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## ***Biodiversity Conservation in Managed Landscapes***

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## 1.0 Introduction

Biodiversity conservation has emerged as one of the most important and controversial global environmental issues in recent years [UNCED]. First, it has been suggested that we are on the verge of mass extinctions, the like of which has not been observed in the fossil record [Wilson, 1985]. Second, it is argued that biodiversity loss matters because it is of fundamental importance to human society. It provides food, shelter, fuel, supports recreation and tourism and is thought to play an important part in global life support and in the functioning of ecosystems [Raven *et al.*, 1992; Lindberg, 1991; Brown *et al.*, 1994].

A decline in habitat is thought to be one of the most significant causes of the loss in terrestrial biodiversity [Wilson, 1998]. A large proportion of the earth's fertile land has been converted into managed agricultural, forest and urban landscape. Recent estimates by the FAO [2004] indicate that some 38% of land globally is now utilised for agriculture. One solution proposed by ecologists is to expand reserves and protected areas. However there are a number of problems with this approach: protected areas cover a limited area – approximately 11% of the earth's surface [WRI, 2005]; protected areas generally exclude economic activities and they can impose costs on land managers and prevent future economic opportunities from taking place. Consequently, it is unlikely that the proportion of land allocated to protected areas will be sufficient to maintain all biodiversity.

In recent years a number of studies indicate that biodiversity conservation must focus on managed human dominated ecosystems [Miller, 1996, Reid, 1996; Daily *et al.*, 2001; Rosenzweig, 2003; Polasky *et al.*, 2005]. Economically valuable managed landscapes do not necessarily have to exclude biodiversity conservation goals. A wide range of species occur in the presence of human activities and much of the world's biodiversity is found in human dominated ecosystems [Pimmental *et al.*, 1992]. Instead of threatening biodiversity, many managed systems may actually enhance biodiversity because of, rather than in spite of, the day to day management activities carried out by land managers. Indeed the phenomenon of land abandonment has become a subject of major concern in many countries because it results in the loss of biodiversity. It is also thought that land managers may conserve biodiversity because it supports the productivity and resilience of the ecosystems they manage and there is now a significant literature on the functional and ecosystem service values associated with biodiversity [Ellis and Fisher, 1987; Daily, 1997; Barbier, 2000; Daily *et al.*, 2000].

However, the intensity and mode of disturbance clearly play an important part in the management of ecosystems. Heavily disturbed agricultural and forest ecosystems in many parts of the world are threatened by human intervention which has resulted in a loss of biodiversity and resilience. Clearly it is important to distinguish between managed landscapes which undergo disturbance in which biodiversity appears to be thriving and those in which it is threatened. In this chapter we explore the relationship between human induced disturbance and biodiversity. We also consider the relationship between disturbance regime and the properties of a managed ecosystem – its productivity, resilience, and stability.

All too frequently the application of “good science” is not in itself sufficient to guarantee desirable environmental outcomes with respect to biodiversity conservation. This also requires an understanding of socioeconomic and policy considerations: how

markets allocate scarce resources, how they influence decisions taken by land managers and why they frequently fail to protect biodiversity and other non-market values. To a degree, most land managers are affected by the market. Thus the chapter also explores the economic linkages between markets and natural resources and to exploiting the powerful creative forces of the market, in a manner which conserves biodiversity whilst also providing useful marketable goods and services. Finally the chapter concludes with some policy recommendations on making markets account for the benefits of biodiversity conservation in managed landscapes. We begin by distinguishing between *genetic* and *functional* diversity.

## 2.0 Genetic and functional diversity in managed landscapes

Several definitions have been proposed to capture the multifaceted nature of biodiversity (ecosystems, species, and genes). This is acknowledged in the definition developed in the convention on biodiversity as follows: '*Biological diversity*' means the variability among living organisms from all sources, including inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and among ecosystems [UNEP, 1995].<sup>1</sup>

A distinction is made in the literature between genetic diversity and functional diversity. Genetic diversity usually refers to the genetic variation that exists within a species (the *gene pool*). Genes are the fundamental unit of biodiversity and the ultimate source of all variation among all animal and plant species [Dobzhansky, 1970; Soulé and Wilcox, 1980]. Genetic diversity has been proposed as the basis on which to make conservation decisions using the evolutionary distinctiveness of taxa when assigning them priorities for preservation [Vane-Wright *et al.*, 1991; Crozier, 1992; Solow *et al.*, 1993; Weitzman, 1998]. Here, the relative ecological value is based on how far away species are from one another genetically and an objective value is assigned to the taxonomic distinctiveness or degree of 'independent evolutionary history' (IEH) that is vested in a species [Vane-Wright *et al.*, 1991].

Conservation organisations frequently employ descriptions and measures of ecosystem diversity based on genetic diversity and they tend to place great emphasis on species and their populations [IUCN, 1988]. Although considerable sums have been allocated towards the conservation of species preservation, there is frequently a bias towards charismatic species, large birds or mammals that are very familiar to the public. Conservation groups and professional conservationists often exploit certain species and ecosystems to further their own conservation goals. Conservationists have called the charismatic species that win the hearts of the general public *flagship species*. This may be at the expense of less well known species that may be critical for the functioning of ecosystems [Metrick and Weitzman, 1994].

Understanding the value of biodiversity to land managers requires a different perspective which is linked to the functional value of biodiversity. How then does functional diversity differ from genetic diversity and if so, why do these differences matter to managers? First, genes are after all just chemicals which have no value in and of themselves. Instead, genes have value in what they do – control the structure and function of life, instead of what they are. Measures of genetic distance may not capture the relative values of species such as the complex functional relationships embodied in ecosystems. Two species might be very similar with respect to genetic distance but they may perform very different functions within the ecosystem. One might be a keystone species which is vital to the wellbeing of the managed ecosystem whilst the other is "functionally redundant". Species diversity is relevant to land

managers because some species appear to play a more important functional role than others. An individual who is evaluating a species in terms of its functional role would be more sensitive to a change in the ecosystems's productivity than would a person focussing on biodiversity. A person assessing an ecosystem from an ecosystem function perspective would be more likely to focus on key species and processes and might overlook the disappearance of a rare species. There is greater emphasis on the biological integrity of the system than simply ensuring that all the biotic elements are present.

Functional diversity refers to the characteristics of ecosystems and includes ecosystem complexity at different levels of organisation such as trophic levels [Cousins, 1991]. This approach uses trophic-level analysis to relate species diversity to functional ecosystem parameters such as food web structure or the transfer of energy, water and chemicals between different trophic levels. Functional diversity can be interpreted as the number of species required for a given ecological process.

In managed ecosystems although every species may have a particular role, it does not follow that these roles are of equal importance. Ecologists acknowledge that some species have a greater ecological impact than one might expect from their abundance or biomass and these have been referred to as keystone species (Power et al., 1996). Some ecosystem studies indicate that only a small number of the numerous species found in ecosystems perform key functions or so called keystone roles and that most species perform a perfunctory role [Holling, 1992]. Beavers have been shown to have a profound impact on streams forests and wetlands through dam construction.

Many species may play keystone roles which involve interdependencies with other species [Daily *et al.*, 1993]. The elimination of any single component of an ecosystem could lead to an unanticipated unravelling of community structure and to local extinctions of some species. Bird dispersers such as the blackcap (*Sylvia atricapilla*) interact with shrub species to influence floristic diversity, spatial patterns of vegetation development and plant dynamics in patchy Mediterranean vegetation in southern France [Debussche and Isenmann, 1994]. Seeds deposited by blackcaps underneath pioneer shrubs (which have positive 'nurse' effects on other plants) were more likely to survive than in the open field and birds may actually trigger dynamic successional processes initiated by pioneer woody perennials in Mediterranean grasslands and shrublands.

The 'keystone role' of a species may also depend on whether a number of other species can assume its functional role within the ecosystem [Schindler *et al.*, 1989]. Functional redundancy is known to occur if other species can perform similar roles [Hutchinson, 1961; Walker, 1992]. A saturating relationship can be expected between the number of species and ecosystem function (see Figure 1) because the more species there are in an ecosystem, the more likely it is that a given species that is deleted or added will be ecologically similar to other species present [Vitousek and Hooper, 1993]. Although there is evidence that the deletion of some species has very little effect on ecosystem functioning, in many diverse tropical forests there are so many rare species that collectively they may have an important impact on the ecosystem. Here, top predators in ecosystems are relatively scarce because they are large in size and at the top of the food chain but may nevertheless be important in terms of ecosystem structure.

INSERT FIGURE 1 ABOUT HERE

Most research has focussed on which species are important here and now. However millions of species have not even been identified let alone evaluated for their potential values to humans. There are difficulties in predicting which species will be important in the future since the present functions performed by a species may provide no clues as to its role when environmental conditions change [Main, 1982; Lovejoy, 1988]. Tree species that colonise gaps in tropical forests and species that require fire to enhance germination provide such examples. The population of *Cactoblastis cactorum*, which is relatively rare in Australia today, would not provide an accurate description of its importance in controlling *Opuntia* in that country in previous decades. However, studies on ecosystem function may reveal clues as to the most sensitive components of food webs, and nutrient and energy flows. Research reveals that the most sensitive components of ecosystems are those in which the number of species performing a particular function is thought to be very small [Schindler, 1990].

Most ecologists recognise that some species play a more important functional role than others. But what does this imply in terms of the properties of an ecosystem? Land managers are principally concerned with ecosystem productivity and its variability. The next section provides a review of the relationship between biodiversity and the stability, resilience and productivity of ecosystems.

## **2.1 Importance of biodiversity in managed landscapes**

The importance of biodiversity is associated with a controversial theoretical debate amongst ecologists which began in the early 1950s: does biodiversity affect the stability of an ecosystem? Holling [1973] refers to stability as a characteristic of the individual populations of an ecosystem. For example, stability is defined as the propensity of a population to return to some kind of equilibrium following a disturbance. The stability of ecosystems may be linked to their biodiversity and it has long been hypothesised that more diverse ecosystems are more stable. A clue as to why this may be the case is illustrated by a natural disturbance that deleted some species from the ecosystem. A diverse system might be little affected by the impact because other species with similar niches could perform similar functions to the missing species. Early advocates of this theory include MacArthur [1955] who postulated that a highly diverse ecosystem would change less upon the removal or addition of a species than would an ecosystem with fewer species. Elton [1958] also suggested that less diversity resulted in less ecological stability.

However these theories were not without their critics. May [1973] challenged this argument and showed that a highly connected system (higher biodiversity) may be less stable than simpler ones and more vulnerable to disturbance because all its components closely interact and are therefore subject to the effects of perturbations. A drought that eliminates key species in a complex ecosystem, for example, will have widespread repercussions on the animals that depend on them.

More recent work [Tilman, 1996] has shown that there exists an important distinction between the properties of a community and its individual species, so although diverse ecosystems are more stable than less diverse ecosystems the populations within them can have great variability. From this perspective, what matters is the stability of the community or ecosystem not their individual populations. There is some experimental evidence to support these assertions. Tilman and Downing (1994) have shown that an ecosystem with many species is

more likely to be stable even though the populations of individual species may experience considerable fluctuations. Resilience is a further factor that refers to properties of the stability of a system.

The traditional concept of resilience is a measure of the speed of return to an equilibrium state after an ecosystem has been disturbed [Pimm, 1984; O'Neill *et al.*, 1986]. Alternative definitions have been proposed by Holling [1973]. He describes resilience as the propensity of an ecosystem to retain its functional and organisational structure following a disturbance. Expressed another way, resilience is the amount of disturbance that can be absorbed before the system changes its structure by changing the variables that control how the system behaves [Holling, 1973]. A characteristic feature of 'Holling-resilience' then is that though the system parameters (net primary production, or system growth rates, species composition) may change after disturbance, a resilient community will return quickly to equilibrium after disturbance is removed. A resilient ecosystem does not necessarily imply that all of its component populations are stable. Environmental perturbation may result in the extinction of an individual species without affecting ecosystem function or resilience. Holling [1973] distinguishes between stability as a property associated with individual populations of an ecosystem, and resilience as a property of an ecosystem.

Early work by Holling [1973] has suggested that, in general, the resilience of an ecosystem is an increasing function of the diversity of that system. There is some empirical evidence to support this view. In a series of field experiments in drought affected grasslands in Minnesota, Tilman [1996] has shown that species poor plots were less productive in terms of biomass than species rich plots (see Figure 2 slide A). He also demonstrated that species poor plots were more greatly harmed by drought (less resistant) took longer to return to pre-drought conditions (less resilient) and were less stable than species rich plots. Tilman *et al.*, [1997] also demonstrated that plots with lower functional diversity had lower productivity in biomass terms than plots with high functional diversity (see Figure 2 slide B).

INSERT FIGURE 2 ABOUT HERE

Having considered some reasons why biodiversity might be important we now provide some evidence as to why managed landscapes might be so significant in supporting biodiversity conservation goals. Managed landscapes which are vital economically in supporting human populations can also make a very important contribution to biodiversity conservation. Biodiversity can coexist alongside human activities and economically valuable managed landscapes do not necessarily have to exclude biodiversity conservation goals. Indeed, there is a significant literature which suggests that many managed systems may actually augment biodiversity and that land abandonment or a decline in management activities can actually threaten biodiversity. We now turn to some examples of how land managers from around the world manage systems which conserve biodiversity. We also consider what can happen to biodiversity when land and management activities are abandoned.

## **2.2 Landscape management and biodiversity**

In many managed landscapes good conservation practice succeeds because it is perceived to coincide with the interests of land managers whose support is vital for

conservation initiatives. Such conservation practices employed may also have been developed to avoid over-utilisation of the resource on which the human population depends. Consequently most biodiversity exists in human dominated ecosystems [Pimmental *et al.*, 1992].

First, some examples of where good conservation practice is coincidental with the interests of land managers is provided, and secondly we look at abandonment. In areas where human populations have long been an intimate part of the landscape and had much to do with its recent evolution, species may have adapted to “managed” landscapes. For example human impacts on biodiversity in the Mediterranean basin may play a positive role where current levels of biodiversity are in part maintained by continued human influence. Pignatti [1978] reports that domestic livestock and an opening up of evergreen oak forests in the Mediterranean provided new opportunities for speciation of herbaceous annual flora. For example, the dehesas of South West Spain have evolved around a distinct and long history of anthropogenic influence. These open wood pasture systems are derived from ancient Mediterranean forests and are managed to support livestock production with some accompanying arable cultivation and silviculture but are widely recognised as being of high conservation value [Baldock *et al.*, 1993; Telleria and Santos, 1995; Díaz *et al.*, 1996].

Floristic diversity is high and dehesa grasslands are remarkable for maintaining some of the most species-rich grasslands outside the tropics, with as many as 60 plant species per m<sup>2</sup> having been recorded [Marañón, 1986; Marañón, 1991]. A number of explanations have been advanced for the high floristic diversity associated with dehesas. The Mediterranean basin acts as a transitional biogeographical location. It has been suggested that its flora which comprises several different genetic elements has been enriched by historical climatic fluctuations during the Quaternary, by complexity of mountain relief and by altitudinal heterogeneity and historical human disturbance [Zohary, 1973; Whittaker, 1977; Marañón, 1986]. Defoliation by domestic herbivores and the occurrence of frequent fires in association with periodic droughts are also thought to have promoted plant diversification particularly of annual species and initiated adaptations to drought, fire and grazing [Pignatti, 1978; Naveh, 1994].

Many bird species from northern Europe overwinter in the dehesas, are reliant upon the dehesas as a food source and Telleria *et al.* [1992] provide evidence, which suggests that dehesas may support more diverse communities of passerines than neighbouring stands of high forest. Dehesa habitat supports 64% of the population of common cranes wintering in Spain (50 000-60 000 birds) which represents 70-85% of the western European population [Alonso *et al.*, 1990]. Cranes rely on acorns, the crane population is not widespread in other habitats and holm oak dehesas are therefore of great importance for this species, considered vulnerable because of their decreasing population trend [Tucker and Heath, 1994]. It is also thought that the distribution of white stork is most strongly associated with open holm oak wood pasture and it has been suggested that conversion of this habitat could lead to a decline in its populations [Carrascal *et al.*, 1993].

