Ecosystem Services and the Economics of Biodiversity Conservation

Ann Kinzig[1], Charles Perrings[1] and Bob Scholes[2]

1. School of Life Sciences, Arizona State University, PO Box 874501, Tempe, AZ 85281, USA

2. CSIR-Natural Resources and Environment, PO Box 395 Pretoria 0001 South Africa

Abstract

The concept of ecosystems services provides a robust and complementary rationale for biodiversity conservation to the traditional arguments based on intrinsic value. In principle, it also provides a mechanism for optimizing investments in biodiversity conservation and directing them to where they are most useful. This requires the valuation of ecosystem services, and in particular, the contribution that biodiversity (in its strict sense) makes to that value. The paper describes a number of key issues in ecosystem and biodiversity valuation.

1. Introduction

One of the consequences of the Millennium Ecosystem Assessment (MA, 2005) has been to force a reappraisal of the rationale for biodiversity conservation. By identifying the role of biodiversity in the provision of services with demonstrable value to people, it has broadened the range of motivations for conservation, and has established an obligation to identify the consequences of change in biodiversity to the wellbeing of people. Justifying conservation no longer relies solely on the notion of biodiversity for biodiversity's sake, or the spiritual or ethical consideration of a right of species to exist independent of their use by people (sometimes referred to as 'intrinsic value'). While this remains an important motivation for conservation it significantly underestimates the value of biodiversity, and is one reason why it has been difficult to secure even the minimum level of protection needed to stem the accelerating wave of species extinctions.

At a time when many conservation biologists have called for 20-30% of the land and sea to be set aside in a highly protected state to ensure that species are adequately buffered against human activities, less than 10% of the global land surface is protected, and a smaller fraction of the oceans. Thus the vast majority of biodiversity, measured in abundance terms rather than simply number of species (Scholes and Biggs 2005) occurs outside of protected areas, in populated, managed, 'working landscapes', and will continue to do so in the future. It is especially here that the utilitarian value of biodiversity is crucial to justifying its conservation.

The Millennium Ecosystem Assessment has challenged science to consider the social costs and benefits of alternative biodiversity conservation strategies, and that means identifying the consequences of biodiversity change for the delivery of ecosystem services. Biodiversity conservation has become an issue amenable to the resource-allocation tools provided by economics. By the same measure, the ecological community has been challenged to identify the consequences of biodiversity change for ecological functioning, and – as importantly – to identify the consequences of changes in ecological functioning for the level and reliability at which ecosystem services are supplied.

A second consequence of the Millennium Ecosystem Assessment has been to direct attention to the services that depend on the variety and proportions of organisms present, rather than on the existence of one or a few species. Historically, individual species have tended to be managed to satisfy demand for particular foods, fuels, fibers, or medicinal compounds or because they have totemic, spiritual, or amenity value. The MA drew attention to the disproportionate benefits that humankind derives from a small number of species. Indeed, the conveniences of modern life would be unattainable without the 'provisioning services' provided by this minority of species. But it also drew attention to the services provided by the existence of species that are substitutes, complements or necessary co-factors for the species we directly rely on for provisioning services. A sufficient analysis of ecosystem services should include not just the provision of consumptive benefits offered by foods, fuels, fibers and medicines or the non-consumptive aesthetic, recreational, spiritual and totemic value offered by individual species or habitats, but also the mechanisms and organisms that sustain the ‘provisioning’ organisms (for instance, by making available the energy or nutrients they need to grow), or that regulate the impact on the provisioning and cultural services of external stresses and shocks (Dirzo and Raven, 2003; MA, 2005). In the Millennium Assessment scheme, the former are known as ‘supporting services’, while the latter are called ‘regulating services’. The regulating ecosystem services determine the capacity of ecosystems both to accommodate shocks, and to respond to changes in environmental conditions without losing functionality (Kinzig et al, 2006). In other words, they determine the distribution of provisioning and cultural services over the expected range of environmental conditions, noting that environmental conditions refers both to natural and social environments (Perrings, 2006). The role of the mix of species – and, we suggest, one of the main reasons why society is ultimately interested in biodiversity conservation – is in assuring the provisioning and cultural services in an uncertain world.

This paper considers the implications of the Millennium Ecosystem Assessment both for conservation objectives and priorities, and for science. It poses the following questions:

1. How does the variety of organisms and pathways affect the capacity of ecosystems to deliver the services that matter to people?
2. What does this mean for the value of biodiversity, and hence for societal decisions about biodiversity conservation?

Ecosystems provide both services and disservices. In addition to the provision of foods, fuels, fibers, amenity and the like, ecosystems are also the source of many diseases and natural disasters. We use the same conceptual framework for both services and disservices, since (a) a decrease in the probability and/or intensity of a disservice is equivalent to a service, and (b) both services and disservices are affected by the way in which people interact with ecosystems. For example, the emergence and spread of zoonotic diseases like the ebola virus, HIV, SARS or avian flu, may turn out to have more impact on human wellbeing over the next few decades than many other environmental threats currently attracting attention. Since emergent zoonotic diseases are a consequence of human interactions with the environment, it follows that there are changes in the way that ecosystems are managed that could reduce that threat (Daszak and Cunningham, 1999, 2000).

