalities, Thresholds and the Marketing of New Aquacultural Products: Theory and Examples” *Economic Theory, Applications and Issues*, Working Paper No.1, Department of Economics, University of Queensland, Brisbane 4072.

- Tisdell, C. A. and Seidl, I. (2001) "Niches and Economic Competition: Implications for Economic Efficiency, Growth and Diversity", *Economic theory, Applications and Issues*, Working Paper No.8, School of Economics, The University of Queensland.
- Tse, K. (1985) *Marks & Spencer: Anatomy of Britain's Most Efficiently Managed Company*, Pergamon Press, Oxford.
- Tullock, G. (1971) "The Coal Tit as a Careful Shopper", *American Naturalist*, **105**, 77-79.
- Worster, D. (1985) *Nature's Economy: A History of Ecological Ideas*, Cambridge University Press, Cambridge, UK.

PREVIOUS WORKING PAPERS IN THE SERIES

ECONOMICS, ECOLOGY AND THE ENVIRONMENT

1. Governance, Property Rights and Sustainable Resource Use: Analysis with Indian Ocean Rim Examples by Clem Tisdell and Kartik Roy, November 1996.
2. Protection of the Environment in Transitional Economies: Strategies and Practices by Clem Tisdell, November 1996.
3. Good Governance in Sustainable Development: The Impact of Institutions by K.C.Roy and C.A.Tisdell, November 1996.
4. Sustainability Issues and Socio-Economic Change in the Jingpo Communities of China: Governance, Culture and Land Rights by Ren Zhuge and Clem Tisdell, November 1996.
5. Sustainable Development and Environmental Conservation: Major Regional Issues with Asian Illustrations by Clem Tisdell, November 1996.
6. Integrated Regional Environmental Studies: The Role of Environmental Economics by Clem Tisdell, December 1996.
7. Poverty and Its Alleviation in Yunnan Province China: Sources, Policies and Solutions by Ren Zhuge and Clem Tisdell, December 1996.
8. Deforestation and Capital Accumulation: Lessons from the Upper Kerinci Region, Indonesia by Dradjad H. Wibowo, Clement a. Tisdell and R. Neil Byron, January 1997.
9. Sectoral Change, Urbanisation and South Asia's Environment in Global Context by Clem Tisdell, April 1997.
10. China's Environmental Problems with Particular Attention to its Energy Supply and Air Quality by Clem Tisdell, April 1997.
11. Weak and Strong Conditions for Sustainable Development: Clarification of concepts and their Policy Application by Clem Tisdell, April 1997.
12. Economic Policy Instruments and Environmental Sustainability: A Second Look at Marketable or Tradeable Pollution or Environmental-Use Permits by Clem Tisdell, April 1997.
13. Agricultural Sustainability in Marginal Areas: Principles, Policies and Examples from Asia by Clem Tisdell, April 1997.
14. Impact on the Poor of Changing Rural Environments and Technologies: Evidence from India and Bangladesh by Clem Tisdell, May 1997.
15. Tourism Economics and its Application to Regional Development by Clem Tisdell, May 1997.
16. Brunei's Quest for Sustainable Development: Diversification and Other Strategies by Clem Tisdell, August 1997.
17. A Review of Reports on Optimal Australian Dugong Populations and Proposed Action/Conservation Plans: An Economic Perspective by Clem Tisdell, October 1997.
18. Compensation for the taking of Resources Interests: Practices in Relations to the Wet Tropics and Fraser Island, General Principles and their Relevance to the Extension of Dugong Protected Areas by Clem Tisdell, October 1997.
19. Deforestation Mechanisms: A Survey by D.H. Wibowo and R.N. Byron, November 1997.
20. Ecotourism: Aspects of its Sustainability and Compatibility by Clem Tisdell, November 1997.