The bird community of western oak woods in the UK, particularly the abundance of the wood warbler (*Phylloscopus sibilatrix*), pied flycatcher (*Ficedula hypoleuca*) and redstart has long been recognised as unique [Hope-Jones, 1972], and some grazing may help to create the open conditions in the understorey and field layer favoured by these species [Stowe, 1987].



Some studies which focus on grazing even report that subspecies of grasses may develop according to the specific ecological conditions that occur in a grazed or mowed sward [Reinhammar, 1995].

The development of Machairs is also thought to be strongly associated with agriculture and human activity, particularly fire and grazing [Mate, 1992; Edwards, *et al.*, 2005]. Machairs, which are priority habitats under the European Habitats Directive, are unique ecosystems confined, in the northern hemisphere, primarily to west and north-west coasts of Ireland and Scotland. Machairs are priority habitats because of the high plant species richness which contain elements of calcareous grassland and sand dune plant communities. We now turn to the issue of abandonment.

Londo [1990] reports that in the absence of management semi-natural grassland communities revert by processes of natural succession to natural woodland and forest and the diversity of herbaceous species falls. Many traditional extensive farming practices have been shown to maintain plant and animal diversity [González Bernáldez, 1991; Naveh, 1994], and where these activities cease, susceptibility to disturbances, especially fire, can be increased [Moreno, 1989]. Fire in turn can have a negative effect on biodiversity [Faraco *et al.*, 1993]. Landscape homogenization can also result from the abandonment of agricultural/pastoral land [Fernandez-Alés *et al.*, 1992]. Without human management diverse plant communities in the Mediterranean basin, for example, become overgrown, and displaced by relatively few, shrubby unproductive species. Livestock may play a positive role in influencing the system.

Bokdam and Gleichman [2000] have suggested that abandonment is a major threat to traditional pastoral landscapes and their wildlife in Europe. They report that increased labour costs have undermined traditional herding systems, which are being replaced by free-ranging grazing systems leading to a decline in species rich open heathland. The management of Mediterranean woodland has become an important issue in many areas because of the abandonment of large areas that were previously exploited by grazing. In many cases impenetrable thickets have developed with continuous accumulation of fuel leading to catastrophic wildfires. Valderrábano and Torrano [2000] evaluate goats as a potential management tool for controlling encroachment of *Genista scorpius* in black pine stands in the Spanish Pyrenees. They report that as a consequence of goat browsing and thinning, dense woodland was opened up and desirable tree growth and development was stimulated.

The relationship between habitat characteristics, weather and spatial variation in animal behaviour was investigated by De Miguel *et al.* [1997]. They suggest that shrub areas provide shelter and represent an important browse resource during winter and that this leads to the occurrence of a diversified landscape with different successional stages (from pastures to clear and dense woodlands) that occur in close proximity which in turn leads to high levels of flora and fauna.

Clearly there is evidence to suggest that biodiversity can coexist in landscapes of economic importance but can land managers from around the world actually use biodiversity to support the productive process? This is the subject of the next section which considers how land managers may conserve biodiversity because it supports the productivity, stability and resilience of the ecosystems they manage.

### **2.3 Landscape management and ecosystem properties**

Biodiversity may be coincident with certain production goals such as improved agricultural productivity, under highly variable environmental and socioeconomic

conditions. For example pastoralists in Africa deliberately maintain as many as a dozen breeds of camel in the Sudan because they are able to exploit the vegetation of extreme environments, including deserts and other uncultivated land. The loss of these hardy animal breeds therefore means a reduction in the area of human habitat [Köhler-Rollefson, 1993].

In dehesa systems good conservation practices that promote biodiversity have arisen because local farmers recognise that a diverse system helps reduce variation in productivity from year to year. Local farmers do not necessarily have biodiversity conservation goals in mind as a management aim. Nevertheless, biodiversity coincides with certain production goals such as improved stability of production under unpredictable environmental conditions. Large differences in climatic, geological and topographical gradients contribute to a considerable degree of variation in productivity across the regional landscape. Climatic factors are instrumental in dictating plant and animal dynamics and productivity. Consequently, a long history of anthropogenic influence has led to the evolution of a high level of management and functional complexity as a means of ensuring stability. Attempts to develop an understanding of the relationship between management practices and environmental variability have prompted research effort into the interactions between the individual components that comprise this complex ecosystem including tree, herbaceous and shrub, and livestock components.

For example, holm oak is managed by farmers because it favours highly productive perennial herbaceous species through improved retention of soil moisture, the modification of microclimate, improved nutrient availability and improved soil properties [Marañon, 1986; Joffre and Rambal, 1993]. Marañon [1986] has observed a much higher phenological diversity in dehesa systems that include a tree component (see Figure 3).

INSERT FIGURE 3 ABOUT HERE

Groups of perennial species may be significant in maintaining productivity because they are able to utilise nutrients and moisture more effectively. These include *Agrostis castellana*, *Dactylis glomerata*, *Lolium perenne* and *Phalaris aquatica* which were all found more frequently beneath tree canopies than in the open field [Montoya and Meson, 1982; Joffre, *et al.*, 1988]. Joffre *et al.* [1988] hypothesised that differences in nitrogen utilisation occurred between annual and perennial species and that the efficiency of nitrogen utilisation by herbaceous species was affected by the tree canopy. They report higher nitrogen mineralisation in grasslands with perennials compared to annuals and greater nitrogen mineralisation below the tree canopy.

Farmers have evolved complex farming systems specifically to be able to exploit resources. Diverse multispecies herbivore systems such as game ranches common to the savannas of Africa may include up to 20 different herbivore species [Cumming, 1993]. Managers exploit differences in grazing habits that can lead to a degree of complementarity in the use of forage resources where the total productivity of the range is seen to increase. Short grass (concentrate) grazers benefit from the modification of sward structure brought about by long grass (bulk) grazers, so that sheep generally perform better when grazed in mixed systems than when grazed alone

[Nolan, and Connolly, 1977]. This is usually only the case when large quantities of unpalatable poor quality fodder are available. McNaughton [1984] reports that in the Serengeti, the larger bulk grazers consume long grass and these are then followed by smaller ungulates that create 'grazing lawns'. These lawns are sources of high quality forage and so herbivores are seen to influence the quality and productivity of the grazing resource. Mixed species grazing systems may also be preferred to single species systems because they improve yields and do not overexploit productive herbaceous species. It has been reported that sheep and cattle may affect the plant community in different ways. Bedell [1973] has shown that sheep can reduce the abundance of clover in a sward but they also increase the amount of *Poa trivialis* [Conway *et al.*, 1972]. In contrast, a high proportion of cattle have been shown to increase the amount of clover relative to grass. In this manner combined cattle and sheep grazing systems may be more productive than single species systems.

Examples of management systems that attempt to encourage diversity in herbivore populations of rangelands to enhance resilience include replacing monocultures of domestic livestock with multispecies game systems and combined cattle/game ranches such as the campfire programme in Zimbabwe [Cumming, 1993]. Scholes and Walker [1993] have suggested that events such as fire and herbivory play an important role in maintaining the diversity and resilience of such systems. Here, the reduction of such perturbations is thought to reduce landscape diversity and the ability of the system to survive similar shocks in the future.

In savannas [Walker *et al.*, 1981] and *Agrostis-festuca* grassland in Britain [Hulme *et al.*, 1999] groups of grass species are important in maintaining the systems productivity. Similarly, insectivorous bird species are considered to be instrumental in controlling outbreaks of forest insect pests in boreal and deciduous forests in North America and Europe [Morris *et al.*, 1958; Tinbergen, 1960; Campbell and Sloan, 1976; Holmes *et al.*, 1979; Takekawa *et al.*, 1982; Holling, 1988; Maquis and Whelan, 1994].

Key plant species may strongly influence successional processes through the provision of so-called *nurse effects*. Several studies have observed a greater number of seedlings beneath mature trees compared to more open areas [Griffin, 1971; Borchert *et al.*, 1989; Espelta *et al.*, 1995]. Similarly, shrub species may influence seedling establishment, acorn consumption and the extent of browsing by herbivores [Morgan, 1991; Callaway, 1992; Herrera, 1995].

Despite the importance of biodiversity in contributing toward ecological services many ecosystems are undergoing profound change due to economic development. Heavily disturbed agricultural ecosystems in many parts of the world are threatened by human intervention which has resulted in a loss of biodiversity, productivity and resilience. Clearly, land managers frequently need to know how biodiversity is affected by the level and intensity of management. The significance of human induced disturbance and environmental perturbation is the subject of the next section.

### **3.0 Ecosystem disturbance and biodiversity**

Considerable insight into an understanding of conservation biology has been gained through a knowledge of the effects of human induced disturbance on biodiversity [Wilson and Johns, 1982]. There is a substantial literature which shows that human induced disturbance and habitat degradation can result in a decline in biodiversity and species extinction.

Highly intensive agricultural practices that reduce spatial complexity leading to homogenisation of the landscape may lead to biodiversity loss. The decline in most of Europe's SPECS (Species of European Conservation Concern) has been linked to land use and management changes with agricultural intensification being cited as the most significant threat to bird populations [Tucker *et al.* 1994]. Arable farming systems in parts of Europe are thought to have played a part in the decline of many species. For example, as a consequence of changing conditions in agricultural fields in Britain many bird species have undergone significant population declines. Fuller *et al.* [1991] report that many British farmland birds have declined dramatically over the last 3 decades as agricultural land use has altered, hedgerows declined, and farms have developed to form larger contiguous areas.

Also, studies of the avifauna of fragmented forests have shown that some species are absent or infrequent in very isolated sites and that smaller woodland size gives rise to less bird species diversity [Moore and Hooper, 1975; Lynch and Whigham, 1984; Opdam *et al.*, 1985; Ford, 1987; van Dorp and Opdam, 1987].

In Galicia, Spain, Hernandez and Silva-Pando [1996] report a decline in the abundance and diversity of shrub species after a period of 3 years' grazing by red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*).

High levels of disturbance are also thought to affect ecosystem productivity. The study of long-term grazing-vegetation interactions using palaeovegetation data in Ireland show that reasonably high populations of giant Irish deer imposed a high pressure on shrubby vegetation and had a profound effect on the change in vegetation communities from Juniper scrub to grassland in Ireland during the Late-glacial interstadial (11 000 – 12 000 BP) [Bradshaw and Mitchell, 1999].

Data from censuses of domestic animals collected for tax purposes as well as from hunting statistics have been combined with palynological reconstructions of vegetation. For example, hunting statistics for moose and roe deer in Sweden suggest dramatic, recent population increases that have probably contributed to the decline of deciduous tree species [Ahlén, 1975].

Peterken and Tubbs [1965] related fluctuating grazing regimes in the New Forest, England (horses, pigs and cattle) to waves of regeneration based on the age structure of existing trees. In Poland pollen data has enabled reconstructions of vegetation successions [Mitchell and Cole, 1998]. This has been combined with data on herbivore densities for forests in Eastern Poland over the last 200 years [Faliński, 1986] and shows that the proportion of conifers, principally *Picea abies*, increased dramatically at the expense of broadleaved species during the period of intensive grazing. Tree regeneration in the subsequent low-intensity grazing period was dominated by broadleaved taxa, initially *Betula*, *Populus* and *Caprinus* and, subsequently, *Tilia* and *Quercus*.

Jane [1994] considered the long-term effects of browsing by red deer (*Cervus elaphus*) on Mountain beech (*Nothofagus solandri*) in New Zealand and concluded that the impact of high deer densities on vegetation remains and can persist for many decades. She suggests that in critical high altitude areas, large reductions in deer densities were required to trigger the regeneration necessary for tree replacement.

Jorritsma *et al.* [1999] used a dynamic simulation model FORGRA to evaluate the impact of grazing on scots pine regeneration in the Netherlands. They showed that even low densities of ungulates could have a significant impact on forest development. Their model indicates that the presence of 1 cow per ha virtually eliminates recruitment entirely. Simulations of the model described above by Kienast *et al.* [1999] confirm these results since they also demonstrated that high browsing

pressure does reduce recruitment and does alter the forest structure considerably, leading to high rates of tree mortality and more open forests. The spatial model developed by Weber *et al.* [1998] was used to determine the effects of grazing intensity and grazing heterogeneity applied to the southern Kalahari and shows that high levels of grazing lead to shrub invasion. Jeltsch *et al.* [1997] also reported that when grazing intensity reaches a critical level, shrub cover increases, drastically lowering the productivity of the range.

Intensive levels of herbivory may reduce plant productivity, survival, reproduction and growth [Fay and Hartnett, 1991; Fox and Morrow, 1992; Relva and Veblen, 1998]. In a long-term experiment to evaluate the impact of domestic livestock on tree species Hester *et al.* [1996] manipulated sheep stocking density and season in an upland broadleaved woodland in Cumbria, UK. They observed that growth and survival to the sapling stage was negatively correlated with grazing intensity and suggest that apart from plots grazed at the lowest animal densities only a small proportion of saplings will attain canopy height. Other studies from around the world implicate browsing by domestic livestock as a cause of poor tree species recruitment [Kingery and Graham, 1991]. Van Hees *et al.* [1996] employed an enclosure to determine the impact of roe (*Capreolus capreolus*) and red deer (*Cervus elaphus*) on beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*), and silver birch (*Betula pendula*) in the Netherlands. They showed that browsing reduced sapling abundance, height, and above ground biomass of all 3 species. Some studies in the UK report a high number of seedlings within fenced enclosures compared to unfenced areas [Sykes and Horrill, 1979; Marrs and Welch, 1991; Staines, 1995]. Historical records have also been used which suggest that deer may prevent natural regeneration of scots pine (*Pinus sylvestris*) in the UK. With respect to stocking densities, studies investigating the impact of ungulates foraging on upland heaths in Scotland suggest that red deer (*Cervus elaphus*) at stocking densities of >1 deer/20 ha can prevent tree regeneration [Staines *et al.*, 1995].

Persistent high levels of disturbance are also thought to affect ecosystem function, particularly where these eliminate important functional groups that affect ecosystem processes. Groups of grass species may be significant in maintaining the productivity of savanna ecosystems [Walker *et al.*, 1981]. Walker *et al.* [1981] found that persistent intensive grazing by settled peasant farmers had lower levels of productivity than moderate opportunistic grazing practices employed by nomadic pastoralists. In the former case, productive functional groups declined because herbivores showed a preference for these species whilst in the latter case these preferred species were able to persist in the sward and adapt to change and instabilities caused by grazing and drought thereby maintaining structural resilience.

Overgrazing may exacerbate the high inter-annual variation in productivity on many rangelands. Walker [1988] has observed a much higher phenological diversity in semi-arid systems not subject to heavy grazing compared to those that are intensively grazed. On lightly grazed areas he noted an even mix of early, mid and late season grasses which were able to respond to rainfall wherever it occurred in the season. Heavy grazing leads to an absence of highly palatable early season species which are replaced by later growing species [Silva, 1987]. The implication being that forage production was lower and more unstable on heavily grazed areas compared to lightly grazed land because the sward was not able to respond to early season rains. In the Serengeti, McNaughton [1985] has also shown that forage production was more stable where the number of species contributing to biomass was high compared to swards where relatively few species contributed to forage production.

Many complex ecosystems that aim to maximise heterogeneity (such as non-equilibrium systems) may be threatened by intensive grazing regimes that attempt to restrict livestock movements. This may have a negative impact on the stability and sustainability of the system. In areas where the fodder resource is widely dispersed seasonally and spatially, restrictions on stock movements by using paddocks can lead to land and vegetation degradation [Hoffman and Cowling, 1990]. Increasing the connectivity of an under-connected system may also cause the system to change to a new stable state. An example of such a change has occurred in semi-arid shrublands, where the erection of fences has restricted animal movements leading to localised feeding and degradation of vegetation and soil resources [Hoffman, 1988].

