

CHAPTER SIX

The links between biodiversity, ecosystem services and human well-being

ROY HAINES-YOUNG

MARION POTSCHIN

*Centre for Environmental Management,
School of Geography, University of Nottingham*

“The degradation of ecosystem services poses a significant barrier to the achievement of the Millennium Development Goals and the MDG targets for 2015” (Millennium Ecosystem Assessment, 2005. p18).

Managing ecosystems for people

No matter who we are, or where we live, our well-being depends on the way ecosystems work. Most obviously, ecosystems can provide us with material things that are essential for our daily lives, such as food, wood, wool and medicines. Although the other types of benefit we get from ecosystems are easily overlooked, they can, for example, also play an important role in regulating the environments in which we live. They can help ensure the flow of clean water and protect us from flooding or other hazards like soil erosion, land-slips and tsunamis. They can even contribute to our spiritual well-being, through their cultural or religious significance or the opportunities they provide for recreation or the enjoyment of nature.

In this chapter, we will look at the good and services that ecosystems can provide and the role that biodiversity may play in producing them¹. There are many different types of arguments we could make about the importance of conserving the earth's biodiversity. Limitations of space mean that we have to focus on just one aspect, that is the contribution that biodiversity makes to people's livelihoods, to their security and to their health. In other words we will concentrate mainly on the *utilitarian* value of biodiversity. In doing so, we will also look at how these ideas link up with those of the ecosystem approach to environmental management and policy, and some of the implications of this idea for how sustainable development is defined. However, while we are selective in the view we take, this does not mean that traditional ideas about the need for conservation are unimportant. Those making the case for biodiversity need to set these issues in a boarder context, and consider whether nature has utilitarian as well as intrinsic values (see for example, Chan et al., 2007).

The current interest in ecosystem services has come from several sources. The most widely acknowledged is perhaps the Millennium Ecosystem Assessment (MA, 2005), which was the first comprehensive global assessment of the implications of ecosystem change for people. It came about as the result of a call in 2000, by the then UN Secretary-General Kofi Annan, to “assess the consequences of ecosystem change for human well-being and the scientific basis for action needed to enhance

¹ While many commentators use the terms 'goods' and 'services' to distinguish between the more tangible and intangible outputs from ecosystems, others treat them as synonyms. In this text we make no distinction between them and use the term 'services' to cover both.

the conservation and sustainable use of those systems and their contribution to human well-being². The work began in 2001 and involved over 1,300 international experts. It resulted in a series of publications in 2005, that described the condition and trends of the world's major ecosystems and the services they provide, and the options available to restore, conserve or enhance their sustainable use.

The key finding of the MA was that currently 60% of the ecosystem services evaluated are being degraded or used unsustainably. It was argued that such a situation has major implications for development, poverty alleviation, and the strategies needed by societies to cope with, and adapt to, long-term environmental change. The key implication, flagged up in our opening quote, was that given such trends it is unlikely that the global community would achieve the so-called Millennium Development Goals that it had set itself in 2000³. The elimination of extreme poverty is a key international challenge, for as the Brundtland Report⁴ argued in 1987, it is one of the major factors leading to environmental degradation and loss of biodiversity. The impacts of biodiversity loss on well-being are uneven across communities, affecting those who depend most on environmental resources such as subsistence farmers and the rural poor (Díaz et al., 2006). A summary of the kinds of pattern we now see emerging is to be found in the first report of the study initiated by the G8+5 meeting in March 2007, on *The Economics of Ecosystems and Biodiversity* (European Commission, 2008).

Although important, the Millennium Ecosystem Assessment is not the only stimulus to the current interest in ecosystem services. In fact, the idea has a longer history. Following Mooney and Ehrlich (1997), Cork et al. (2001) trace the development of the concept to the 1970 Study of Critical Environmental Problems (SCEP, 1970), which first used the term '*environmental services*'. It is possible that elements of the idea can be found earlier even, in Leopold's *Sand County Almanac* (Grumbine, 1998). Nevertheless, Holdren and Ehrlich (1974) went on to refine the list of services proposed in the SCEP study, referring to them as '*public service functions of the global environment*'. Westman (1977) later reduced this to '*nature's services*' and finally the term '*ecosystem services*' was used by Ehrlich and others in the early 1980s (Mooney and Ehrlich, 1997). The concept is also specifically covered by the principles underlying the Ecosystem Approach as set out in the Convention for Biological Diversity (CBD)⁵.