2. The Millennium Ecosystem Assessment

The Millennium Ecosystem Assessment distinguishing between four broad categories of benefit derived from ecosystems: provisioning services, regulating services, cultural services and supporting services. Of the four categories, the first is most familiar and has in the past often been referred to as ‘goods’ (as in ‘environmental goods and services’).. Provisioning services cover the renewable resources that have been the focus of much work in environmental and resource economics in the last three decades of the 20th century, including foods, fibres, fuels, water, biochemicals, medicines, pharmaceuticals and genetic material. Many of these products are more-or-less directly consumed, and are subject to reasonably well-defined property rights. They are often priced in reasonably well-functioning markets, and even though there may be externalities in their production or consumption, those prices bear some relation to the scarcity of resources. Where no direct market exists, their value can be estimated by other fairly straightforward means, such as working out the price of an equivalent service that does have a market. Data regarding the supply of provisioning services are thus relatively easily obtained.

The other three ecosystem service categories are less familiar. Cultural services comprise a category that captures many of the non-use or passive use values of ecological resources. Cultural services include the spiritual, religious, aesthetic, educational, scientific, inspirational and recreational well-being that people derive from the ‘natural’ world. They include the sense of place that people have, as well as the cultural importance of landscapes and species. It has been noted that the diversity of ecosystems is reflected in the diversity of human cultures. Cultural services include both traditional and scientific information, awareness and understanding of ecosystems and their individual components offered by functioning ecosystems. One modern expression of cultural services – nature-based tourism – involves well-developed markets. Others do not. While intellectual property rights are increasingly well-defined (largely to protect the patent rights of corporations seeking to develop novel products from biochemical and genetic material drawn from ecosystems), most cultural services are still regulated by custom and usage, or by traditional taboos, rights and obligations. Nevertheless, they are directly used by people, and so are amenable to valuation by methods designed to reveal people's preferences.

The category of supporting services captures the ecosystem processes that underpin all other services. Examples offered by the MA include soil formation, primary production, decomposition, nutrient and water cycling. These services play out at quite different spatial and temporal scales. For example, nutrient cycling involves the maintenance of the roughly twenty nutrients essential for life, in appropriate relative concentrations for the organisms that use them. For nutrients that are not readily transported in the atmosphere or water the service is often localized, and is therefore at least partially captured, for instance by the price of the land on which it takes place. (Fertile lands are higher priced than infertile land). Carbon cycling, on the other hand, operates at a global scale due to its stable atmospheric form, and is very poorly captured in any set of prices. Nitrogen cycling falls in between, since there is a regional-scale atmospheric loop in its cycle. Since these services are not directly consumed themselves, their value is embedded in the provisioning and cultural services.

The remaining category, the regulating services, are even harder to measure and value. The regulating services alter the reliability of supply of provisioning or cultural services. This may be by changing the consequence of extreme events, or by changing the likelihood that environmental conditions will move outside the range of comfort for humans or their domesticates. The examples described by the Millennium Ecosystem Assessment included the following: air quality regulation (by affecting the chemicals contributed to and extracted from the atmosphere); climate regulation (through the way that ecosystem processes affect climate both locally and globally); water regulation (through the impact of land cover and soil micro-organisms on flooding, or aquifer recharge); erosion regulation (through the role of plants, insects and other soil biota in soil retention); water purification and waste treatment services (through impacts of the biota on water pollution and filtration in inland waters and coastal ecosystems); disease regulation (through the impact of changes in the abundance of human pathogens, such as cholera, or disease vectors such as mosquitoes); pest regulation (through the effect of predators and competitors on the prevalence of crop and livestock pests and diseases; and natural hazard regulation (through a wide range of buffering functions of biota, for example in coastal ecosystems where mangroves and coral reefs can reduce the damage caused by hurricanes and storm surges).

The MA’s report on changes in the availability of all of the above categories of services is patchy, reflecting the relative abundance of information on provisioning services, and the paucity of knowledge on most of the others. Its report on their value is even sketchier. This is partly because most effort in valuing ecosystem services has gone into understanding of human preferences for services that are directly consumed (or directly experienced in a non-consumptive way). Comparatively little effort has gone into understanding the indirect linkages between ecological functioning, ecosystem services and the production and consumption of marketed goods and services. Almost no effort has gone into understanding the value of the role of the environment in either mitigating or exacerbating the risks we face. This is what the regulating services do.

3. Ecosystem services: the scientific challenge

A fundamental problem confronting ecologists is to understand the linkages between biodiversity, ecosystem functioning and the provision of ecosystem services. This is part of a broader challenge to understanding the interdependence between biodiversity, ecosystem functioning, ecosystem services, economic, technical and institutional change at the global scale (Dirzo and Loreau, 2005). There have been a number of recent attempts to clarify the linkages between biodiversity change and ecosystem functioning (Loreau et al, 2002; Caldeira et al, 2005; Hooper et al, 2005; Spehn et al, 2005).