There is evidence that overgrazing may trigger the transition from one ecosystem to another for example from forest to grassland or grassland to a shrubby semi-desert [Holling, 1973; Westoby *et al.*, 1989]. This evidence suggest that state and transition models (STM) are appropriate in many rangeland situations where vegetation is best described by a set of discrete “states” and a set of discrete “transitions” between states. During a transition the system jumps to another state if a threshold is exceeded and these can be triggered by fire, rainfall or grazing and the system never rests halfway through a transition. They use a STM in eastern Australia to show how once ecological thresholds are exceeded the system shifts from a woodland with a grass understorey to a less productive shrubby state. Ecological thresholds suggest that there are limits to the ability of ecosystems to withstand environmental perturbation. If such limits are exceeded, ecosystems may shift to a less productive phase.

In some circumstances human management and spatial landscape change may undermine ecosystem processes. For example some empirical studies have demonstrated that habitat fragmentation may reduce parasitism rates on herbivorous insects at different spatial scales [Kruess and Tschardt, 1994; Roland and Taylor, 1997]. Similarly, silvicultural practices may reduce parasitism rates of spruce bark beetle (*I. typographus*) in central Sweden [Weslien and Schroeder, 1999].

Clearly persistent intensive use of resources can degrade ecosystems and impact negatively on key functional groups. However, the level and nature of disturbance appears to be an important factor. Some examples of *managed* ecosystems indicate that an element of disturbance caused by human intervention may actually enhance biodiversity. In the next section we explore the impact of low and moderate levels of disturbance on biodiversity, productivity and resilience.

### **3.1 Moderate ecosystem disturbance and biodiversity**

MacArthur and Wilson [1967] suggest that some disturbance can promote diversity because different species respond to disturbance in different ways. They first characterised species as either *r* or *K* strategists which have evolved mechanisms to optimise resources in quite different environments. The former refer to species that attempt to maximise growth in an unconstrained environment, reproduce quickly, disperse widely, and are of smaller size and shorter lifespan. On the other hand *K* strategists include species that optimise growth in a climax successional phase or a crowded environment, are highly adapted to stable equilibrium conditions, are less flexible, more vulnerable to change, are generally longer lived, and do not disperse as well. High levels of disturbance may lead to species poor habitats since they favour the persistence of competitive, opportunistic *r* species better adapted to cope with disturbance [Miller, 1982]. Conversely, undisturbed environments that do not

undergo change may support less diversity because they favour the persistence of *K* strategists. Linder *et al.* [1997] examined the effects of fire history on stand structure and plant diversity in Swedish forest reserves. They concluded that the reintroduction of fire represents an important means of disturbance that was necessary to promote diversity of flora and fauna in the area. Continued fire suppression has changed successional patterns and altered stand structure. Late successional species such as spruce dominate due to lack of fire, and pioneer species such as pine, silver birch and aspen are decreasing in number because they require fire disturbance to regenerate. This appears to accord with MacArthur and Wilson's [1967] theory where undisturbed environments may therefore support less diversity because climax species are favoured. Linder *et al.* [1997] recommend prescribed burning to ensure a relatively wide range of successional stages to promote biodiversity over the longer term.

Higher habitat diversity due to moderate disturbance can also be explained by niche relations and the manner in which species divide up limited resources for their survival [Schmida and Wilson, 1985]. They may divide up the available space (e.g. by selecting different habitats) or energy resources (e.g. by adopting different diets). Some studies serve to demonstrate that moderate levels of human activity may enhance biodiversity by opening up new niches, providing new food or protection from predators and by diversifying micro-habitats. For example structural heterogeneity is thought to be important for bird species diversity and vegetation indexes have been developed to quantify structural diversity particularly in relation to bird species [MacArthur and MacArthur, 1961; Willson, 1974; Blondel and Curvillier, 1977; Erdelen, 1984]. Several studies indicate that a decline in structural diversity [James and Wamer, 1982; Terborgh, 1985; Ratcliffe, 1993; Telleria and Carrascal, 1994] and floristic diversity [Lynch and Whigham, 1984] leads to less bird species diversity. This is confirmed by Casey and Hein [1983] and Dambach [1944] who all reported that heavily browsed woodland by deer supported fewer bird species than woodland that was not grazed (although see DeGraaf *et al.* [1991]).

Schemske and Brokaw [1981] provide empirical evidence to show that moderate disturbance in tropical forests caused by natural tree falls resulted in the greatest diversity of bird species. Clout and Gaze [1984] in New Zealand found that the highest levels of bird diversity were recorded in disturbed productive forests while undisturbed mature forests contained less bird diversity though were populated predominantly by native bird species. Sternberg *et al.* [2000] conducted a 4 year study on the response of a Mediterranean herbaceous community to grazing management in north-eastern Israel. Contrasting different grazing treatments they found that low and high grazing regimes reduced herbaceous diversity but that moderately grazed areas increased diversity.

The study of long-term grazing-vegetation interactions ( $10^2 - 10^6$  years) using palaeovegetation data permits the reconstruction of vegetation and herbivore abundance and associations. Data from Jutland in Denmark from the Holocene about 5000-7000 years ago suggests that large forest herbivores did not have a significant influence on regional forest structure [Bradshaw and Mitchell, 1999]. This is because either large predators held populations at modest levels or the diversity of grazing species held populations at stable, low populations of individual species.

Moderate levels of insect herbivory may actually increase productivity. For example, Holling [1978] carried out an experiment on the defoliation of balsam fir (*Abies balsamea*) by spruce budworm. The larvae result in the death of mature trees aged 55-60 years though young trees are unaffected. Saplings grow rapidly after

mature forest is damaged, and the forest is restored by its juvenile population. In the short term there is a shortfall in the production of timber, but over the longer term wood production remains unaffected. In fact, production rates of the juvenile forest remain above that of the mature forest because in a mature stand, most trees have passed their rapid-growth phase. Mattson and Addy [1975] reached similar conclusions in their study on the effects of forest tent caterpillars on Aspen.

French *et al.* [1997] conducted a study on the development of scots pine in the Cairngorm mountains in Scotland and found that provided grazing/browsing pressure remains at a low level recruitment is possible. Similarly Sun *et al.* [1997] evaluated the effects of cattle grazing and seedling size on the establishment of *Araucaria cunninghamii* in a silvo-pastoral system in northeast Australia. They report that grazing did not cause unacceptable mortality due to the fact that the tree has prickly needles, which prevented browsing by cattle. They recommend that grazing does not affect recruitment and can begin immediately after tree planting provided that a moderate stocking rate is used.

Modelling has shown that plant populations may be little affected by low levels of herbivory. Kienast *et al.* [1999] used a succession model – FORECE – to assess the long-term dynamics of alpine forests in central Europe. They report that moderate levels of browsing posed no threat to the long-term survival of these forests and did not alter the successional sequence of forest development.

Recent developments on the functional complexity of ecosystems show that small disturbances may actually enhance ecosystem function and increase resilience. Holling *et al.* [1986; 1994] suggest that some natural disturbances initiated by fire, wind and herbivores, are an inherent part of the internal dynamics of ecosystems and in many cases set the timing of successional cycles as depicted in Figure 4. Exploitation involves processes which lead to a rapid colonisation of an ecosystem by species during its disturbed state. Conservation refers to the slow accumulation of stored “capital” in the form of nutrients and biomass and the building of increasingly complex structures and thus the system becomes more connected and stable. The release of stored capital is triggered by disturbance in the form of fire, grazing or damage by herbivores. Resources are thereby released and made available for the next exploitative phase. The productivity and stability of the ecosystem is determined by phase 1 and 2 whereas the resilience of the system is affected by phase 3 and 4. These natural perturbations are part of ecosystem development and evolution, and seem to be crucial for maintaining ecosystem resilience and integrity [Costanza, *et al.*, 1993]. In the absence of such shocks, the system will become highly connected and this will provoke even larger perturbations that are more destructive to the ecosystem because they reduce the ability of the system to survive similar shocks in the future [Scholes and Walker, 1993].

INSERT FIGURE 4 ABOUT HERE

Some empirical studies reveal that herbivores may enhance a systems ability to resist environmental perturbation. For example, in their work on Florida Mangroves Simberloff *et al.* [1978] reported that the action of isopod and other invertebrate root borers resulted in new growth of roots at the point of attack. More extensive root systems in mangroves result in greater stability and resistance to storms and therefore benefit the plant.



Hulme *et al.* [1999] carried out a study to evaluate the effects of sheep grazing on the productivity of upland *Agrostis-festuca* grassland in Britain. The experiment controlled sheep grazing at light, heavy and moderate levels. Both low and high levels of grazing resulted in the spread of less desirable species such as *Nardus stricta* and *Molinia caerulea*. Moderate levels of grazing maintained preferred species such as *Festuca rubra*, and *Agrostis capillaris* and prevented the spread of *Nardus stricta* and *Molinia caerulea*.

Non-equilibrium rangeland systems as practised by nomadic pastoralists in parts of Africa have evolved opportunistic management regimes that employ moderate levels of grazing intensity which do not eliminate keystone elements but instead maintain the resilience of these components. Scholes and Walker [1993] have suggested that events such as fire and herbivory may play an important role in maintaining the diversity and resilience of such systems. Nutrient release following small fires supports a flush of new growth without destroying all of the old growth. Rangeland patches are affected but the forage resource remains intact. Small fires prevent the accumulation of forest biomass, which fuels very large fires that can decimate large areas of rangeland [Scholes and Walker, 1993] or whole forests [Holling *et al.*, 1994]. Such events may affect the parameters of the system and cause it to cross a threshold into an alternative state, which may alter the system's capacity to provide ecological services. For example, the Yellowstone National Park in the US employed a 'natural burn' policy of management that culminated in catastrophic forest fires.

As seen human induced perturbation on managed ecosystems is a critical factor in maintaining biodiversity. However, the application of best scientific practice by land managers may not in itself be sufficient to achieve biodiversity conservation goals. This is because markets may fail to account for the value of biodiversity to society. It is essential therefore that land managers are aware of the limitations and opportunities of the market. The next section explores the economic linkages between markets and biodiversity.

#### **4.0 Biodiversity in managed landscapes: economic issues**

As seen above, biological resources in many of the world's low intensity managed habitats represent a significant contribution to economic activity. However, many of the world's traditional low intensity managed habitats are threatened by development – a change in land use management due to the prospect of increased private returns. According to the economic theory of general equilibrium, the search for opportunities for increased private returns can ensure that resources are allocated to the highest value use available, so that economic efficiency is achieved. This result depends on a number of conditions. If these conditions are fully met, land use change motivated by private profit need not be a cause for concern. However, managed landscapes, in common with most environmental goods, have characteristics that ensure that the necessary conditions will never be fully met in practice. In general terms, this failure implies that any resulting allocation of resources is likely to be economically inefficient, meaning that it would be possible to re-allocate resources in such a way as to make (at least one member of) society 'better off'.

Some mention of the distinction between economic efficiency and equity is worthwhile at this point. Economists place great emphasis on economic efficiency but this will not necessarily result in a fair outcome. For a society to be sustainable, its welfare should not be declining over time [WCED, 1987; Pezzey, 1989]. In theory there are potentially a number of efficient time paths which are sustainable. However,

efficiency does not necessarily guarantee sustainability between say current and future generations in terms of the distribution of natural resources such as biodiversity [Perman *et al.*, 2003; Common and Perrings, 1992].

In the case of managed landscapes, the danger is that land use change guided by market signals alone may lead not to beneficial development but to loss of valuable and possibly irreplaceable resources. The necessary conditions that must hold in order for market-led development to be benign (and their absence in practice) are typically discussed under two headings. These are (i) market failure and (ii) policy failure.

#### **4.1 Causes of biodiversity loss: market and policy failure**

Market failure occurs when private decisions based on a set of prices, or lack of them, do not generate an efficient allocation of resources [Hanley, *et al.*, 1997]. With respect to biodiversity the concern is that market prices are not reliable indicators of social cost. Social cost refers to the opportunities forgone by society in committing resources in some way [Coase, 1960] and social cost in this study is taken to mean the true value that society as a whole places on natural resources. Private cost, on the other hand, refers simply to the financial cost faced by the private individual or firm undertaking the land use change, at current and expected market prices.

This divergence between private and social cost occurs because managed biodiverse landscapes generate benefits to society in addition to those that are transacted in the market system: external benefits. An absence of such external effects is one of the necessary conditions for market efficiency referred to in the previous section. Typically, the reason these benefits remain external to the market system is that they have the characteristics of public goods, in particular they are indivisible and perhaps also non-excludable, making their exchange in markets unlikely (see Table 1).

INSERT TABLE 1 ABOUT HERE

The public good nature of biodiversity creates difficulties for its valuation. These will be discussed in some detail in the sections that follow but can also be shown diagrammatically as in Figure 5. Because managed landscapes provide high levels of *unpriced* public benefits, in terms of wildlife and landscape quality, private agents will have no incentive to take account of these benefits in decisions over land use.

INSERT FIGURE 5 ABOUT HERE

Conventional economic theory seeks to cast government in the role of an objective and well-informed ‘third force’ (in addition to individuals and firms), with some ability to intervene to correct for market failures. Government or policy failure occurs when policy decisions required to correct for market failure are not implemented and fail to fully recognise, or incorporate, the values associated with environmental resources. Policy failure may also arise where government decisions themselves induce economic inefficiencies. For example, agri-environment policies, through creating incentives for farmers to expand production may result in a greater

privately optimal level of degradation than would be the case in the absence of such policies. Poorly formulated policy instruments and incentives may distort the allocation of resources unintentionally. Simpson *et al.* [1998] suggest that high stocking rates are caused by incentives to graze moorland to achieve profit maximisation, encouraged by support from the CAP. They indicate that increases in the ewe flock across the Northern Isles (in Orkney from 37 000 in 1983 to nearly 55 000 in 1992, and in Shetland from 116 000 in 1982 to 156 000 in 1993) was in response to the EU's sheep meat regime introduced in the early 1980's. The scheme offered headage payments and a variable premium in fat lamb sales. They suggest that the policy has been sufficient to increase stocking levels and hence heather utilisation rates, across the Northern Isles. McNeely [1993] suggests that in Botswana, national and European Union subsidies have led to excessive uncontrolled grazing of rangelands and degradation of grazing savanna which have affected the long-term productivity of the resource. Subsidies that aim to promote cash crops to secure export revenue may result in land degradation, soil nutrient losses, and a reduction in the resilience of ecosystems [Grainger, 1990]. Royalties in forestry can lead to excessive rates of deforestation [Repetto, 1989; Barbier, *et al.*, 1991].

The catch-all term 'market failure' is defined so as to refer to all situations where the market signals perceived by private individuals fail to coincide with social values (and fail to produce economic efficiency). However, some necessary conditions for market efficiency, which may be violated in practice, tend to be omitted from discussions of market failure, and are worth briefly mentioning here. The discussion above relates mainly to what might be called the 'complete set of markets' condition [Common, 1995].

Also important is the 'complete information' condition, requiring not only that prices be widely known, but also that they reflect the full implications of any reallocation of resources. It is clear from the discussion above that in the case of managed landscapes, such knowledge is available only in partial and uncertain form, and is not reflected in actual market prices. The effect of such uncertainty is discussed below.

The so-called 'rationality condition' may also be violated for environmental goods such as managed landscapes and associated biodiversity. The link between market efficiency and the (constrained) satisfaction of the wants of individuals and of the society of which they are members relies upon a number of assumptions about the nature of individuals' preferences. Rationality of preferences includes the ability and willingness always to make comparisons between goods. We will see below that stated preferences for environmental resources can include a refusal to do this, on the grounds that a biological resource should be preserved 'in its own right'. To the extent that individuals do not in fact have 'rational' preferences, market outcomes will tend to deviate from socially desired outcomes.