As described elsewhere in this volume, 'The Ecosystem Approach' emerged as a topic of discussion in the late 1980s and early 1990s amongst the research and policy communities concerned with the management of biodiversity and natural resources (see also Hartje et al., 2003). People argued that a new focus was required to achieve robust and sustainable management and policy outcomes. An Ecosystem Approach, it was suggested, would deliver more *integrated* policy and management at a landscape-scale and be more firmly directed towards human well-being.

According to the CBD, the Ecosystem Approach seeks to put human needs at the centre of biodiversity management. If we are to ensure that decisions take full account of the value of natural resources and biodiversity, then the links between biodiversity and well-being must be clear – hence the emphasis that the Convention places on identifying the benefits from nature. Under the Convention, the Ecosystem

² <http://www.millenniumassessment.org/en/About.aspx> (accessed 24th July, 2008)

³ <http://www.un.org/millenniumgoals/> (accessed 24th July, 2008)

⁴ <http://www.worldinbalance.net/pdf/1987-brundtland.pdf> (accessed 24th July, 2008)

⁵ <http://www.cbd.int/ecosystem/principles.shtml> (accessed 24th July, 2008)

Approach forms the basis for considering all the services provided to people by biodiversity and ecosystems in a holistic framework (Secretariat of the Convention for Biological Diversity, 2004).

The design of environmental management strategies or policies for future development often involves weighing up the consequences of proposed actions. We need to consider impacts upon ecosystems as well as the social and economic systems to which they are linked – so that the choices society makes are as well informed as possible (Potschin and Haines-Young, 2006). Thus questions about what kinds of service an ecosystem can provide, how much of these services we need now and in the future, and what might threaten their output are fundamental. Ecologists have much to contribute to such debates. Decisions about policy and management may ultimately be a matter of societal choice but as the Ecosystem Approach recognises, those decisions have to be grounded on a good understanding of biophysical limits that constrain ecological processes and the spatial and temporal scales at which they operate. Thus before we can take the Ecosystem Approach forward, we need to explore the science that underpins these ideas.

What is an ecosystem service?

Although we can define an ecosystem service in fairly simple terms, as ‘the benefits ecosystems provide’ (MA, 2005, p.1), it can become quite difficult to be precise about what an ecosystem service is when we try to apply the idea. A number of scientists have attempted to construct typologies of ecosystem services, that is a categorization of different types of service, and it is useful to start by looking at what has been achieved.

In the typology suggested by the MA, four broad types of service were recognized, namely: those that cover the material or *provisioning* services; those that cover the way ecosystems *regulate* other environmental media or processes; those related to the *cultural* or spiritual needs of people; and finally the *supporting* services that underpin these other three types. Examples of services under each of these broad headings, and their relationship to different components of human well-being are illustrated in Figure 1 and Table 1. The typology shown in Table 1 is from Kremen (2005), but it is based on the MA. It is particularly useful because it also attempts to detail some of the ecological and spatial characteristics of the services.

>>>Insert Figure 1 about here

>>>Insert Table 1 about here

It is important to note several things about the typology and relationships shown in Figure 1. First, ‘biodiversity’ *per se* is not a service; rather, the MA represents the services as flowing directly from the presence of life on earth. This is an important point, because it suggests that ecosystem services depend fundamentally on the structures and processes generated by living organisms and their interactions with, and processing of, abiotic materials. As a result some commentators (Swallow et al., 2007; Smith, 2006) think it may be useful to distinguish between ecosystem services that are a consequence of biodiversity, and a more general class of ‘environmental services’, like wind or hydraulic potential, that have a more indirect connection. Wind or hydraulic flows may be affected by the presence of living organisms, but ecological processes are not primarily responsible for them.