However, we still do not have a clear idea of what an interest in maintaining the flow of particular ecosystem services means for the conservation of biodiversity.

To illustrate the problem, Table 1 summarizes what we know about the importance of suites of species for the production of a sub-set of the major provisioning services. The size of the dot in each cell indicates the relative contribution of that category (for example, a taxonomic group or ecosystem) to the direct provisioning of the service. Note that the contribution must be direct to avoid 'double counting'—thus, while bacteria are necessary to grow plants, for instance, they do not get a dot for food production because they do not themselves constitutes a significant source of human nutrition. The bacterial contribution to food production is a supporting service under the MA scheme, and its value is accounted for in the value of the food.

Whether the dot is black or white indicates something about the type of biodiversity required. A black dot indicates that many or all of the species in the indicated category provide the service. A white dot indicates that only a restricted sub-set of species within the category—a particular functional group, or species with certain characteristics—can provide the service.

The background shade of the cell indicates something about our current understanding of the level of biodiversity needed to maintain the service over the expected range of environmental conditions. Dark grey indicates that high proportion of all species within the category should be conserved to maintain the service in question. That is, there is little redundancy among species in service provisioning. Mid grey indicates that there is some redundancy for the service in question: some intermediate level of species richness must be maintained. Light grey indicates high redundancy – it is thought that any of the many species in the group are capable of providing the service. Note that the shade of cells including white dots reflect the restricted set of species; even if dark grey or mid grey, it may be that only a few species within the overall category are needed.

Table 1: The importance (symbol size), number of species involved (black,white) and degree of redundancy (cell shade) of species or ecosystems involved in supplying provisioning services

	Food	Fiber	Fuel	Genetic Resources	Biochemicals & Pharmaceuticals	Ornamental Resources	Fresh Water
Taxonomic Group							
Bacteria				●	●		●
Protists				●	●		•
Fungi				●	●		●
Invertebrates							
Plants	○	○	○	●	●	○	●
Vertebrates	○			●	●		
Ecosystems							
Marine	○			●	●		
Freshwater	○			●	●		
Forests		○	○	●	●	○	●
Grassland & Savanna	○			●	●	○	●
Desert				●	●	○	•
Tundra				●	●		•
Mountain				●	●	○	●
Agroecosystems	●	○	○	●			•
Urban ecosystems	○			○		○	•
Species Interactions							
Plant-insect	●						
Plant-microbial	●						
Abiotic Features							
Soil Properties							●

4. Ecosystem services: the valuation challenge

Perrings (2006) identifies the major challenges to economics from the Millennium Ecosystem Assessment to be the following:

1. to understand the consequences of ecological change induced by current economic activity;
2. to understand the distribution of possible outcomes attaching to alternative activities and, where feasible, the probabilities attaching to those outcomes; and
3. to develop appropriate mitigating or adaptive policies.

A number of studies have drawn attention to the changes in ecosystem services and the importance of quantifying the value of these changes to human societies in terrestrial (e.g. Daily et al, 1997; Daily, 1997), marine (e.g. Duarte, 2000) and agroecosystems (Björklund et al, 1999). There have been several attempts to estimate the value of ecosystem services for the whole world, or large parts of it (Costanza et al, 1997; Bolund and Huhammar, 1999; Norberg, 1999; Limburg and Folke, 1999; Woodward and Wui, 2001). There are serious concerns over the reliability of such estimates. The Millennium Ecosystem Assessment did not attempt a comprehensive and systematic 'total' valuation of ecosystem services, because their judgement was that the theory, methods and data sources were insufficiently developed to support a credible effort of that sort.

One source of concern is the fact that most studies of ecosystem services have focused on a single dimension of the problem only. Turner *et al* (2003) drew attention to the fact that few studies had considered the multiple functions that any ecosystem supports, and fewer still had estimated ecosystem values 'before and after' environmental changes had taken place. Daily *et al* (1997) had emphasized that most ecosystem services were the result of a complex interaction between natural cycles operating over a wide range of space and time scales. Waste disposal, for example, depends both on highly localized life cycles of bacteria as well as the global cycles of carbon and nitrogen. The same cycles are implicated in the provision of a range of other services. By ignoring multiple services, and multiple scales, many valuation studies underestimate the importance of the underlying ecosystem stocks to the economy.