## **4.2 Valuing biodiversity**

The main point that is frequently made by environmental economists working on valuation with regards to market and policy failure is that private resource users do not attribute sufficient weight to biodiversity. Valuation, it is argued, aims to redress this imbalance and sets out to determine what weight should be given to biodiversity in the interests of society as a whole.

The literature indicates that a variety of methods have been employed to estimate wildlife values in managed landscapes. Studies on wildlife value have

focused on their *use* and *non-use* values. These values are based on an individual's willingness to pay (WTP) or willingness to accept (WTA) compensation. Gross willingness to pay might include the cost of travel, purchase of equipment to participate in the recreation activity, actual fees associated with the activity and consumer surplus. The concept of "Total Economic Value" (TEV) has been used to describe the components of value as shown in Figure 6. Use values associated with managed landscapes refer to the actual and or planned use of a service by an individual and include recreational activities such as bird watching or hunting. Use values also include the following: option value, i.e. the value of the option to guarantee use of the service by the individual in the future [Weisbrod, 1964]; quasi option value, i.e. the value of future information protected by preserving the resource now, given the expectation of future growth in knowledge relevant to the implications of development [Arrow and Fisher, 1974; Perman, *et al.*, 2003].

INSERT FIGURE 6 ABOUT HERE

More recently, empirical studies on wildlife values have placed emphasis on non-use values. These refer to situations where an individual knows a biological resource exists and will continue to exist, independently of any actual or prospective use by the individual and where that individual would feel a 'loss' if the resource were to disappear [Brown, 1990]. Existence value arises when the utility function of a consumer is enhanced by the knowledge that a certain wildlife species exists. As indicated in Figure 7 below, non-use values thus refer to situations in which individuals would like to see a biological resource preserved 'in its own right'. Non-use values include the following: *bequest value*: the value of ensuring that the resource remains intact for one's future heirs [Krutilla, 1967]; *existence value*: the value that arises from ensuring the survival of a resource [Pearce and Turner, 1990; Perman, *et al.*, 2003]. Existence value is usually assumed to embody some form of altruism, either for other human beings or for a concern for non-human entities. For example some of the literature distinguishes between philanthropic motives based on the provision of services to other people, and altruistic behaviour solely concerned with nature. The sum of all use values and non-use values is referred to as total economic value (TEV).

In the literature, two classes of use value are sometimes defined – direct use value and indirect – use value. This is illustrated in Figure 7. Direct use value is the same as that outlined above and includes, for example, harvesting timber from a forest or the use of recreation services provided by a national park. Indirect use value on the other hand refers to the life support services provided by ecosystems. These include ecosystem functions such as flood control, catchment protection, nutrient cycling and carbon sequestration. The biological diversity of managed landscapes may serve an important role in maintaining ecosystem functions and thus serve to support the productive process.

INSERT FIGURE 7 ABOUT HERE

### **4.3 Measuring biodiversity values**

Early studies on wildlife values employed revealed preference methods, such as the so-called travel cost method (TCM). This technique was first proposed for use in recreation studies and was subsequently refined and applied in empirical studies by Clawson and Knetsch [1966]. The method is based on the premise that it should be possible to infer values placed by visitors on environmental outdoor recreation services from the costs that they have incurred in order to experience these sites. Such costs include costs associated with travelling to a recreation site and the imputed value of people's time. A statistical relationship between observed visits and the cost of visiting a site is determined. This is then used to construct a demand curve from which consumer surplus can be measured. The current value of the resource and value of alternative policies affecting the resource can then be evaluated using consumer surplus calculated from the demand curves. The advantage of TCM is that the data collected involves actual consumer behaviour. Its chief disadvantage is that it does not accurately value trips for multiple purposes. TCM has been used extensively in the UK and USA for valuing the non-market benefits associated with national parks and managed landscapes including public forests [Bowes and Krutilla, 1989; Benson and Willis, 1991; Whiteman, 1991].

A second method of estimating wildlife value is a stated preference method, the contingent valuation method (CVM). This involves the construction of a hypothetical or simulated market for an environmental or wildlife resource. Contingent valuation techniques use surveys to elicit individuals' preferences for public goods by finding out what they would be willing to pay (WTP) for them, or what they would be willing to accept as compensation (so that they would not be worse off) for specified changes in them. This approach circumvents the absence of markets for public goods by presenting consumers with hypothetical markets in which they have the opportunity to purchase the good. Willingness to pay is determined either through a written questionnaire or using bidding games implemented by personal interviews. Demand curves are then constructed, and consumer surplus used as a measure of use and non-use value. The CVM has the advantage of utilizing all the structural characteristics of demand analysis. Its chief disadvantage is that respondent bias may exist, pointing out the importance of the art of questionnaire design. Despite its widespread use CVM is extremely controversial and the values derived from the technique are treated with some scepticism by many economists [van Rensburg *et al.*, 2002; Mill *et al.*, 2007]. Some go as far as to suggest that the technique should not be used as the basis for policy decisions [Hausman, 1993].

The contingent valuation method began to be used widely from the mid-1970's [Randall *et al.*, 1974; Brookshire *et al.*, 1976]. Other detailed accounts of the method can be found in Mitchell and Carson [1989], Hanley and Spash [1993], Bateman and Willis [1995], van Rensburg *et al.* [2002], and Mill *et al.* [2007]. Relatively few contingent valuation studies relate specifically to biodiversity [Diamond and Hausman, 1994; Hanneman, 1994; Portney, 1994].

### **4.4 The value of species and habitats**

Many empirical studies applied to wilderness areas indicate that the value of recreational and other non-marketed direct values derived from areas of high nature conservation value can be significant and may compare favourably with competing commercial uses of the same resource. For example, Hanley and Craig [1991] contrasted the tradeoffs implicit in permitting or prohibiting afforestation with respect to the flow country, in Northern Scotland (the largest body of blanket peat bog in the

northern hemisphere). The development would generate employment and produce timber but displace extensive populations of internationally rare breeding birds. They demonstrated that the total recreational value of the resource exceeded the benefits derived from afforestation at discount rates of 6, 4, and 3%. Similarly, Willis [1991] established that the total recreational value of the Forestry Commission estate in the UK exceeded the value of timber sales.

Garrod and Willis [1997] carried out one of the few examples of contingent ranking techniques applied specifically to biodiversity. They employed a discrete choice contingent ranking approach to estimate the general public's WTP to increase the area of Forestry Commission forests managed under 3 forest management standards designed to offer increasing levels of biodiversity at the expense of commercial timber production. This method enables relative preferences for different forest management standards to be measured at the same time as WTP to promote biodiversity. They suggest that the benefits of changing forest management to meet these standards far outweigh the financial costs involved.

Some of the benefits associated with biodiversity can be deciphered from expenditure on the preservation of endangered species. Several empirical CVM studies have been used to determine values related to the conservation of individual and endangered species in protected areas [Stoll and Johnson, 1984; Brown and Henry, 1993]. Research on endangered or threatened species includes the value of preserving the whooping crane (*Grus americana*) population at the Arkansas National Wildlife Refuge in Texas for viewers and non-viewers [Bowker and Stoll, 1988] at about US\$6 per person per year. Similarly, Boyle and Bishop [1987] estimated the value of preserving the bald eagle at US\$17.46 per person per year.

A study conducted by Brown *et al.* [1994] values the northern spotted owl and its ancient old growth forest habitat using the contingent ranking approach. In this study, respondents were offered 5 different policies. Associated with each policy were the cost of the policy, the area preserved, the estimated number of owl pairs preserved and their probability of survival. They estimated existence values for conserving the northern spotted owl at about US\$20 per person per year. Probabilistic theoretical models have been used to determine the benefits of important wildlife species such as the northern spotted owl in old naturally regenerated red wood forests and have demonstrated the high marginal cost of preservation [Montgomery *et al.*, 1994]. Estimates based on the probability of survival and a reduction in timber stumpage supply, give an estimated welfare cost of US\$21 billion to ensure an 82% chance of the species surviving. Increasing the chance of survival from say 90% to 95% was estimated to cost an additional US\$13 billion.

#### **4.5 Indirect use values and ecosystem function**

Much of the discussion in section 2 of this paper dealt with the properties of ecosystems including their productivity, resilience and stability. There is a significant literature on the value of ecosystem services including indirect values [Ellis and Fisher, 1987; Barbier, 1994; Bell, 1997; Daily, 1997; Barbier, 2000; Daily *et al.*, 2000]. Indirect values associated with biodiversity can be measured using surrogate market approaches using the production function approach. Information about a marketed good (timber, crops or livestock sales) is used to infer the value of a related non-marketed good (e.g. forest, agricultural or wetland habitat). The basic assumption underlying this approach is that, if for instance biodiversity supports agricultural or forest production, then this ecological service provides an additional environmental input into the agricultural or forest enterprise.

For example, the stability of a managed ecosystem constitutes an indirect use value and represents an important function to land managers. As seen above, biodiversity may mitigate large inter-annual variation in productivity [McNaughton, 1985; Walker, 1988]. For instance, the economic value of a change in diversity can be evaluated from the change in livestock liveweight gain associated with a decline in forage biomass as a result of a decline in grassland diversity.

A number of studies in the applied economics literature have used the stochastic production function approach suggested by Just and Pope (1978) to capture the value of crop diversity. These studies indicate that genetic variability within and between crop species confers the potential to resist stress, provide shelter from adverse conditions, and increase the resilience and sustainability of agro-ecosystems. Plot studies indicate that intercropping can reduce the probability of absolute crop failure and that crop diversification increases crop income stability (Walker *et al.*, 1983). Therefore, the greater is the diversity between and/or within species and functional groups, the greater is the tolerance to pests. This is because pests easily spread through crops with the same genetic base (Sumner, 1981; Altieri and Lieberman, 1986).

Crop diversity may enhance farm productivity, stabilise farm income and reduce the risk of outright crop failure [Long *et al.*, 2000]. The existence of a limited number of crops grown in an area makes these crops more vulnerable to diseases and pests. By maintaining proper crop rotations diversity can improve soil productivity and reduce the need for agro-chemical applications. Land managers also recognise that soil and climatic conditions can vary considerably. In such circumstances, growing different crops and crop varieties can lead to more efficient use of resources. Some crops can be grown on fertile land while others can utilize marginal areas. Therefore, the greater the variability of soil and climatic conditions, the greater the impact biodiversity will have on improved agricultural production.

For example, Smale *et al.* [1998], report that crop diversity is positively related to the mean of yields and negatively correlated with the variance of yields in rain fed districts of the Punjab in Pakistan. Di Falco and Perrings [2003; 2005] found cereal diversity to be positively correlated with yields and negatively correlated with revenue variability in two studies in southern Italy. Di Falco and Chavas [2006], point out increased crop diversity may also reduce the likelihood of complete crop failure. Diversity is important also for commercial farmers, since they are dependent on diversity in the breeding pool, regardless of whether it is provided on or off farm.

Other examples of indirect values associated with diversity include mycorrhizae which are important for the functioning of ecosystems and can be considered as a complementary input to timber production. They represent an indirect use value. Silvicultural practices that eliminate mycorrhizae from the system will involve the loss of timber revenue. Although mycorrhizae are not consumed themselves, they are essential for the growth of many timber species which are harvested and they are necessary to support the production process that produces goods and services that are consumed directly.

Similarly, the importance of bird species used as a biological control agent can be captured from increased timber sales associated with insect pest reduction. Takekawa and Garton [1984] used the substitution method to determine the value of a bird species, the evening grosbeak (*Hesperiphona vespertina*) in controlling spruce budworm populations affecting stands of douglas fir (*Pseudotsuga menziesii*) in Washington. They substituted the costs of insecticide to produce the same mortality

that birds cause and established that it would cost at least \$1,820 per square km per year over a 100 year rotation.

## **5.0 Biodiversity in managed landscapes: policy issues**

Section 4 to 4.1 indicated why markets may fail to protect biodiversity and sections 4.2 to 4.5 give some examples of how economic tools can provide a useful means by which to measure the non - benefits and costs associated with biodiversity and thereby go some way toward dealing with market failure. A further solution is to develop economic incentives and instruments which correct for market failure. In what follows we consider the importance of policy with respect to biodiversity conservation.

The aims of a society may be formulated within the framework of national environmental policy. Policy can be regarded as “the compendium of statements, laws and other actions concerning government’s intentions for a particular human activity under its jurisdiction” [Miller, 1999].

Objectives concerning natural resources are not necessarily static. History indicates that environmental policies have changed progressively with time in response to changes in society. This has led to changes in the public demands placed on environmental resources. Human populations are concerned with using environmental resources as a means of survival but also increasingly to meet recreation and conservation goals.

In managed landscapes there is also public concern about the importance of ecological functions – water quality, biodiversity, aesthetic values and international and national organisations are under increasing public pressure to take action to develop economic incentives to protect public values on privately managed land [WCED, 1987].

## **5.1 Economic instruments**

In what follows we outline two types of policy instruments of relevance to land managers – economic incentives and command and control regulations. We discuss economic incentives first.

McNeely [1988] has defined incentives as “an inducement, which is specifically intended to incite or motivate governments, local people, and international organisations to conserve biological diversity”. The idea behind economic incentives being to increase the cost of non-compliance with environmental standards yet allowing the producer the flexibility to employ the least cost method of meeting these standards. By increasing the cost of non-compliance the producer has a private incentive to meet the standards set by the policy instrument. One of the advantages of incentive systems is that they are seen by economists as a cost effective alternative to inflexible command and control environmental regulations [Hanley *et al.*, 1997]. However in practice subsidies are much more widely used because of the resistance to other instruments by the agricultural sector [Hanley and Spash, 1993].

Many incentives are based on the level of opportunity costs or *financial costs* forgone by the producer. For example the financial costs of conservation as estimated by Willis and Benson [1988] in the UK are offered to farmers as compensation for not developing their land. This is based on profits forgone under a management agreement. The current financial cost is the difference between the value of the output (less inputs) of the land under intensive management minus the value of output



(less inputs) under a conservation regime. A complete financial evaluation of conservation also needs to include administrative costs, legal fees, labour and material costs for the maintenance of habitats [Willis and Benson, 1988].

Once the specific costs to the producer are known, policy instruments can be formulated which are targeted at the producer and which persuade producers to achieve the desired environmental objectives. Typically, agri-environmental policies employ market based instruments such as subsidies that create economic incentives which allow individual producers to choose freely to adjust their activities thereby producing an environmental improvement [Barbier *et al.*, 1994]. Taxes as opposed to subsidies are generally preferred by economists because the latter inject income and lead to expansion of the sector under consideration. Subsidies can attract new entrants which may lead to greater aggregate levels of environmental damage and to other market distortions [Hanley *et al.*, 1997].

An example of such a broad appraisal is agri-environment policy used to maintain ecologically important habitats such as the Environmentally Sensitive Area Scheme (ESA) in the UK. Specific areas of land providing habitats for valuable species are identified as conservation areas under which agricultural management practices are regulated. Typically the policy is aimed at the farmer or forester to meet the desired environmental objectives where for example farmers might be expected to employ 'traditional' agronomic practices. The producer is then expected to change his management methods in accordance with certain regulations specified under a 'management agreement'. Such management agreements usually involve an identification of, for example the farming practices necessary to achieve environmental objectives and then stipulate how they should be put into practice. In order to specify guidelines for 'good environmental practice', policy makers need to understand the relationship between management practices and the species, population or community concerned. For example the specific relationships between farm management methods and the species composition of grasslands.

An example of this includes the use of stocking restrictions to encourage heather moorland in the UK. The model developed by Simpson *et al.* [1998] crucially relates heather productivity and survival to varying intensities of the management variable (in this case stocking rate). Reductions in stocking rate can then be used to target farmers who are able to manage heather sustainably under, say, a management agreement.