The second important point to note about the typology shown in Figure 1 is that the supporting services have a different relationship to human well-being than the other three types of service. As the diagram suggests, they do not directly benefit people,

but are part of the often complex mechanisms and processes that generate them. As Banzhaf and Boyd (2005), Boyd and Banzhaf (2005, 2006) and Wallace (2007) have noted, the MA and the wider research literature is in fact extremely ambiguous about how to distinguish between the mechanisms by which services are generated (called by some ecosystem functions) and the services themselves. This situation prevails despite the many attempts to provide systematic typologies of ecosystem functions, goods and services (Binning et al., 2001; Daily, 1997; de Groot, 1992; de Groot et al., 2002; MA, 2005).

The problem is an important one to resolve, because unless we can be clear about what a service actually is, it is difficult to say what role 'biodiversity' plays in its generation. Wallace (2007) has been one of the most recent to comment on the problems that the MA typology poses. He suggests that if we are to use the idea of ecosystem services to help us make decisions, then it is essential that we are able to classify them in ways that allow us to make comparisons and so evaluate the consequences of different management or policy strategies. The main problem with the MA typology, according to Wallace (2007, 2008), is that it confuses *ends* with *means*; that is the benefit that people actually 'enjoy' and the mechanisms that give rise to that service. A service is something that is consumed or experienced by people. All the rest, he argues, are simply part of the ecological structures and processes that give rise to that benefit.

Service cascades

A way of representing the logic that underlies the ecosystem service paradigm and the debates that have developed around it is shown in Figure 2. The diagram makes a distinction between ecological structures and processes created or generated by living organism and the benefits that people eventually derive. In the real world the links are not as simple and linear as this. However, the key point is that there is a kind of cascade linking the two ends of a 'production chain'. The idea is best illustrated by an example.

>>>Insert Figure 2 about here

The presence of ecological structures like woodlands or other habitats such as wetlands in a catchment may have the capacity (function) of slowing the passage of surface water. This function can have the potential of modifying the intensity of flooding. It is something *humans* find useful – and not a fundamental property of the ecosystem itself – that is why it is sometimes helpful to separate this capability out and call it a function. However, whether this function is regarded as a service or not depends upon whether 'flood control' is considered as a benefit. People or society will value this function differently in different places at different times. Therefore in defining what the 'significant' functions of an ecosystem are and what constitutes an 'ecosystem service', an understanding of spatial context (geographical location), societal choices and values (both monetary and non-monetary) is as important, as knowledge about the structure and dynamics of ecological systems themselves.

In following the 'cascade' idea through it is important to note the particular way that the word 'function' is being used, namely to indicate some capacity or capability of the ecosystem to do something that is potentially useful to people. This is the way commentators like de Groot et al. (2002) and others (e.g. Costanza et al., 1997; Daily 1997) use it in their account of services. However, as Jax (2005) notes the term function can mean a number of other things in ecology. It can mean something like 'capability' but it is often used more generally also to refer to processes that operate within an ecosystem (like nutrient cycling or predation). This is the way Wallace

(2007) uses it, although he suggests that we drop the term altogether to avoid confusion. We cannot, however, be prescriptive about the way scientists use words – this is how concepts develop. We have simply included the idea of functions as capabilities in Figure 2 to help those less familiar with the field to pick their way through current debates.

The second important idea that the cascade model tries to flag up is that services do not exist in isolation from people's needs. We have to be able to identify a specific benefit or beneficiary to be able to say clearly what is, or is not, a service. It is this property which makes Banzhaf and Boyd (2005, p.12), suggest that service typologies are difficult to construct. They sum it up by claiming that identification of what is an ecosystem service depends on context because they are '*contingent*', that is depend on, '*particular human activities or wants*'. The problem, which is also recognised by Wallace (2007), is illustrated by Figure 3. This diagram shows the different roles that 'water quality' can have in the analysis of ecosystem services and societal benefits.