A second concern is that many valuation studies depend on elicitation of the preferences of people who have little conception of the role of ecosystem stocks in the generation of ecosystem services, or of the link between those services and the production of commodities (Winkler, 2006a). The problem here is that ecosystems and the services they provide are, for the most part, intermediate inputs into goods and services that are produced or consumed by economic agents. As with other intermediate inputs, their value derives from the value of those goods and services. To illustrate, consider the following simplified description of the decision-maker's problem.

$$Max_{\mathbf{h}(t)} \int_0^\infty u\left(\mathbf{q}\left(\mathbf{x}\left(\mathbf{s}(t)\right)\right), \mathbf{h}(t)\right) e^{-\delta t}\, dt$$

where utility (u) depends on a vector of produced goods **q**, a vector of marketed inputs **x**, the state of the environment **s,** the harvest of ecosystem resources, **h,** and the discount rate, δ. This is subject to the dynamics of the natural environment, summarized by the equations of motion:

$$\frac{ds_i}{dt} = f_i\left(\mathbf{s}(t)\right) - h_i(t),\ i = 1,\ldots,n$$

The value of the *n* ecosystem stocks in this problem is their social opportunity cost, measured by the shadow price (or costate variable) obtained from the solution to the optimization problem. Specifically, if the costate variables in the solution to the problem are denoted λ_i, then they will evolve as follows:

$$\frac{d\lambda_i}{dt} = \lambda_i\left(\delta - f_i^{'}\right) - \sum_j \frac{du}{dq_i}\frac{dq_i}{d\mathbf{x}}\frac{d\mathbf{x}}{ds_i},\ i = 1,\ldots,n$$

and in the steady state, λ_i takes the value:

$$\lambda_i = \frac{\sum_j \frac{du}{dq_i}\frac{dq_i}{d\mathbf{x}}\frac{d\mathbf{x}}{ds_i}}{\delta - f_i^{'}}, \; i = 1,\ldots,n$$

So the value of the i^{th} ecosystem stock depends (a) on its regeneration rate relative to the yield on produced capital, indicated by the discount rate, and (b) on its marginal impact on the production of the set of marketed outputs, **q**, through the effect it has both on other ecosystem stocks, **s**(*t*), and on marketed inputs, **x**.

The second concern relates to the establishment of values. Stated preference methods have been used to value the outputs of activities for which there are no well-functioning markets, and then the value of underlying regulating and supporting ecosystem services have been derived from this. Allen and Loomis (2006), following Goulder et al (1997), use such an approach to derive the value of species at lower trophic levels from the results of surveys of willingness to pay for the conservation of species at higher trophic levels. Specifically, they derive the implicit willingness to pay for the conservation of prey species from direct estimates of willingness to pay for top predators (which tend to be more charismatic and well-known). They refer to this as a form of quasi-benefit transfer. They make the point that it is not necessary for people to understand the trophic structure of an ecosystem, since their willingness to pay for top predators effectively captures their willingness to pay for the whole system. While this ignores any value attaching to the diversity of species or to other ecosystem services other than habitat provision, it is at least a constructive use of stated preference methods.

Where prices are known for the outputs of activities, then derived demand (production function) methods are appropriate. A growing number of studies use this approach (e.g. Barbier, 2000; Nunes et al, 2006; Matete and Hassan, 2006). These studies identify values for ecosystem services that represent at least part of the shadow value of those resources. Like the study by Allen and Loomis (2006) they apply knowledge of ecosystem functioning and processes to derive the value of supporting and regulating ecosystem services. To this point, however, there are very few studies of the value of regulating services in changing the distribution of outcomes. Studies that derive the value of ecosystem services look for the partial derivative of the production function with respect to the service to be valued, but do not consider the marginal impact of a change in the service on the second (or higher) moments of the distribution of output.

A third concern relates to the way that valuation studies address the problem of uncertainty (Winkler, 2006b). Since the value of ecosystem stocks is the discounted stream of net benefits they provide, it is sensitive to uncertainty about the environmental and market conditions under which they will be exploited. Most valuation studies simply sidestep the problem. Others address it indirectly through the discount rate. Since uncertainty is typically an increasing function of time, if the future is discounted sufficiently heavily the more uncertain consequences of the use of ecosystem stocks are effectively ignored. Where uncertainty about the future consequences of the use we make of the environment includes the likelihood of severe and irreversible consequences, this is not satisfactory. Since social-ecological systems are complex, coupled and adaptive, the capacity to predict the future consequences of current actions is limited at best. Such systems have the usual properties of non-linearity, path dependence and sensitivity to initial conditions. Any estimate of the value of stocks is conditioned on the capacity to predict those consequences, as is the choice between adaptation to and mitigation of those consequences.

A fourth concern relates to the increasing reliance on value transfer techniques in ecosystem service valuation studies. Value transfer (the transfer of value estimates obtained for one service in one location to the same service in other locations) may be sensible in the case of carbon sequestration services, since carbon dioxide mixes relatively rapidly and completely in the global atmosphere and thus the contribution of carbon sequestration to the general circulation system is independent of where it takes place (e.g. Songhen and Brown, 2006). However, it makes less sense where the benefits of ecosystem services depend heavily on local conditions.