Typically, agri-environment policy under a management agreement involves reductions in farm intensity in exchange for compensatory payments. In order to do this a precise estimate of the changes in management intensity to meet environmental objectives are required. This then enables the specific costs to the producer to be calculated based on opportunity cost pricing procedures. In the example described above Simpson *et al.* [1998] suggest that in order to meet conservation guidelines for heather conservation ewe stocking rates will have to be reduced to between 13 and 91% on Orkney and between 5 and 89% on Shetland. They report that such a reduction would in most cases result in major financial losses to farmers who would need to be compensated if they were to comply with their recommendations.

This process of European agricultural reform has influenced the objectives of the common agricultural policy (CAP) which have undergone significant changes in recent years. The aims of the CAP are now strongly oriented towards environmental conservation rather than agricultural productivity. The development of these initiatives has provoked many EU countries to adopt environmental policies specifically aimed at encouraging producers to adopt less intensive agronomic and

silvicultural practices [Hanley, 1995]. The status of environmental objectives therefore is increasingly recognised to be as important as other goals such as rural income stability, employment and support for agricultural commodities. As a consequence, the monitoring and evaluation of environmental policy includes an increasing environmental component. The appraisal of agri-environment policy needs to include an assessment of physical economic targets but also needs to meet environmental objectives.

The second type of instrument includes command and control regulations. Situations may occur where economic activities need to be restrained in areas that are especially rich in biodiversity to protect the resource for present and future generations and yet it may not be possible to control market behaviour using incentives. Command and control environmental regulations may be used in such circumstances. Regulatory control involves the direct limitation or reduction of activities which degrade an environmental resource in accordance with some legislated or agreed standard [Barbier *et al.*, 1994].

This is especially important where development initiatives that threaten biological diversity involve uncertainty. In the case of risk, as opposed to uncertainty, it is possible to completely list the range of possible outcomes, and to assign an estimated probability to each outcome. Given this information, and preferences over risk and return, rational decision making is possible. In circumstances of uncertainty, however, where the range of possible outcomes is unknown it is not possible to determine the expected profitability of a project. Although in the case of species extinctions a probability can be attached to the loss of species, the total consequence of this in terms of the loss of environmental services and ecosystem support and duration of these effects cannot be known with certainty. Decision making in the presence of uncertainty relies not on rational comparison of all options, but on adoption of some decision rule that has appealing properties [Common, 1995]. It has been argued that a precautionary approach to the conservation of biological resources should be adopted.

The policy of taking action before uncertainty about possible environmental damages is resolved has been referred to as the 'precautionary principle'. One justification for this is that the costs of damage to biological resources may exceed the costs of preventative action [Taylor, 1991]. Also, irreversible damage may occur such as species extinctions. The emphasis is thus on avoiding potentially damaging situations in the face of uncertainty over future outcomes. It has been proposed for decisions taken over the convention on biodiversity and has been used in conjunction with the Montreal protocol [Myers, 1992; Haigh, 1993].

Ciriacy-Wantrup [1968] and Bishop [1978] have proposed 'the safe minimum standards' approach, which involves setting quantitative, and qualitative limits for, say, the preservation of species and their habitats. A program is developed to maintain such limits unless the costs of doing so are 'unacceptably high'. Hanley *et al.* [1991] indicate that sites of special scientific interest (SSSI) in the UK provide an example of this approach in practice. These sites may be lost if the costs of conservation are prohibitive in terms of the government's conservation budget, but they are still protected regardless of any cost-benefit analysis having been undertaken.

## **6.0 Conclusions**

Rapidly increasing human populations and associated economic development around the world have imposed real pressures on natural habitat and its biodiversity. This is a

subject of major concern to policy makers and the public at large because it is recognised that biodiversity loss could seriously diminish the options open to future generations. All too often market and policy imperfections obscure the social costs of managed lands giving rise to inefficient land use and biodiversity loss.

Protected areas represent a high cost solution to biodiversity conservation in many areas. They impose considerable costs on producers, limit future development options, reduce the supply of market produce and they fail to engage land managers in conservation initiatives.

Joint production of commercial goods and biodiversity in managed landscapes represents an important alternative to reserves. Indeed there is evidence to suggest that biodiversity can coexist in landscapes of economic importance and that it is important in supporting productive processes in managed areas. However, highly intensive managed systems may pose a threat to biodiversity in some areas and it is vital that managers and policy makers work together to develop strategies to avoid such losses.

Policy makers should contribute to this process by developing instruments which internalise biodiversity values into market behaviour. This will help to avoid intervention failure and perverse incentives which lead to biodiversity loss, ensuring that biodiversity values are protected and provided efficiently.

Uncertainty over the benefits and costs of biodiversity and its role in the functioning of ecosystems point toward the need for a diversified strategy which includes protected areas as well as privately managed land used for production. In the absence of a concerted effort by policy makers and land managers, the opportunity to develop initiatives which include private lands in such a strategy to achieve biodiversity conservation goals will be missed.

## References

- Acherar, M. and Rambal, S. 1992. Comparative water relations of four Mediterranean oak species. *Vegetatio* 99-100: 177-184.
- Acocks, J.P.H. 1966. Non selective grazing as a means of veld reclamation. *Proceedings of the Grassland Society of Southern Africa* 1: 33-49.
- Ahlén, I. 1975. Winter habitats of moose and deer in relation to land use in Scandinavia. *Viltrevy* 3: 1-88.
- Alonso, J.A., Alonso, J.C. and Muñoz-Pulido, R. 1990. Areas de invernada de la grulla común *Grus grus* en España. In Alonso, J.A. and Alonso, J.C. (ed). *Distribución y demografía de la grulla común (Grus grus) en España*. ICONA, Madrid.
- Altieri, M. and Liebman, M. (eds) 1986. Insect, Weed, and Plant Disease Management in Multiple Cropping Systems. In Francis, C. *Multiple Cropping Systems*. Macmillan, New York.
- Appleton, Z.E.N. and Crabtree, J.R. 1991. *The farm woodland scheme: an economic appraisal*. SAC Economic Report 27. Scottish Agriculture College, Perth.
- Arrow, K.J. and Fisher, K.C. 1974. Environmental preservation, uncertainty and irreversibility. *Quarterly Journal of Economics* 88: 312-319.
- Baldock, D., Beaufoy, G., Bennet, G. and Clark, J. (eds) 1993. *Nature conservation and new directions in the EC common agricultural policy*. Institute for European Environmental Policy, HPC, Arnhem.
- Barbero, M., Loisel, R. and Quézel, P. 1992. Biogeography, ecology and history of Mediterranean *Quercus ilex* ecosystems. *Vegetatio* 99-100: 19-34.
- Barbier, E.B., 1994. Valuing Environmental Functions: Tropical Wetlands. *Land Economics* 70: 155-173.
- Barbier, E.B., 2000. Valuing the environment as input: review of applications to mangrove-fishery linkages. *Ecological Economics* 35: 47-61.
- Barbier, E.B., Burgess, J.C. and Folke, C. 1994. *Paradise lost? The ecological economics of biodiversity*. Earthscan, London.
- Barbier, E.B., Burgess, J.C. and Markyanda, A. 1991. The economics of tropical deforestation. *Ambio* 20: 55-58.
- Bateman, I. 1992. The United Kingdom. In Wibe, S. and Jones, T. (eds.) *Forests: market and intervention failures, five Case Studies*, Earthscan, London.
- Bateman, I and Willis, K. 1995. *Valuing environmental preferences: theory and practice of the contingent valuation method*. Oxford University Press, Oxford.
- Bedell, T.E. 1973. Botanical composition of a subclover-grass pasture as affected by single and dual grazing by cattle and sheep. *Agronomy Journal* 65: 502-504.
- Behnke, R.H. and Scoones, I. 1993. Rethinking range ecology: implications for rangeland management in Africa. In Behnke, R.H., Scoones, I. And Kerven, C. (eds) *Range ecology at disequilibrium*. Overseas Development Institute, London.
- Bell, F.W., 1997. The economic value of saltwater marsh supporting marine recreational fishing in the Southeastern United States. *Ecological Economics* 21: 243-254.
- Benson, J. and Willis, K. 1991. The demand for forests for recreation. In forestry expansion: a study of technical economic and ecological factors. Forestry Commission, Edinburgh.
- Bignal, E.M. and McCracken, D.I. 1996. Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology* 33: 413-424.

- Bishop, K.D. 1992. Britain's new forests: public dependence on private interest? In Gilg, A.W. (ed). *Restructuring the countryside: environmental policy in practice*. Avebury Studies Green Research.
- Bishop, R. 1978. Endangered species and uncertainty: the economics of a safe minimum standard. *American Journal of Agricultural Economics* 60: 10-18.
- Blondel, J and Curvillier, R. 1977. Une méthode simple et rapide pour décrire les habitats d'oiseaux: le stratiscope. *Oikos* 29: 326-331.
- Bockstael, N., Constanza, R., Strand, I., Boynton, W., Bell, K. and Wainger, L. 1995. Ecological economic modelling and valuation of ecosystems. *Ecological Economics* 14: 143-159.
- Bokdam, J. and Gleichman, M. 2000 Effects of grazing by free ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology* 37: 415-431.
- Borchert, M.I., Davis, F.W., Michaelsen, J. and Oyler, L.D. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. *Ecology* 70: 389-404.
- Bowes, M. and Krutilla, J. 1989. *Multiple use management: the economics of public forestlands*. Resources for the Future, Washington, DC.
- Bowker, J. and Stoll, J.R. 1988. Use of dichotomous choice nonmarket methods to value the whooping crane resource. *American Journal of Agricultural Economics* 70: 372-381.
- Boyle, K.J. and Bishop, R.C. 1987. Valuing wildlife in benefit-cost analyses: a case study involving endangered species. *Water Resources Research* 23: 943-950.
- Bradshaw, R. and Mitchell, F.J.G. 1999. The palaeoecological approach to reconstructing former grazing-vegetation interactions. *Forest Ecology and Management* 120: 3-12.
- Brookshire, D., Ives, B. and Schulze, W. 1976. The valuation of aesthetic preferences. *Journal of Environmental Economics and Management* 3: 325-346.
- Brown, G.M. 1990. Valuation of genetic resources. In Orians, G.H., Brown, G.M., Kunin, W.E. and Swierbinski, J.E. (eds) *The preservation and valuation of biological resources*. University of Washington Press, Seattle.
- Brown, G.M. and Henry, W. 1993. The economic value of elephants. In Barbier, E.B. (ed) *Economics and Ecology: new frontiers and sustainable development*. Chapman and Hall, London.
- Brown, G.M., Layton, D. and Lazo, J. 1994. Valuing habitat and endangered species. *Discussion Paper 94-1* (January). Institute for Economic Research, University of Washington.
- Bullock, C. and Kay, J. 1996. Preservation and change in the upland agricultural landscape: valuing the benefits of grazing extensification. Mimeo, MLURI, Aberdeen.
- Callaway, R.M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73: 2118-2128.
- Campbell, R.W. and Sloan, R.J. 1976. Influence of behavioural evolution on gypsy moth pupal survival in sparse populations. *Environmental Entomology* 5: 1211-1217.
- Carrascal, L.M., Bautista, L.M. and Lázaro, E. 1993. Geographical variation in the density of the white stork *Ciconia ciconia* in Spain: influence of habitat structure and climate. *Biological Conservation* 65: 83-87.

- Casey, D and Hein, D. 1983. Effects of heavy browsing on a bird community in deciduous forest. *Journal of Wildlife Management* 47: 351-396.
- Ciriacy-Wantrup, S. 1968. *Resource conservation: economics and policies*. University of California, Berkely.
- Clawson, M. and Knetsch, J. 1966. *Economics of outdoor recreation*. John Hopkins University Press, Baltimore.
- Clout, M.N. and Gaze, P.D. 1984. Effects of plantation forestry on birds in New Zealand. *Journal of Applied Ecology* 21: 795-815.
- Coase, R. 1960. 'The problem of social cost'. *Journal of Law and Economics* 3: 1-44.
- Common, M. 1995. *Sustainability and Policy: Limits to Economics*. Cambridge University Press, Cambridge, UK.
- Common, M. and Perrings, C. 1992. Towards an ecological economics of sustainability. *Ecological Economics* 6: 7-34.
- Conway, A., McLoughlin, A. and Murphy, W.E. 1972. Development of a cattle and sheep farm. Animal Management series No. 2, An Foras Taluntais, Dublin.
- Costanza, R., Kemp, W.M. and Boynton, W.R. 1993. Predictability, scale and biodiversity in coastal and estuarine systems. In Perrings, C., Mäler, K.-G., Folke, C., Jansson, B.O. and Holling, C.S. (eds) *Biodiversity loss: ecological and economic issues*. Cambridge University Press, Cambridge.
- Coughenour, M.B. 1991. Spatial components of plant-herbivore interactions in pastoral, ranching and native ungulate ecosystems. *Journal of Range Management* 44: 530-542.
- Cousins, S.H. 1991. Species diversity measurement: choosing the right index. *Tree* 6: 190-192.
- Crabtree, J.R. and Appleton, Z. 1992. Economic evaluation of the farm woodland scheme in Scotland. *Journal of Agricultural Economics* 43: 355-367.
- Crabtree, J.R., Chalmers, N. and Barron, N. 1998. Information for policy design: modelling participation in a farm woodland incentive scheme. *Journal of Agricultural Economics* 49: 306-320.
- Crozier, R.H. 1992. Genetic diversity and the agony of choice. *Biological Conservation* 61: 11-15.
- Cumming, D.H.M. 1993. Multispecies systems: progress, prospects and challenges in sustaining range animal production and biodiversity in east and southern Africa. *Proceedings of the 7<sup>th</sup> World Conference on Animal Production*, Edmonton, Alberta.
- Daily, G.C., Ehrlich, P.R. and Haddad, N.M. 1993. Double keystone bird in a keystone species complex. *Proceedings of the Natural Academy of Sciences* 90: 592-594.
- Daily, G.C., (ed) 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC.
- Daily, G.C., Soderqvist, T. Aniyar, S. Arrow, K. Dasgupta, P. Ehrlich, P.R. Folke, C. Jansson, A. Jansson, B.O. Kautsky, N. Levin, S. Lubchenco, J. Maler, K.G. Simpson, D. Starrett, D. Tilman, D. and Walker. B. 2000. The value of nature and the nature of value. *Science* 289: 395-396.
- Daily, G.C., Ehrlich, P.R. and Sanchez-Azofeifa, G.A. 2001. Countryside biogeography: use of human dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications* 11: 1-13.
- Dambach, C.A. 1944. A ten-year ecological study of adjoining grazed and ungrazed woodlands in northeastern Ohio. *Ecological Monographs* 14: 69-105.