21. A Report Prepared for the Queensland Commercial Fisherman's Organisation by Gavin Ramsay, Clem Tisdell and Steve Harrison (Dept of Economics); David Pullar and Samantha Sun (Dept of Geographical Sciences and Planning) in conjunction with Ian Tibbetts (The School of Marine Science), January 1998.
22. Co-Evolutions in Asia, Markets and Globalization by Clem Tisdell, January 1998.
23. Asia's Livestock Industries: Changes and Environmental Consequences by Clem Tisdell, January 1998.
24. Socio-Economics of Pearl Culture: Industry Changes and Comparisons Focussing on Australia and French Polynesia by Clem Tisdell and Bernard Poirine, August 1998.
25. Asia's (Especially China's) Livestock Industries: Changes and Environmental Consequences by Clem Tisdell, August 1998.
26. Ecotourism: Aspects of its Sustainability and Compatibility with Conservation, Social and Other Objectives, September 1998.
27. Wider Dimensions of Tourism Economics: A Review of Impact Analyses, International Aspects, Development Issues, Sustainability and Environmental Aspects of Tourism, October 1998.
28. Basic Economics of Tourism: An Overview, November 1998.
29. Protecting the Environment in Transitional Situations, November 1998.
30. Australian Environmental Issues: An Overview by Clem Tisdell, December 1998.
31. Trends and Developments in India's Livestock Industries by Clem Tisdell and Jyothi Gali, February 1999.
32. Sea Turtles as a Non-Consumptive Tourism Resource in Australia by Clevo Wilson and Clem Tisdell, August 1999.
33. Transitional Economics and Economics Globalization: Social and Environmental Consequences by Clem Tisdell, August 1999.
34. Co-evolution, Agricultural Practices and Sustainability: Some Major Social and Ecological Issues by Clem Tisdell, August, 1999.
35. Technology Transfer from Publicly Funded Research for improved Water Management: Analysis and Australian Examples by Clem Tisdell, August 1999.
36. Safety and Socio-Economic Issues Raised by Modern Biotechnology by Dayuan Xue and Clem Tisdell, August 1999.
37. Valuing Ecological Functions of Biodiversity in Changbaishan Mountain Biosphere Reserve in Northeast China by Dayuan Xue and Clem Tisdell, March 2000.
38. Neglected Features of the Safe Minimum Standard: Socio-economics and Institutional Dimension by Irmi Seidl and Clem Tisdell, March 2000.
39. Free Trade, Globalisation, the Environment and Sustainability: Major Issues and the Position of WTO by Clem Tisdell, March 2000.
40. Globalisation and the WTO: Attitudes Expressed by Pressure Groups and by Less Developed Countries by Clem Tisdell, May 2000.
41. Sustainability: The Economic Bottom Line by Clem Tisdell, May 2000.
42. Trade and Environment: Evidence from China's Manufacturing Sector by Joseph C. H. Chai, June 2000.
43. Trends and Development in India's Livestock Industry by Clem Tisdell and Jyothi Gali, August 2000.
44. Tourism and Conservation of Sea Turtles by Clem Tisdell and Clevo Wilson, August 2000.
45. Developing Ecotourism for the Survival of Sea Turtles by Clem Tisdell and Clevo Wilson, August 2000.
46. Globalisation, WTO and Sustainable Development by Clem Tisdell, August 2000.

47. Environmental Impact of China's Accession to WTO in the Manufacturing Sector by Joseph Chai, August 2000.
48. Effects of Cartagena Biosafety Protocol on Trade in GMOs, WTO Implications, and Consequences for China (English version) by Dayuan Xue and Clem Tisdell, August 2000.
49. Effects of Cartagena Biosafety Protocol on Trade in GMOs, WTO Implications, and Consequences for China (Chinese version) by Dayuan Xue and Clem Tisdell, August 2000.
50. The Winnipeg Principles, WTO and Sustainable Development: Proposed Policies for Reconciling Trade and the Environment by Clem Tisdell, September 2000.
51. Resources Management within Nature Reserves in China by Dayuan Xue, October 2000.
52. Economics, Educational and Conservation Benefits of Sea Turtle Based Ecotourism: A Study Focused on Mon Repos by Clem Tisdell and Clevo Wilson, October 2000.
53. Why Farmers Continue to use Pesticides despite Environmental, Health and Sustainability Costs by Clevo Wilson and Clem Tisdell, November 2000.
54. Wildlife-based Tourism and Increased Tourist Support for Nature Conservation Financially and Otherwise: Evidence from Sea Turtle Ecotourism at Mon Repos by Clem Tisdell and Clevo Wilson, November 2000.
55. A Study of the Impact of Ecotourism on Environmental Education and Conservation: The Case of Turtle Watching at an Australian Site by Clem Tisdell and Clevo Wilson, December 2000.
56. Environmental Regulations of Land-use and Public Compensation: Principles with Swiss and Australian Examples by Irmi Seidl, Clem Tisdell and Steve Harrison.
57. Analysis of Property Values, Local Government Finances and Reservation of Land for National Parks and Similar Purposes by Clem Tisdell and Leonie Pearson, March 2001.
58. Alternative Specifications and Extensions of the Economic Threshold Concept and the Control of Livestock Pests by Rex Davis and Clem Tisdell, May 2001.
59. Conserving Asian Elephants: Economic Issues Illustrated by Sri Lankan Concerns by Ranjith Bandara and Clem Tisdell, June 2001.
60. World Heritage Listing of Australian Natural Sites: Tourism Stimulus and its Economic Value by Clem Tisdell and Clevo Wilson, September 2001.
61. Aquaculture, Environmental Spillovers and Sustainable Development: Links and Policy Choices by Clem Tisdell, October 2001.