>>>Insert Figure 3 about here

In Figure 3 clearly the quality of the water body plays an important role in the ecosystem service 'supply chain' that produces the benefits we might recognise as 'recreational angling' and 'the provision of drinking water'. However, only in the case of drinking is the water **directly** consumed, and so only here is 'the water body's quality' to be regarded as a service. Wetlands and natural riparian land cover are important assets that help deliver that service, but they are not, according to Banzhaf and Boyd (2005) services in themselves. By contrast, for recreational angling the water body's quality is no longer the service. Here the things being used directly are the fish population (bass) and elements of the environment such as the presence of the surrounding vegetation which may influence the quality of the angling experience. The value of the water body's quality is taken account of in the service represented by the fish stock. Thus in this situation the quality of the water is more of a function or capability of the ecosystem; it is needed to produce the service. Notice also in Banzhaf and Boyd's (2005) scheme that services and benefits are quite distinct. As Fisher and Turner (2008) note, a benefit is something that directly impacts on the welfare of people, like more or better drinking water or a more satisfying fishing trip. For them, in contradistinction to the definition given by the MA, a service is not a benefit – but something that changes the level of well-being (welfare).

Evolving Service Typologies

So what might the ecologist make of such a discussion? The simple message is that while the idea of ecosystems producing services is an attractive one, as with all things, the scientist has to be careful to specify clearly what he or she is looking at. This is particularly so in a new field like this, where concepts are developing rapidly. However, the conclusion that ecosystem services appear to be defined by human activities and needs appears fairly sound. This observation has a number of implications that are useful if we are to make progress:

- The contingent nature of services suggests that it is unlikely that we can ever devise any simple, generic checklist of services that ecosystems or regions might support, as many commentators have tried to do. Rather the task seems to be one of treating things like the MA list of services more as a menu of **service-benefit themes**, and of using the cascade to examine how particular systems operate in particular places. We must treat concepts like 'processes', 'functions', 'services' and 'benefits' more as prompts to help sort

out the complexities of a given problem rather than as a set of water-tight definitions that the world has to be squeezed into.

- While it is important to identify the 'final product' that is consumed or used by people, so that we can value or look at the adequacy of different levels of service output, we should not overlook the importance of the other ecosystem components on which it depends. In fact, as Fisher and Turner (2008), and Costanza (2008) have argued, services do not have to be utilised directly by people. These workers prefer to think of intermediate and final services or products, rather than getting trapped in arguments about what is and is not a service (see Figure 2). This is probably helpful, because in many cases the contribution that biodiversity makes to well-being, is only part of a much larger system that may include social and economic elements.

It is likely that typologies of ecosystem services will continue to evolve. And, as Costanza (2008) has pointed out, we may envisage other ways of categorising them besides the type of listing suggested by the MA or Wallace (2007). For example, Costanza (2008) suggests that ecosystem services can also be classified according to their *spatial* characteristics (Table 2). Some, like carbon sequestration, are global in nature; since the atmosphere is so 'well-mixed' all localities where carbon is fixed is potentially useful. By contrast, others, like waste treatment and pollination depend on proximity. "Local proximal" services are, according to Costanza (2008), dependent on the co-location of the ecosystem providing the service and the people who receive the benefit. He also distinguishes services that 'flow' from the point of production to the point of use (like flood regulation) and those that are enjoyed at the point of where they originate ('in situ' services). Finally he identifies services like cultural and aesthetic ones, which depend on the movement of users to specific places.

>>>Insert Table 2 about here

To emphasise his point about the need for different classification schemes, Costanza (2008) also highlights classifications of services that try to describe the degree to which users can be excluded from accessing them, or the extent to which users may interfere with each other when they enjoy the service (Table 3). Those goods and services that are privately owned sold on a market are classified as 'excludable'. The owner or provider can regulate access to the service, normally via price. Moreover, with such services, consumers are often 'rivals' in that if one consumes or enjoys the good the other cannot because the service or good is finite. Most provisioning services fall into this category. A variation on this type of service is something like 'observing wildlife', which is in principle excludable but non-rival; what one person observes does not prevent others from experiencing the same thing. The problem with many ecosystem services, and this is the significance of this type of classification for ecosystem managers, is that some services are open access or 'common pool' resources, from which it is very difficult to exclude potential users. While users may or may not interfere with each other in using them, on the whole it is very difficult to quantify their value to society or have these values included in decision making. As Hardin (1968) pointed out many years ago, the fate of such common pool resources is often one of progressive degradation or loss. Marine fisheries are examples of rival, non-excludable services. Many of the regulating services, like flood protection are open access but non-rival.