- Debussche, M. and Isenmann, P. 1994. Bird-dispersed seed rain and seedling establishment in patchy mediterranean vegetation. *Oikos* 69: 414-426.
- Degraaf, R.M., Healy, W.M. and Brooks, R.T. 1991. Effects of thinning and deer browsing on breeding birds in New England oak woodlands. *Forest Ecology and Management* 41: 179-191.
- De Miguel, J.M., Rodriguez, M.A. and Gómez-Sal, A. 1997. Determination of animal behaviour-environment relationships by correspondence analysis. *Journal of Range Management* 50: 85-93.
- Di Falco, S and Chavas, J-P. 2006. Crop Biodiversity, farm productivity and the management of environmental risk in rainfed agriculture. *European Review of Agricultural Economics* 33: 289-314.
- Di Falco, S. and Perrings, C. 2003. Crop genetic diversity, productivity and stability of agroecosystems: a theoretical and empirical investigation. *Scottish Journal of Political Economy* 50: 207-216.
- Di Falco, S. and Perrings, C. (2005), Crop biodiversity, risk management and the implications of agricultural assistance. *Ecological Economics* 55: 459-466.
- Diamond, P.A. and Hausman, J.A. 1994. Contingent valuation: is some number better than no number? *Journal of Economic Perspectives* 8: 19-44.
- Díaz, M., González, E., Muñoz-Pulido, R. and Naveso, M.A. 1996. Habitat selection patterns of common cranes *Grus grus* wintering in holm oak *Quercus ilex* dehesas of central Spain: effects of human management. *Biological Conservation* 75: 119-123.
- Dobzhansky, T. 1970. *Genetics of the evolutionary process*. Columbia University Press. New York.
- EC Council 1988. Regulation 1094/88. *Official Journal* 106/28.
- Edwards, K.J., Whittington, G. and Ritchie, W. 2005. The possible role of humans in the early stages of machair evolution: palaeoenvironmental investigations in the Outer Hebrides, Scotland. *Journal of Archaeological Science* 32: 435-449.
- Ellis, G.M. and Fisher, A.C. 1987. Valuing the Environment as an Input. *Journal of Environmental Management*, 25: 149-156.
- Ellis, J.E. and Swift, D.M. 1988. Stability of African pastoral systems: alternate paradigms and implications for development. *Journal of Range Management* 41: 450-459.
- Elton, C. 1958. *The ecology of invasions of animals and plants*. Chapman and Hall, London.
- Erdelen, M. 1984. Bird communities and vegetation structure: I. Correlations and comparisons of simple and diversity indices. *Oecologia* 61: 277-284.
- Espelta, J.S., Riba, M. and Retana, J. 1995. Patterns of seedling recruitment in West-Mediterranean *Quercus ilex* forests influenced by canopy development. *Journal of Vegetation Science* 6: 465-472.
- Faliński, J.B. 1986. Vegetation dynamics in temperate lowland forests. Dr W Junk, Dordrecht.
- FAO. 2004. (<http://www.faostat.fao.org/>, updated February 2004).
- Faraco, A.M., Fernandez, F. and Moreno, J.M. 1993. Post-fire dynamics of pine woodlands and shrublands in the *Sierra de Gredos*. In Traubaud, L. and Prodon, R. (eds), *Fire in Mediterranean ecosystems*. Ecosystems Research Report 5: 101-113.
- Fay, P.A. and Hartnett, D.C. 1991. Constraints on growth and allocation patterns of *Silphium integrifolium* (Asteraceae) caused by a cynipid gall wasp. *Oecologia* 88: 243-250.

- Fernandez, R., Martin, A., Ortega, F. and Ales, E.E. 1992. Recent changes in landscape structure and function in a Mediterranean region of SW Spain (1950-1984). *Landscape Ecology* 7: 3-18.
- Ford, H.A. 1987. Bird communities on habitat islands in England. *Bird Study* 34: 205-218.
- Fox, L.R. and Morrow, P.A. 1992. Eucalypt responses to fertilization and reduced herbivory. *Oecologia* 89: 214-222.
- French, D.D, Miller, G.R. and Cummins, R.P. 1997. Recent development of high-altitude *Pinus sylvestris* scrub in the Northern Cairngorm mountains, Scotland. *Biological Conservation* 79: 133-144.
- Fuller, R.J., Hill, D. and Tucker, G.M. 1991. Feeding the birds down on the farm: perspectives from Britain. *Ambio* 20: 232-237.
- Garrod, G.D. and Willis, K.G. 1997. The non-use benefits of enhancing forest biodiversity: a contingent ranking study. *Ecological Economics* 21: 45-61.
- Gasson, R. and Hill, P. 1990. An economic evaluation of the farm woodland scheme. F.B.U. Occasional Paper 17. Wye College.
- González Bernáldez, F. 1991. Ecological consequences of the abandonment of traditional land use systems in central Spain. In Baudry, J. and Bunce, R.G.H. (eds) *Land abandonment and its role in conservation*. 23-29. Options Méditerranéennes Ser. A15.
- Gourlay, D. 1996. Loch Lomond and Stewarty ESAs: a study of public perceptions of policy. Unpublished PhD dissertation, School of Agriculture, University of Aberdeen.
- Grainger, A. 1990. *The threatening desert - controlling desertification*. Earthscan, London.
- Great Western Community Forest. 1992. *Great western community forest and the farmer*. Great Western Community Forest, Swindon.
- Griffin, J.R. 1971. Oak regeneration in the upper Carmel valley, California. *Ecology* 52: 862-868.
- Guyer, C. and Edwards, C. 1991. Farmer response to the farm woodland scheme in Northern Ireland: Part 2 results. *Agroforestry in the UK*, Newsletter to the UK Agroforestry Research Discussion Forum 2: 20-21.
- Haigh, N. 1993. *The precautionary principle and British environmental policy*. Institute for European Environmental Policy, London.
- Hanley, N. and Craig, S. 1991. Wilderness development decisions and the Krutilla-Fisher model: the case of Scotland's flow country. *Ecological Economics* 4: 145-164.
- Hanley, N., Munro, A., Jamieson, D. and Ghosh, D. 1991. Environmental economics and sustainable development in nature conservation. Unpublished NCC Report.
- Hanley, N., Munro, A., Jamieson, D. and Ghosh, D. 1991. Environmental economics and sustainable development in nature conservation. Unpublished NCC Report.
- Hanley, N.D. 1995. Rural amenities and rural development: empirical evidence. Synthesis Report to the Rural Development Programme, OECD, Paris.
- Hanley, N., Shogren, J.F. and White, B. 1997. Environmental economics: in theory and practice. Macmillan, London.
- Hanley, N., Kirkpatrick, A.H., Simpson, I.A., Oglethorpe, D. and MacDonald, A.J. 1996. Ecological-economic modelling of the conservation of threatened



- habitats: heather moorland in the Northern Isles of Scotland. *Biodiversity and Conservation* 5: 1207-1967.
- Hanley, N and Spash, C. 1993. *Cost-benefit analysis and the environment*. Edward Elgar, Cheltenham.
- Hanley, N., MacMillan, D., Wright, R.E, Bullock, C., Simpson, I., Parsisson, D. and Crabtree, B. 1998. Contingent valuation versus choice experiments: estimating the benefits of environmentally sensitive areas in Scotland. *Journal of Agricultural Economics* 49: 1-15.
- Hanemann, W.M. 1994. Valuing the environment through contingent valuation. *Journal of Economic Perspectives* 8: 19-44.
- Hanson, J.D., Skiles, J.W. and Parton, W.J. 1988. A multi-species model for rangeland plant communities. *Ecological modelling* 44: 89-123.
- Hatch, G.P. and Tainton, N.M. 1990. A preliminary investigation of area-selective grazing in the southern tall grassveld of Natal. *Journal of the Grassland Society of Southern Africa* 7: 238-247.
- Hausman, J. A. (ed) 1993. *Contingent valuation: a critical assessment, contributions to economic analysis*. North Holland Publishers, Amsterdam.
- Hernandez, M.P.G. and Silva-Pando, F.J. 1996. Grazing effects of ungulates in a Galician oak forest (Northwest Spain). *Forest Ecology and Management* 88: 65-70.
- Herrera, J. 1995. Acorn predation and seedling production in a low-density population of cork oak (*Quercus-suber* L). *Forest Ecology and Management* 76: 197-201.
- Hester, A. J. Mitchell, F.J.G. and Kirby, K.J. 1996. Effects of season and intensity of sheep grazing on tree regeneration in a British upland woodland. *Forest Ecology and Management* 88: 99-106.
- Higgins, S.I., Turpie, J.K., Constanza, R., Cowling, R.M., Le Maitre, D.C., Marais, C. and Midgley, G.F. 1997. An ecological economic simulation model of mountain fynbos ecosystems: dynamics valuation and management. *Ecological Economics* 22: 155-169.
- Hoffman, M.T. 1988. Rationale for Karoo grazing systems: criticisms and research implications. *South African Journal of Science* 84: 556-559.
- Hoffman, M. T. and Cowling, R.M. 1990. Vegetation change in the semi-arid eastern karoo over the last 200 years: an expanding karoo - fact or fiction? *South African Journal of Science* 86: 286-294.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecological Systems* 4: 1-24.
- Holling, C.S. (ed) 1978. *Adaptive environmental assessment and management*. John Wiley and Sons, Chichester, England.
- Holling, C.S. 1986. Resilience of ecosystem: local surprise and global change. In Clark, E.C, and Munn, R.E. (eds). *Sustainable development of the biosphere*. 292317. Cambridge University Press, Cambridge.
- Holling, C.S. 1988. Temperate forest insect outbreaks, tropical deforestation and migratory birds. *Memoirs of the Entomological Society of Canada* 146: 21-32.
- Holling, C.S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. *Ecological Monographs* 62: 47-52.
- Holling, C.S., Schindler, D.W., Walker, B.W. and Roughgarden, J. 1994. Biodiversity in the functioning of ecosystems: an ecological primer and synthesis. In Perrings, C., Mäler, K.-G., Folke, C., Jansson, B.O. and Holling,

- C.S. (eds) *Biodiversity loss: ecological and economic issues*. Cambridge University Press, Cambridge.
- Holmes, R.T., Schultz, J.C. and Nothnagle, P. 1979. Bird predation on forest insects: an enclosure experiment. *Science* 206: 462-463.
- Hoogervorst, N.J.P. 1993. Integration of economic and ecological modelling for agriculture in the Netherlands. Paper presented at the Integrating economic and ecological indicators symposium, resource Policy consortium, May, World Bank Washington, DC.
- Hope-Jones, P. 1972. Succession in breeding bird populations of sample Welsh oakwoods. *British Birds* 65: 292-299.
- Hulme, P.D., Pakeman, R.J., Torvell, J.M., Fisher, J.M. and Gordon, I.J. 1999. The effects of controlled sheep grazing on the dynamics of upland *Agrostis-Festuca* grassland. *Journal of Applied Ecology* 36: 886-900.
- Hutchinson, G.E. 1961. The paradox of the plankton. *American Naturalist* 95: 137-147.
- IUCN 1988. General Assembly of the International Union for Conservation of Nature and Natural resources, Costa Rica.
- James, F.C. and Wamer, N.O. 1982. Relationships between temperate forest bird communities and vegetation structure. *Ecology* 63: 159-171.
- Jane, G.T. 1994. The impact of browsing animals on the stand dynamics of monotypic mountain beech (*Nothofagus solandri*) forests in Canterbury, New Zealand.
- Jeltsch, F., Milton, S.J., Dean, W.R.J., and van Rooyen, N. 1997. Analysing shrub encroachment in the southern Kalahari: a grid based modelling approach. *Journal of Applied Ecology* 34: 1497-1509.
- Joffre, R., Vacher, J., Los-Ilanos, C. and Long, G. 1988. The dehesa: an agrosilvopastoral system of the Mediterranean region with special reference to the *Sierra Morena* area of Spain. *Agro-forestry systems* 6: 71-96.
- Joffre, R. and Rambal, S. 1993. How tree cover influences the water balance of Mediterranean rangelands. *Ecology* 74: 570-582.
- Jorritsma, I.T.M., van Hees, A.F.M. and Mohren, G.M.J. 1999. Forest development in relation to ungulate grazing: a modelling approach. *Forest Ecology and Management* 120: 23-24.
- Just, R.E. and Pope, R.D. 1978. Stochastic representation of production functions and econometric implications, *Journal of Econometrics* 7: 67-86.
- Kienast, F., Fritschi, J., Bissegger, M. and Abderhalden, W. 1999. Modelling successional patterns of high-elevation forests under changing herbivore pressure - responses at the landscape level. *Forest Ecology and Management* 120: 35-46.
- Kingery, J.L. and Graham, R.T. 1991. The effect of cattle grazing on ponderosa pine regeneration. *Forestry Chronicle* 67: 245-248.
- Köhler-Rollefson, I. 1993. Traditional pastoralists as guardians of biological diversity. *Indigenous Knowledge and Development Monitor* 1: 14-16.
- Kruess, A. and Tschardtke, T. 1994. Habitat fragmentation, species loss and biological control. *Science* 264: 1581-1584.
- Krutilla, J.V. 1967. Conservation reconsidered. *American Economic Review* 57: 778-786.
- Law, R. and Morton, R.D. 1993. Alternative permanent states of ecological communities. *Ecology* 74: 1347-1361.

- Leiva, M.J. and Fernández-Alés, R. 1998. Variability in seedling water status during drought within a *Quercus ilex* subsp. *Ballota* population, and its relation to seedling morphology. *Forest Ecology and Management* 111: 147-156.
- Lindberg, K. 1991. *Policies for maximising nature tourism's ecological and economic benefits*. World Resources Institute, Washington DC.
- Linder, P., Elfving, B. and Zackrisson, O. 1997. Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* 98: 17-33.
- Londo, G. 1990. Conservation and management of semi-natural grasslands in Northwestern Europe. In Bohn, U. and Neuhäusl, R. (eds) *Vegetation and Flora of Temperate Zones*. Academic publishing, the Hague.
- Long, J., Cromwell, E. and Gold, K. 2000. "On-farm Management of Crop Diversity: An Introductory Bibliography". Overseas Development Institute for ITDG. London.
- Lovejoy, T.E. 1988. Diverse considerations. In Wilson, E.O. and Peter, F.M. (eds) *Issues in risk assessment*. National Academy Press, Washington, D.C.
- Lynch, J.F. and Whigham, D.F. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* 28: 287-324.
- McNaughton, S.J. 1984. Grazing lawns: animals in herds plant form and co-evolution. *American Naturalist* 124: 863-886.
- McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55: 259-294.
- McNeeley, J.A. 1988. *Economics and biological diversity*. IUCN, Gland.
- McNeeley, J.A. 1993. Economic incentives for conserving biodiversity: lessons for Africa. *Ambio* 22: 144-150.
- MacArthur, R.H. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36: 533-536.
- MacArthur, R.H. and MacArthur, J.W. 1961. On bird species diversity. *Ecology* 42: 594-598.
- MacArthur, R.H. and Wilson, E.O. 1967. *The theory of island biogeography*. Princetown University Press, Princetown.
- Main, A.F. 1982. Rare species: precious or dross? In Groves, R.H. and Ride, W.D.L. (eds) *Species at risk: research in Australia*. Australian Academy of Science, Canberra.
- Maquis, R.J. and Whelan, C.J. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75: 2007-2014.
- Marañón, M. 1986. Plant species richness and canopy effect in the savannah-like dehesa of South west Spain. *Ecologia Mediterranea* 12: 131-141.
- Marañón, T. 1991. Diversidad en comunidades de pasto mediterráneo: modelos y mecanismos de coexistencia. *Ecologia* 5: 149-157.
- Marrs, R.H. and Welch, D. 1991. *Moorland wilderness: the potential effects of removing domestic livestock, particularly sheep*. ITE report to the Department of the Environment.
- Mate, I.D. 1992. The theoretical development of machair in the Hebrides. *Scottish Geographical Magazine* 108: 35-38.
- Mattson, W.J. and Addy, N.D. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190: 515-522.
- May, R.M. 1973. *Stability and complexity in model ecosystems*. Princetown University Press, New Jersey.