5. The value of biodiversity in reducing risk

The above difficulties apply to the valuation of all ecosystem services. The valuation of biodiversity-based services involves an additional set of complexities. In some special cases it is the diversity itself that is valued by consumers: examples might be ornithological or botanical tourism[1], and bioprospecting. In most other cases the value is indirect, or embedded in the provisioning or cultural services that are ultimately consumed. But then it is often two steps removed from the market, since the main contribution of biodiversity is to the regulating and supporting services, which in turn are mainly valued through the provisioning services.

All organisms belong and contribute to the collective noun we call biodiversity, but the value of the *diversity* part of it is not simply the sum of the value of the *bio* components, which is in any case already captured in the value of provisioning and cultural services. It is common cause that human life depends absolutely on the presence and sufficient abundance of certain other organisms (since we are not autotrophs), so at some minimum level the utilitarian value of those organisms is infinite. It is also our current understanding that the number of species in this category is quite small: possibly 10,000 species or perhaps fewer- less than 1% of known species. Even within that small subset, there is apparently a high degree of substitutability. One species will do nearly as well as another in satisfying human basic needs, if not preferences. Ecologically, the diversity of species within that subset derives its value from a number of different things:

1. Almost all provisioning services, even if ultimately delivered by one species, depend on processes mediated by an unseen set of symbionts, mutualists or commensual species. These processes can usually *only* be performed by a species belonging to a so-called 'functional types' (or 'guilds'), although there is often a high degree of species substitutability within a functional type. These dependencies substantially enlarge the 'iceberg' of necessary species beyond its obvious tip, but the indispensable functional types can act in support of many different species delivering the provisioning service.

[1] Nature-based tourism in general is only weakly dependent on biodiversity. A large part depends only on the presence of clean water, a pleasant beach or snowfield and an agreeable climate. Another large part values a moderate level of landscape diversity (particularly topographic grandeur). Even wildlife tourism requires only modest levels of biodiversity (5-10 species), provided it is of the charismatic type. Adding more diversity does not proportionately increase its value.

2. Having more species increases the efficiency with which resources can be converted into an ecosystem service. Experimental evidence is that this effect is quite small: the productivity of biodiverse ecological communities is typically only 10% higher than the average for monocultures, to the extent that the difference is often indistinguishable in relation to natural variability, and is seldom greater the best-performing monoculture. The effect saturates rapidly (<10 species). The leading explanation for this phenomenon is that narrow niches are more efficient at resource conversion than broad niches; thus a set of partly-overlapping narrow niches capture and convert more resource than a single broad one.
3. The *constancy of supply* of an ecosystem service in a temporally variable environment is increased by having a number of species providing that service, with partially overlapping niches. The same applies for all the supporting services that underlie the provisioning service. This mechanism differs from the one described above because it does not raise the mean level of service delivery, but decreases the variance. An increase in reliability in supply has an 'insurance value', discussed below. Spatial heterogeneity plays an analogous role is stabilizing the supply of services in a an environment with patchily-distributed abiotic resources.
4. The availability of alternate pathways by which provisioning or supporting services can be supplied provides a fail-safe mechanism analogous to the much-vaunted pathway diversity of the internet. This is quite similar to the mechanism described in (3), except that it does not depend on niche differences, but on differential susceptibility to damage by disturbance, including overharvesting, or perhaps because of spatial separation.
5. The regulation of certain disservices, notably the outbreak of pests and diseases, is thought to be provided by foodweb complexity. Simple predator-prey systems are typically prone to 'boom-and-bust' epidemiology, whereas the presence of multiple predators and prey, in several trophic levels, with features such as prey-switching, have much less spikey dynamics.

From an economic perspective, the most significant of these effects is the impact of diversity within functional groups on the capacity of ecosystems to provide goods and services over a range of environmental conditions. This is a portfolio effect. One way of capturing this has been to extend the Capital Asset Pricing Model of financial economics to a Biological Capital Asset Pricing Model (B-CAPM) where the optimal species portfolio varies with the random state of the environment (e.g. "wet" periods versus "dry" periods) (cf. Brock & Xepapadeas, 2002). Species that appear redundant in "normal" times have a key role to play in preserving the viability of the whole ecosystem during "abnormal" times. The portfolio of species changes with the extinction or local extirpation of species as a consequence of habitat destruction, or the effects of the dispersion of species through the growth of the global trade system. In all cases, it affects the capacity of ecosystems to support the production of valued services over a range of environmental conditions. An increase in the rate at which species are dispersed across a spatially heterogeneous landscape, for example, affects the functional compensation between species. Depending on the rate of dispersion, this may either increase or decrease the number of functionally redundant 'insurance' species, and hence the resilience of the affected ecosystem. The link between resilience and functional redundancy lies in the fact that species that are functionally redundant in some environmental conditions may protect the functioning of the system under other environmental conditions. Indeed, degrees of redundancy, coupled with spatial patchiness and the capacity to disperse underlie the notion that biodiversity provides the system with functional insurance (Balmford et al. 2002). Loreau et al (2003) show that ecological productivity and resilience in a spatially heterogeneous system depends on the rate at which species disperse. Low and high dispersion rates lead to competitive exclusion, intermediate rates increase local biodiversity and hence (possibly) resilience.