- Metrick, A. and Weitzman, M.L. 1994. Patterns of behaviour in biodiversity preservation. Policy Research Working Paper 1358. Environment, Infrastructure, and Agriculture Division, The World Bank, Washington, D.C.
- Mill, G.A., van Rensburg, T.M., Hynes, S. and Dooley, C. Preferences and multiple use forest management in Ireland: a contingent valuation approach. Forthcoming in *Ecological Economics* in 2007.
- Miller, K.R. 1996. Conserving biodiversity in managed landscapes. In Szaro R.C. and Johnston, D. W. (eds.). *Biodiversity in Managed Landscapes: Theory and Practice*. Oxford University Press, Oxford, UK.
- Miller, T.E. 1982. Community diversity and interaction between the size and frequency of disturbance. *American Naturalist* 120: 533-542.
- Miller, H.G. 1999. Forest policy: the international and British dimensions. Department of Forestry, University of Aberdeen.
- Mitchell, R. and Carson, R. 1989. *Using surveys to value public goods: the contingent valuation method*. Resources for the Future, Washington, D.C.
- Mitchell, F.J.G. and Cole, E. 1998. Reconstruction of long-term successional dynamics of temperate woodland in Bialowieza forest, Poland. *Journal Ecology* 86: 1042-1059.
- Montgomery, C.A., Brown, G.M. and Adams, D.M. 1994. The marginal cost of species preservation: the northern spotted owl. *Journal of Environmental Economics and Management* 26: 111-128.
- Montoya, J.M. and Meson, M.L. 1982. Intensidad y efectos de la influencia del arbolado de las dehesas sobre la fenología y composición específica del sotobosque. *Anal INIA Ser Forestal* 5: 43-60.
- Moore, A.D. 1990. The semi-Markov process: a useful tool in the analysis of vegetation dynamics for management. *Journal of Environmental Management* 30: 111-130.
- Moore, A.D. and Noble, I.R. 1990. An individualistic model of vegetation stand dynamics. *Journal of Environmental Management* 31: 61-81.
- Moore, N.W. and Hooper, M D. 1975. On the number of bird species in British woods. *Biological Conservation* 8: 239-250.
- Moreno, J.M. 1989. Los ecosistemas terrestres mediterráneos y el fuego. *Politica Científica* 18: 46-50.
- Morgan, R.K. 1991. The role of protective understorey in the regeneration system of a heavily browsed woodland. *Vegetatio* 92: 119-132.
- Morris, C. and Potter, C. 1995. Recruiting the new conservationists: Farmers' adoption of agri-environmental schemes in the UK, *Journal of Rural Studies* 11: 51-63.
- Morris, R.F., Cheshire, W.F., Miller, C.A. and Mott, D.G. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* 39: 487-494.
- Mott, J.J. 1986. Patch grazing and degradation in natural pastures of the tropical savannas in northern Australia. In Horne, F., Hodgson, J., Mott, J.J. and Brougham, R. (eds) *The Plant-Animal Interface*. Winrock International, Morrilton, Arkansas.
- Myers, N. 1992. Population/environment linkages: discontinuities ahead. *Ambio* 21: 116-118.
- Naveh, Z. et al., 1979. Structural and floristic diversity of shrublands and woodlands in northern Israel and other Mediterranean areas. *Vegetatio* 41: 171-190.

- Naveh, Z. 1994. The role of fire and its management in the conservation of Mediterranean ecosystems and landscapes. In Moreno, J.M. and Oechel, W.C. (eds). *The role of fire in Mediterranean-type ecosystems*. Springer Verlag, New York.
- Ni Dhubhain, A. and Gardiner, J.J. 1994. *Farm forestry in the rural economy*. Discussion paper presented at AES Conference, Exeter.
- Nolan, T. and Connolly, J. 1977. Mixed stocking by sheep and steers - a review. *Herbage Abstracts* 47: 367-379.
- Oglethorpe, D.R. and Sanderson, R.A. 1999. An ecological-economic model for agri-environmental policy analysis. *Ecological Economics* 28: 245-266.
- Oliveira, G., Correia, O.A., Martins-Loucao, M.A. and Catarino, F.M. 1992. Water relations of cork-oak (*Quercus suber* L.) under natural conditions. *Vegetatio* 99-100: 199-208.
- O'Neill, R.V., DeAngelis, D.L., Waide, J.B. and Allen, T.F.H. 1986. *A hierarchical concept of ecosystems*. Princetown University Press, Princetown.
- Opdam, P., Rijsdijk, G. and Hustings, F. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biological Conservation* 34: 333-351.
- Pearce, D.W. and Turner, R.K. 1990. *Economics of natural resources and the environment*. Harvester Wheatsheaf, Hemel Hempstead, UK.
- Perman, R., Ma, Y., McGilvray, J. and Common, M. 2003. *Natural resource and environmental economics*. Pearson, Education, New York, Longman.
- Perrings, C. and Walker, B. 1997. Biodiversity, resilience and the control of ecological-economic systems: the case of fire-driven rangelands. *Ecological Economics* 22: 73-83.
- Peterken, G.F. and Tubbs, C.R. 1965. Woodland regeneration in the new forest, Hampshire, since 1650. *Journal of Applied Ecology* 2: 159-170.
- Pezzey, J. 1989. *Economic analysis of sustainable growth and sustainable development*. Environment Department Working Paper No 15. The World bank, Washington, DC.
- Pignatti, S. 1978. Evolutionary trends in Mediterranean flora and vegetation. *Vegetatio* 37: 175-185.
- Pimm, S.L. 1984. The complexity and stability of ecosystems. *Nature* 307: 321-326.
- Pimmental, D., Stachow, U., Takacs, D.A., Brubaker, H.W., Dumas, A.R., Meaney, J.J., O'Neill, J.A. Onsi, D.E. and Corzilius, D.B. 1992. Conserving biological diversity in agricultural/forestry systems. *Bioscience* 42: 354-362.
- Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P. and Starfield, A. 2005. Conserving species in a working landscape: land use with biological and economic objectives. *Ecological Applications*: 1387-1401.
- Portney, P.R. 1994. The contingent valuation debate: why economists should care. *Journal of Economic Perspectives* 8: 3-18.
- Power, M. E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenko, J. and Paine, R.T. 1996. Challenges in the quest for keystones. *BioScience* 46: 609-20.
- Ramakrishnan, P.S. 1992. *Shifting agriculture and sustainable development: an interdisciplinary study from north-eastern India*. Parthenon Publishing Group, Park Ridge, NJ.
- Randall, A., Ives, B. and Eastman, C. 1974. Bidding games for the valuation of aesthetic environmental improvements. *Journal of Environmental Economics and Management* 1: 132-149.

- Ratcliffe, P.R. 1993. Biodiversity in Britain's forests. The Forest Authority, Edinburgh.
- Raven, R.H., Beese, K., Eisner, T., Morin, N., Duncan, T., Hobbs, S.L.A., Hodges, J., Rall, W.F., Colwell, R.R. and Swings, J. 1992. Biotechnology and genetic resources: United States- Commission of the European Communities Workshop, October 21-22, Airlie, Virginia, USA. Commission of the European Communities. Brussels, Belgium.
- Reid, W.V. 1996. Beyond protected areas: changing perceptions of ecological management objectives. In Szaro, R.C. and Johnston, D. W. (eds.). *Biodiversity in Managed Landscapes: Theory and Practice*. Oxford University Press, Oxford, UK.
- Reinhammar, L-G. 1995. Evidence for two distinct species of *Pseudorchis* (Orchidaceae) in Scandinavia. *Nordic Journal of Botany* 15: 469-481.
- Relva, M.A. & Veblen, T.T. 1998. Impacts of introduced large herbivores *Austrocedrus chilensis* forests in northern Patagonia, Argentina. *Forest Ecology and Management* 108: 27-40.
- Repetto, R. 1989. Economic incentives for sustainable production. In Schramme, G. and Warford, J.J. (eds) *Environmental management and economic development*. Johns Hopkins for the World Bank, Baltimore.
- Ring, C.B., Nicholson, R.A. and Launchbaugh, J.L. 1985. Vegetational traits of patch grazed rangelands in west-central Kansas. *Journal of Range Management* 38: 51-55.
- Roland, M.A. and Taylor, P.D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386: 710-713.
- Rosenzweig, M.L. 2003. Win-Win Ecology: *How the Earth's Species Can Survive in the Midst of Human Enterprise*. Oxford University Press, Oxford, UK.
- Sala, O.E., Chapin III, F.S., Gardner, R.H., Lauenroth, W.K., Mooney, H.A. and Ramakrishnan, P.S. 1999. Global change, biodiversity and ecological complexity. In Walker, B., Steffen, W., Canadell, J. and Ingram, J. (eds) *The terrestrial biosphere and global change: implications for natural and managed ecosystems*. Cambridge University Press, Cambridge, UK.
- Sandys, P. 1994. The woodland grant scheme: a review from the perspective of owners and managers. *Quarterly Journal of Forestry* 88: 20-26.
- Schemske, D.W. and Brokaw, N. 1981. Treefalls and the distribution of understorey birds in a tropical forest. *Ecology* 62: 938-945.
- Schindler, D.W. 1990. Experimental perturbations of whole lakes as tests of hypotheses concerning ecosystem structure and function. *Proceedings of 1987 Crafoord Symposium*. *Oikos* 57: 25-41.
- Schindler, D.W., Kasian, S.E.M. and Hesslein, R.H. 1989. Biological impoverishment in lakes of the northeastern United States from acid rain. *Environmental Science and Technology* 23: 573-580.
- Schmida, A. and Wilson, M.V. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12: 1-20.
- Scholes, R.J. and Walker, B.H. 1993. An African savanna: synthesis of the Nylsvlei study. CUP, Cambridge.
- Scottish Office Agricultural and Fisheries Department. 1994. Shetland Islands environmentally sensitive area: explanatory leaflet for farmers and crofters.
- Scottish Office Agricultural and Fisheries Department. 1995a. *Habitats scheme: explanatory leaflet for farmers and crofters*.

- Scottish Office Agricultural and Fisheries Department 1995b. Heather moorland scheme: *explanatory leaflet for farmers and crofters*.
- Silva, J. 1987. Responses of savanna to stress and disturbance: species dynamics. In Walker, B.H. (ed) *Determinants of tropical savannas*. IRL Press, Oxford.
- Simberloff, D., Brown, B.J. and Lowrie, S. 1978. Isopod and insect root borers may benefit Florida mangroves. *Science* 201: 630-632.
- Simpson, I.A., Kirkpatrick, A.H., Scott, L., Gill, J.P., Hanley, N. and MacDonald, A.J. 1998. Application of a grazing model to predict heather moorland utilization and implications for nature conservation. *Journal of Environmental Management* 54: 215-231.
- Solow, A., Polasky, S. and Broadus, J. 1993. On the measurement of biological diversity. *Journal of Environmental Economics and Management* 24: 60-68.
- Soulé, M.E. and Wilcox, B. A. (eds). 1980. *Conservation biology, an evolutionary ecological perspective*. Sinauer Associates, Sunderland Massachusetts.
- Smale, M., Hartell, J., Heisey, P.W., Senauer, B. 1998. The contribution of genetic resources and diversity to wheat production in the Punjab of Pakistan. *American Journal of Agricultural Economics*, 80: 482-493.
- Staines, B.W. 1995. The impact of red deer on the regeneration of native pinewoods. In Forestry Commission. Our pinewood heritage. Conference proceedings, 1994. Inverness. Forestry Commission, RSPB,SNH. Surrey.
- Staines, B.W., Balharry, R. and Welch, D. 1995. The impact of red deer and their management on the natural heritage in the uplands. In Thompson, D.B.A. Hester, A.J. and Usher, M.B. (eds.) *Heaths and moorlands: cultural landscapes*. Scottish Natural Heritage, Edinburgh.
- Standiford, R.B. and Howitt, R.E. 1992. Solving empirical bioeconomic models: a rangeland management application. *American Journal of Agricultural Economics* May 1992: 421-433.
- Sternberg, M., Gutman, M., Perevolotsky, A., Ungar, E.D. and Kigel, J. 2000. Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. *Journal of Applied Ecology* 37: 224-237.
- Stoll, J.R. and Johnson, L.A. 1984. Concepts of value, non-market valuation and the case of the whooping crane. *Transactions of the Forty Ninth American Wildlife and Natural Resources Conference* 49: 382-393.
- Stowe, T.J. 1987. The management of sessile oakwoods for pied flycatchers. *RSPB Conservation Review* 1: 78-83.
- Sumner, D.R., B. Doupnik and M.G. Boosalis 1981. Effects of tillage and multicropping on plant diseases, *Annual Review of Phytopathology*, 19. 167-187.
- Sun, D., Dickinson, G.R. and Bragg, A.L. 1997. Effect of cattle grazing and seedling size on the establishment of *Araucaria cunninghamii* in a silvo-pastoral system in Northeast Australia. *Journal of Environmental Management* 49: 435-444.
- Sykes, J. M. and Horrill, A.D. 1979. Regeneration of native pinewoods *Institute of Terrestrial Ecology Annual Report 1978*. 103-106.
- Tainton, N.M., Zacharias, P.J.K. and Hardy, M.B. 1989. The contribution of veld diversity to the agricultural economy. In Huntley, B.J. (ed) *Biotic diversity in Southern Africa: concepts and conservation*. Oxford University Press, Cape Town.

- Takekawa, J.Y. and Garton, E.O. 1984. How much is an evening grosbeak worth? *Journal of Forestry* 82: 426-428.
- Takekawa, J.Y., Garton, E.O. and Langelier, L.A. 1982. Biological control of forest insect outbreaks: the use of avian predators: 47<sup>th</sup> North American Wildlife Conference. 393-409.
- Taylor, P. 1991. The precautionary principle and the prevention of pollution. *ECOS* 124: 41-46.
- Telleria, J.L., Santos, T., Sanchez, A. and Galarza, A. 1992. Habitat structure predicts bird diversity distribution in Iberian forests better than climate. *Bird Study* 39: 63-68.
- Telleria, J.L. and Carrascal, L.M. 1994. Weight-density relationships between and within bird communities: implications of niche space and vegetation structure. *The American Naturalist* 143: 1083-1092.
- Telleria, J.L. and Santos, T. 1995. Effects of forest fragmentation on a guild of wintering passerines: the role of habitat selection. *Biological conservation* 71: 61-67.
- Terborgh, J. 1985. Habitat selection in Amazonian birds. In Cody, M.L. (ed) *Habitat selection in birds*. Academic Press, Orlando.
- Terradas, J. and Save, R. 1992. The influence of summer and winter stress and water relationships on the distribution of *Quercus ilex* L. *Vegetatio* 99-100: 137-145.
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77: 350-363.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1302.
- Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. *Archives Neerlandaises de Zoologie* 13: 265-243.
- Tschirhart, J. and Crocker, T.D. 1987. Economic valuation of ecosystems. *Transactions of the American Fisheries Society* 116: 469-478.
- Tucker, G.M. and Heath, M.F. 1994. *Birds in Europe: their conservation status*. Birdlife international, Cambridge.
- Turner, R.K. (ed) 1993. *Sustainable environmental economics and management*. Belhaven Press, London.
- UNEP, 1995. *Global biodiversity assessment*. Cambridge University Press, Cambridge.
- Usher, M. B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. *Journal of Applied Ecology* 3: 355-367.
- Valderrábano, J. and Torrano, L. 2000. The potential for using goats to control *Genista scorpius* shrubs in European black pine stands. *Forest Ecology and Management* 126: 377-383.
- Van Dorp, D. and Opdam, P.F.M. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecology* 1: 59-73.
- Van Hees, A.F.M., Kuiters, A.T. and Slim, P.A. 1996. Growth and development of silver birch, pedunculate oak and beech as affected by deer browsing. *Forest Ecology and Management* 88: 55-63.
- Van Rensburg, T.M., Mill, G.A., Common, M. and Lovett, J. 2002. Preferences and multiple use forest management. *Ecological Economics* 43: 231-244.