In order to identify the optimal level of biodiversity conservation we need to develop predictive models of the impact of biodiversity change on ecosystem services. The application of dynamic niche modeling techniques to predict species response to changes in climate and other determinants of the distribution and abundance of species has improved the capacity to connect land-use change, biodiversity distributions, and ecological functioning (Pearson and Dawson 2003; Wilson et al 2005; Sutherland 2006). In the same way, we need to be able to identify the effect of biodiversity change on the capacity of socio-ecological systems to absorb anthropogenic and environmental stresses and shocks without loss of value. This parallels work on the resilience of coupled systems within the Resilience Alliance (Kinzig et al. 2006; Scheffer et al. 2000; Walker et al. 2004; Walker et al. 2006) and is, again, grounded in an analysis of the linkages among biodiversity change, ecological functioning, ecosystem processes, and the provision of valued goods and services. If we are to understand and enhance the resilience of coupled systems we need robust models of the linkages between biodiversity and ecosystem services (Loreau et al. 2002; Naeem and Wright 2003; Reich et al. 2004; Hooper et al.

2005), and between biodiversity change and human well-being (Kontoleon et al. 2006; Finnoff and Tschirhart 2006; Baumgartner 2006).

The growth and increasing integration of the global economic system is responsible for increasing levels of stress on the world's biodiversity. Anthropogenic climate change, the growth in the complexity, reach and volume of international trade and travel, the increased fraction of the land and sea resources that are appropriated for human use, biotechnological innovation, the depletion of freshwater resources and the growth in emissions to the environment of a range of byproducts of human activities, all affect biodiversity and the ecosystem services it supports. Since human activities depend on these services, this matters. For a number of reasons, the effects are uncertain.

In addition to the natural variability that affects many processes, some sources of stress are novel, and therefore lack historical precedent. New technological products and processes, and the new and rapid dispersal pathways provided by trade and transport pose risks for which organisms are unprepared by their evolutionary environment. Other sources of stress, such as climate change, have approximate precedents, but the risk profile has changed because they are concomitant with habitat fragmentation, biological simplification in highly managed ecosystems, and a variety of other stresses, such as pollution and overharvesting. The contemporary risks may be difficult to estimate from palaeo-environmental data. We need to be able to characterize the risks affecting biodiversity and ecosystem services, including those that arise from scientific uncertainties

Biodiversity change theoretically and empirically alters the capacity to cope with disturbance and change. In extreme cases this may force a regime shift or change of state. More generally, it will affect ecosystem functioning and thus ecological services. Understanding ecosystem responses to biodiversity change requires new theoretical and experimental work linking (a) food-web structure and ecosystem functioning in systems with multiple trophic levels; (b) biodiversity and functioning of microbial communities; (c) biodiversity and ecosystem functioning at the landscape scale using spatially explicit models (Loreau et al, 2001). It also requires research into the dynamics, stability and emergent properties of stressed ecosystems (Scheffer et al., 2001). Since there are no standardized procedures to analyze uncertainty that may arise from qualitatively different causes (eg chaotic dynamics, phase transitions, hysteresis effects and emergent properties) it may be important to adopt case-specific procedures.

Considerable attention has recently been paid in the decision-sciences to the implications of qualitative differences in available information for decision-making under uncertainty. This includes research on alternative tools for decision-making under fundamental uncertainty, including robust control theory (Roseta-Palma & Xepapadeas, 2003; Brock & Xepapadeas, 2003), ambiguity theory and adaptations of weighted expected utility theory (Horan, Perrings et al., 2003). There is, however, a clear need to develop more robust tools for decision-making, both to identify the trade-offs involved in alternative biodiversity conservation strategies, and to evaluate the temporal and spatial spread of biodiversity risks.

References

Allen, B.P.and J.B. Loomis 2006. Deriving values for the ecological support function of wildlife: An indirect valuation approach, Ecological Economics 56: 49– 57.

Balmford A., A. Bruner,P. Cooper, R. Costanza, S. Farber, R. E. Green, M. Jenkins, P. Jefferiss, V. Jessamy, J. Madden, K. Munro, N. Myers, S. Naeem, J. Paavola, M. Rayment, S. Rosendo, J. Roughgarden, K. Trumper, R. K. Turner. Economic reasons for conserving wild nature. Science 297: 950-953.

Barbier, E., 2000. Valuing the environment as input: review of applications to mangrove–fishery linkages. Ecological Economics 35: 47–61.

Baumgartner, S. 2006. The insurance value of biodiversity in the provision of ecosystem services. Natural Resources Modeling, in press.

Björklund J., K.E. Limburg and T. Rydberg, 1999. Impact of production intensity on the ability of the agricultural landscape to generate ecosystem services: an example from Sweden, Ecological Economics 29; 269–291.