- Vane-Wright, R.I., Humphries, C.J. and Williams, P.H. 1991. What to protect? Systematics and the agony of choice. *Biological conservation* 55: 235-254.
- Vitousek, P.M. and Hooper, D.U. 1993. Biological diversity and terrestrial ecosystem biogeochemistry. In Schulze, E.-D and Mooney, H.A. (eds) *Biodiversity and ecosystem function*. Springer-Verlag, Berlin.
- Walker, B.H., Ludwig, D., Holling, C.S. and Peterman, R.M. 1981. Stability of semi-arid savanna grazing systems. *Ecology* 69: 473-498.
- Walker, B.H. 1988. Autoecology, synecology, climate and livestock as agents of rangelands dynamics. *Australian Range Journal* 10: 69-75.
- Walker, B.H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18-23.
- Walker, B.H. 1993a. Rangeland ecology: understanding and managing change. *Ambio* 22: 80-87.
- Walker, B.H. 1993b. Stability in rangelands - ecology and economics. *Proceedings of the 17th International Grasslands Congress*. Palmerston North, New Zealand.
- Walker T.S., Singh, R.P. and Jodha. N.S. 1983. *Dimensions of farm level diversification in the semi arid tropics of rural south India*. Economic Program Progress report, 51 ICRISAT, Patancheru, India.
- Watkins, C., Williams, D. and Lloyd, T. 1996. Constraints on farm woodland planting in England: a study of Nottinghamshire farmers. *Forestry* 69: 167-176.
- WCED 1987. *Our common future*. The World Commission on Environmental Development. Oxford, OUP.
- Weber, G.E., Jeltsch, F., van Rooyen, N. and Milton., S.J. 1998. Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. *Journal of Applied Ecology* 35: 687-699.
- Weisbrod, B. 1964. Collective consumption services of individual consumption goods. *Quarterly Journal of Economics* 77: 71-77.
- Weitzman, M. L. 1998. The Noah's ark problem. *Econometrica* 66: 1279-1298.
- Weslien, J. and Schroeder, M. 1999. Population levels of bark beetles and associated insects in managed and unmanaged spruce stands. *Forest Ecology and Management* 115: 267-275.
- Westoby, M., Walker, B.H. and Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42: 266-274.
- Whitby, M. 1996. *The European environment and CAP reform. Policies and prospects for conservation*. CAB International, Oxon.
- Whittaker, R.H. 1977. Evolution of species diversity in land communities. *Evolutionary Biology* 10: 1-67.
- Whiteman, A. 1991. A cost-benefit analysis of forest replanting in east England. Forestry Commission development Division. Edinburgh.
- Willis, K.G. and Benson, J.F. 1988. Financial and social costs of management agreements for wildlife conservation in Britain. *Journal of Environmental Management* 26: 43-63.
- Willis, K.G. 1991. The recreational value of the Forestry Commission estate in Great Britain: a Clawson-Knetsch travel cost analysis. *Scottish Journal of Political Economy* 38: 58-75.

- Willis, K.G., Garrod, G.D. and Saunders, C.M. 1995. Benefits of environmentally sensitive area policy in England: a contingent valuation assessment. *Journal of Environmental Management* 44: 105-125.
- Willson, M.F. 1974. Avian community organization and habitat structure. *Ecology* 55: 1017-1029.
- Wilson, E.O. 1985. The biological diversity crisis. *BioScience* 35: 700-706.
- Wilson, E.O. (ed). 1988. Biodiversity. National Academy Press, Washington, DC.
- Wilson, W.L. and Johns, A.D. 1982. Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest and plantations in east Kalimantan, Indonesia. *Biological Conservation* 24: 205-218.
- World Resources Institute (WRI). 2005. Earth Trends: The Environmental Information Portal. (<http://earthtrends.wri.org/>)
- Zohary, M. 1973. *Geobotanical foundations of the Middle East. Vol 1.* Gustav Fisher Verlag, Stuttgart.

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<sup>1</sup> Biodiversity thus represents the diversity of all life being a characteristic property of nature, rather than a resource. The term also has a broader meaning for the set of organisms themselves. For example, a biodiverse tropical rainforest, therefore, refers to the quality or range of diversity within it.

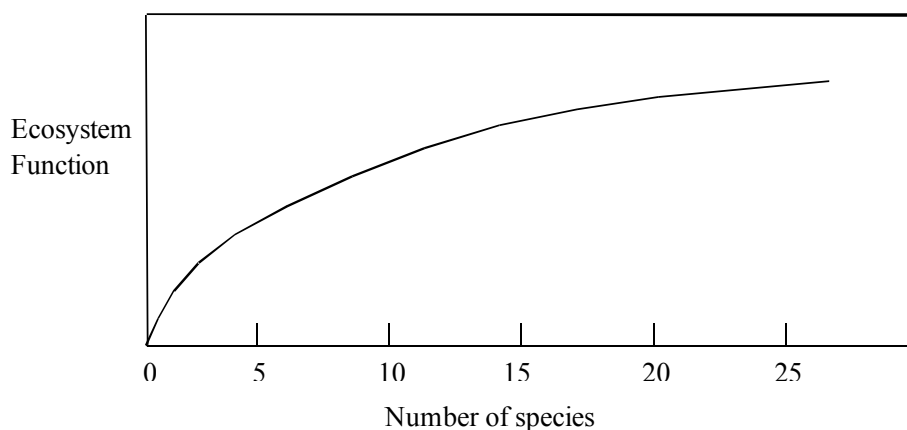


Figure 1 Conceptual relationship between the number of species and ecosystem functioning. Source: [Sala *et al.*, 1999; Vitousek and Hooper, 1993]

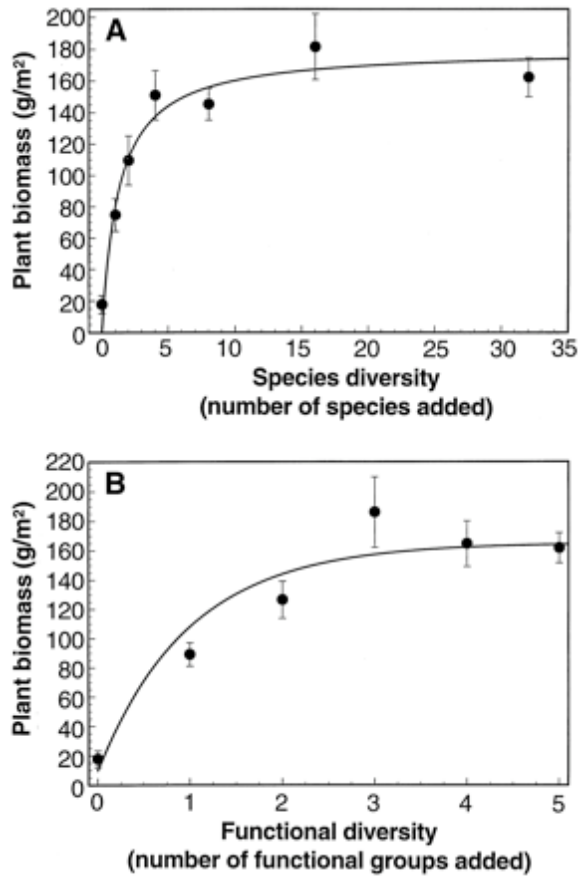


Figure 2 (A) Dependence of 1996 aboveground plant biomass (that is, productivity) (mean and SE) on the number of plant species seeded into the 289 plots. (B) Dependence of 1996 aboveground plant biomass on the number of functional groups seeded into each plot. Curves shown are simple asymptotic functions fitted to treatment means. Source Tilman *et al.*, [1997].

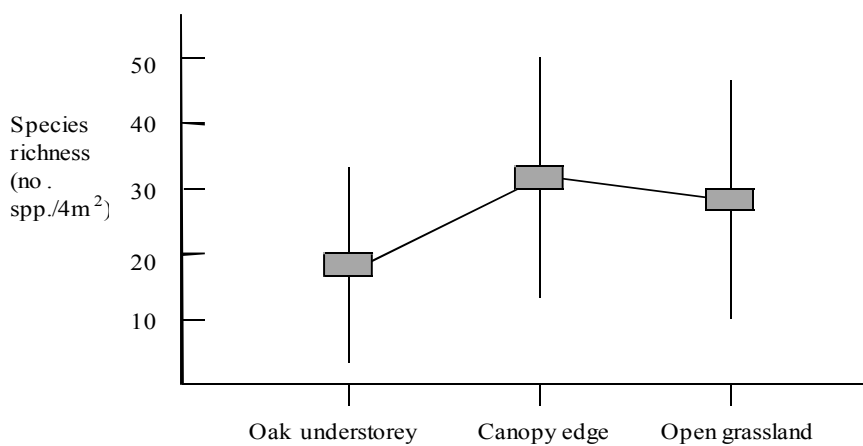


Figure 3 Average species richness (number of species in 4m<sup>2</sup> plots) in 3 habitats: oak understory, canopy edge and open grassland. Mean SE. and range have been drawn. Source: Maranon [1986].

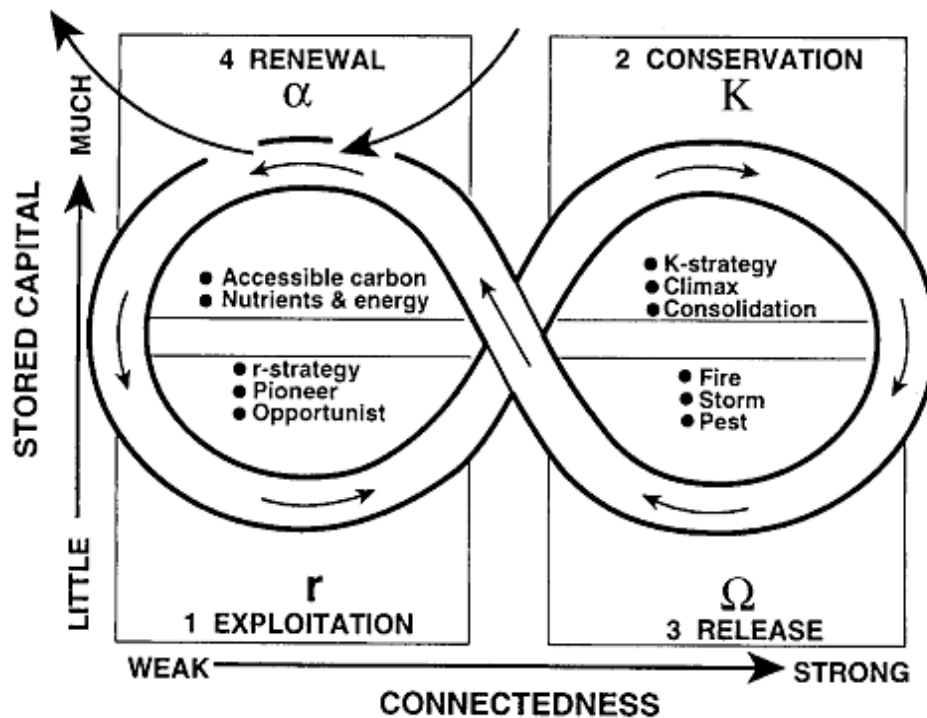


Figure 4 The four ecosystem functions, the flow of events among them and their relationship with stored capital and degree of connectedness. Arrows indicate an ecosystem cycle. The cycle reflects changes in two attributes (1) *vertical* axis: the amount of accumulated capital (nutrients, carbon) stored in variables that are the dominant structuring variables at that moment, and (2) *horizontal* axis: the degree of connectedness among variables. The arrows entering and leaving a phase indicate where the system is most sensitive to external influence. Source: Holling [1986].

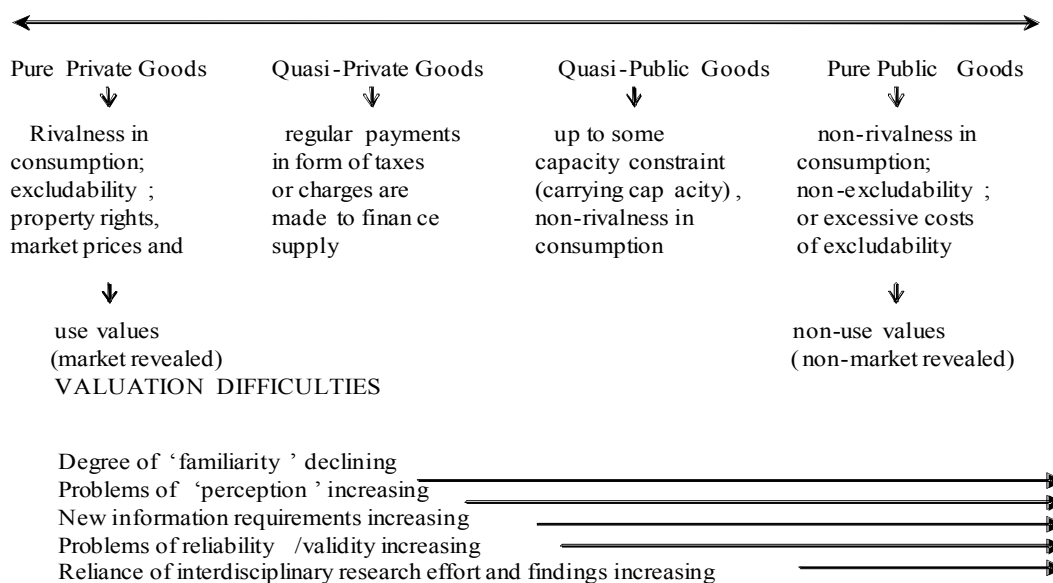


Figure 5 Environmental commodities spectrum and the valuation problem. Source: Turner [1993]

$$TEV = F(\text{Use value}, \text{Non-use value})$$

$$TEV = F(DUV, IUV, OV, QOV, BV, EV)$$

Where:

- TEV = Total Economic Value
- DUV = Direct Use Value
- IUV = Indirect Use Value
- OV = Option Value (including bequest value)
- QOV = Quasi Option Value
- BV = Bequest Value
- EV = Existence Value

Figure 6 Components of Total Environmental Value

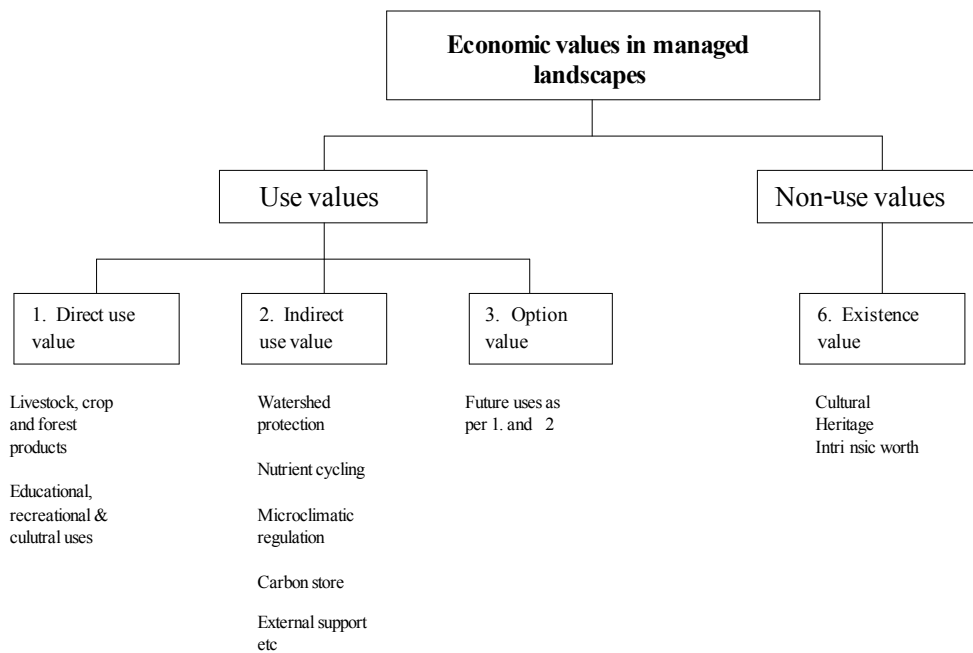


Figure 7 Economic values in managed landscapes. Source: adapted from Barbier [1994].

Table 1. Characteristics of public and private goods

	Excludable	Non-excludable
Rivalrous	Pure private good	Open access resource
Non-rivalrous	Congestible resource	Pure public good