Bolund, P. and S. Hunhammar 1999. Ecosystem services in urban areas, Ecological Economics 29: 293–301.

Brock, W. and A. Xepapadeas 2003..Regulating Nonlinear Environmental Systems under Knightian Uncertainty, in R. Arnott, B. Greenwald, R. Kanbur and B. Nalebuff, Eds, Economics for an Imperfect World: Essays In Honor of Joseph Stiglitz, MIT Press, forthcoming.

Caldeira, M. C. , Hector, A. Loreau, M., and Pereira, J. S. (2005) Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. Oikos 110: 115-123.

Carpenter, S.R. and W.A. Brock. 2006. Rising variance: A leading indicator of ecological transition. Ecology Letters 9: 311-318.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R.V. O'Neill, J. Paruelo, R.G. Raskin, P. Sutton, M. van den Belt, 1997. The value of the world's ecosystem services and natural capital. Nature 387: 253–260.

Daily, G.C., 1997. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, DC.

Daily, G.C; S. Alexander, P.R. Ehrlich, L. Goulder, J. Lubchenco, P.A. Matson, H.A. Mooney, S. Postel, S.H. Schneider, D. Tilman, G.M. Woodwell, 1997. Ecosystem Services: Benefits Supplied to Human Societies by Natural Ecosystems Issues in Ecology 1(2):1-18.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife: threats to biodiversity and human health. Science 287:443-449.

Daszak, P., A. A. Cunningham, and A. D. Hyatt. 2001. Viral emergence within the human-wildlife continuum. In B. Dodet, editor. Emergence and Control of Zoonotic Ortho- and Paramyxoviruses. John Libbey Eurotext, Paris.

Daszak, P., A.A. Cunningham, and A. D. Hyatt. 2000. Emerging infectious diseases of wildlife: threats to biodiversity and human health. Science 287:443-449.

Daszak, P., and A.A. Cunningham. 1999. Extinction by infection. Trends in Ecology & Evolution 14:279.

Finnoff, D. and J. Tschirhart. 2006. Using oligopoly theory to examine individual plan versus community optimization and evolutionary stable objectives. Natural Resource Modeling, in press.

Goulder, L.H. and D. Kennedy, 1997. Valuing ecosystem services: philosophical bases and empirical methods. In: Daily, G.C. (Ed.), Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, D.C.: 23–47.

Heal G., B. Walker, S. Levin, K. Arrow, P. Dasgupta, G. Daily, P. Ehrlich, K.-G. Maler, N. Kautsky, J. Lubchenco, S. Schneider, D. Starrett, 2004, Genetic diversity and interdependent crop choices in agriculture, Resource and Energy Economics 26 (2004) 175–184.

Heal, G.M., E.B. Barbier, K.J. Boyle, A.P. Covich, S.P. Gloss, C.H. Hershner, J.P. Hoehn, C.M. Pringle, S. Polasky, K. Segerson, and K. Shrader-Frechette. 2005. Valuing Ecosystem Services: Toward Better Environmental Decision Making. Washington, D.C.: The National Academies Press.

Hooper, D. U., Chapin III , F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., and Wardle, D. A. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75 (1): 3-35.

Horan R.D., Perrings C., Lupi F. and Bulte E.H. 2002. Biological pollution prevention strategies under ignorance: the case of invasive species, American .Journal of Agricultural Economics 84: 1303-1310.

Kinzig, A. P., P. Ryan, M. Etienne, H. Allyson, T. Elmqvist, and B. H. Walker. 2006. Resilience and regime shifts: assessing cascading effects. Ecology and Society 11(1): 20. [online] URL: http://www.ecologyandsociety.org/vol11/iss1/art20/.

Kleinen, T., Held, H. & Petschel-Held, G. 2003. The potential role of spectral properties in detecting thresholds in the earth system: application to the thermohaline circulation. Ocean Dynamics, 53, 53-63.

Kontoleon, A. U. Pascual and T. Swanson (eds) 2006. Frontiers of Biodiversity Economics, Cambridge, Cambridge University Press.

Limburg K. and C.Folke, 1999 The ecology of ecosystem services: introduction to the special issue, Ecological Economics 29: 179–182

Loreau, M., M. T. K. Arroyo, D. Babin, R. Barbault, M. Donoghue, M. Gadgil, C. Häuser, C. Heip, A. Larigauderie, K. Ma, G. Mace, H. A. Mooney, A. Oteng-Yeboah, C. Perrings, P. Raven, J. Sarukhan, P. Schei, R. J. Scholes, R. T. Watson, (2006) The need for an international panel on biodiversity, Nature, in press.

Loreau, M., Mouquet N., Gonzalez, A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. PNAS 22: 12765-12770.

Loreau, M., Naeem, S. and P. Inchausti (eds). 2002. Biodiversity and Ecosystem Functioning: Synthesis and Perspectives. Oxford University Press, Oxford

Matete, M. and R. Hassan 2006. Integrated ecological economics accounting approach to evaluation of inter-basin water transfers: An application to the Lesotho Highlands Water Project, Ecological Economics, in press.

Naeem, S. and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. Ecology Letters 6: 567-579.

Norberg, J. 1999. Linking Nature's services to ecosystems: some general ecological concepts, Ecological Economics 29: 183–202.

Núñez, L. Nahuelhual, L. and Oyarzún, C. 2006. Forests and water: The value of native temperate forests in supplying water for human consumption, Ecological Economics 58: 606– 616.

Pearson, R.G. and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology & Biogeography 12 (5), 361-371.

Pearson, R.G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology & Biogeography 12(5):361–371.

Perrings C. 2005. Economics and the value of biodiversity and ecosystem services. In J.-P. de Luc (ed) Biodiversity Science and Governance: Proceedings of the International Conference, Paris, Museum National d'Histoire Naturelle, Paris: 109-118.

Perrings C. 2006. Ecological economics after the Millennium Ecosystem Assessment, International Journal of Ecological Economics and Statistics 6: 8-22.

Reich, P. B., D. Tilman, S. Naeem, D. S. Ellsworth, J. Knops, J. Craine, D. Wedin, and J. Trost. 2004. Species and functional group diversity independently influence biomass accumulation and its response to CO2 and N. Proceedings of the National Academy of Sciences of the United States of America 101:10101–10106.

Rodrıguez, L.C. U. Pascual, H.M. Niemeyer 2006. Local identification and valuation of ecosystem goods and services from Opuntia scrublands of Ayacucho, Peru, Ecological Economics 57: 30– 44.

Roseta Palma, C. and A. Xepapadeas, 2002. Robust Control in Water Management, Wageningen International Conference on "Risk and Uncertainty in Environmental and Resource Economics," June 2002.

Scheffer, M., Carpenter, S.R., Foley, J., Folke, C. & Walker, B. 2001. Catastrophic shifts in ecosystems. Nature, 413, 591-596.

Scheffer, M., W. Brock, and F. Westley. 2000. Socioeconomic mechanisms preventing optimum use of ecosystem services: an interdisciplinary theoretical analysis. Ecosystems 3:451-471.

Sohngen, B. and S. Brown, 2006. The influence of conversion of forest types on carbon sequestration and other ecosystem services in the South Central United States, Ecological Economics 57: 698– 708.

Spehn, E. M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Giller, P. S., Good, J., Harris, R., Högberg, P., Huss-Dannell, K., Jumpponen, A., Koricheva, J., Leadley, P. W., Loreau, M., Minns, A., Mulder, C. P. H., O'Donovan, G., Otway, S. J., Palmborg, C., Pereira, J. S., Pfisterer, A. B., Prinz, A., Read, D. J., Schulze, E.-D., Siamantziouras, A.-S. D., Terry, A. C., Troumbis, A. Y., Woodward, F. I., Yachi, S., and Lawton, J. H. (2005) Ecosystem effects of biodiversity manipulations in European grasslands. Ecological Monographs 75 (1): 37-63.

Sutherland, W. 2006. Predicting the ecological consequences of environmental change: a review of the methods. Journal of Applied Ecology 43:4, 599-616.

Turner, R.K., J. Paavola, P. Cooper, S. Farber, V. Jessamy, S. Georgiou 2003. Valuing nature: lessons learned and future research directions, Ecological Economics 46: 493-510.

Walker B & Meyers JA. 2004 Thresholds in ecological and social-ecological systems: A developing database. Ecol. Soc., 9(2):3, [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art3

Walker, B. H., C. S. Holling, S. R. Carpenter, and A. P. Kinzig. 2004. Resilience, adaptability, and transformability. Ecology and Society 9(2): 5. [online] URL: http://www.ecologyandsociety.org/vol9/iss2/art5/.

Walker, B. H., L. H. Gunderson, A. P. Kinzig, C. Folke, S. R. Carpenter, and L. Schultz. 2006. A handful of heuristics and some propositions for understanding resilience in social-ecological systems. Ecology and Society 11(1): 13. [online] URL: http://www.consecol.org/vol11/iss1/art13/.

Walker, B.H. and J. A. Meyers. 2004. Thresholds in ecological and social-ecological systems: A developing database. Ecology and Society 9(2):3, www.ecologyandsociety.org/vol9/iss2/art3

Wilson, R. W., D. Gutiérrez, J. Gutiérrez, D. Martínez, R. Agudo, and V. J. Monserrat. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. Ecology Letters 8:11:1138–1146

Winkler, R. 2006a Valuation of ecosystem goods and services Part 1: An integrated dynamic approach, Ecological Economics, in press.

Winkler, R. 2006b Valuation of ecosystem goods and services Part 2: Implications of unpredictable novel change, Ecological Economics, in press.

Woodward, R.T. and Yong-Suhk Wui 2001. The economic value of wetland services: a meta-analysis, Ecological Economics 37: 257–270.