>>>Insert Table 3 about here

A key theme of the Ecosystem Approach is the emphasis it gives to holistic or 'joined up' thinking. If ecologists are to engage effectively in such work then they must connect with other disciplines to understand how they also look at the world.

Although ecologists and natural resource managers have been actively involved in the debate about ecosystem services, it is important to note that the way the concepts and terminology is developing is also being shaped by geographers, economists and a range of other social and natural sciences. Many disciplines are all interested in the problems that arise at the interface of people and the environment. If we are to discover and describe fully the importance of biodiversity to human well-being then we have to understand just how the connections to well-being are made. In the last part of this chapter we will therefore look at what progress has been achieved in understanding the role of biodiversity in the production of ecosystem services.

Biodiversity, ecosystem function and service output

How sensitive is ecosystem service output to changes in biodiversity? The assumption that they are is implicit in many of the arguments people make about conserving and restoring ecological systems, but what evidence is there to support this assertion?

>>>Insert Figure 4 about here

A review by Schwartz et al. (2000) takes stock of the evidence linking biodiversity and ecosystem function over the previous decade or so, and in particular the implications it has for the conservation debate. The review is a useful starting point, because these authors set out very clearly the kind of issue experimental and observational studies face in resolving these key questions. Schwartz et al. (2000) suggest that in order to use the link between biodiversity and ecosystem function as the basis for arguing that the conservation of biodiversity is important, two conditions need to be met. Crucially, we would need to show that the maintenance of ecosystem function and the output of ecosystem services are dependent on a *wide range of native species*. They also note that while a number of different types of relationships between biodiversity and ecosystem function are possible, for the conservation case to be strengthened a *direct and positive association* needs to be observed.

Figure 4 illustrates the kinds of relationship between biodiversity and ecosystem function that might exist. Curves A and B are those suggested by Schwartz et al. (2000). We have added a third relationship to those they suggested, which we will discuss later; for the moment let us consider only A and B.

The important difference between curves A and B in Figure 4 is that in A ecosystem function is highly sensitive to variations in biodiversity, and in B there is a 'saturation' effect, ecosystem function is only dependent upon biodiversity at low levels of species richness. Schwartz et al. (2000) note that the difficulty of observing relationships like curve B for the advocates of conservation is that it suggests that systems can lose much of their diversity without affecting their functioning (operation) and potentially the benefits they provide for people. In these situations we appear to be buffered from the effects of biodiversity loss.

From their review of a range of empirical studies and modelling exercises, Schwartz et al. (2000) concluded that few studies supported the hypothesis that there was a simple, direct linear relationship between species richness and some measure of ecosystem functioning like productivity, biomass, nutrient cycling, carbon flux or nitrogen use. Instead the evidence available to them suggested that these functions did not increase proportionally above a threshold that represented a fairly low

proportion of the local species pool. Others who have questioned the existence of the relationship include Aarssen, (1997), Grime, (1997), Huston, (1997) and Wardle et al., (1997). Some have even suggested that any observed positive association is an artefact or sample effect. By considering a greater number of species one is, for example, more likely to include highly productive ones (Huston & McBride, 2002; Thompson et al., 2005).

In reviewing these arguments about the links between biodiversity and ecosystem functioning, it is important to note that there is considerable disagreement about what the evidence shows because the problem is such a complex one. Loreau et al. (2001) have, for example, suggested that any simple resolution of the question is difficult because there is considerable uncertainty about how results 'scale up' to whole landscapes and regions, and how far one can generalise across ecosystems and processes; Swift et al. (2004) makes a similar point in the context of agricultural systems. We might add that a further complexity arises because of the very different ways in which 'biodiversity' is measured.

Biodiversity in the sense of species richness may be important for ecosystem functioning, but so might other aspects of ecosystem structure. As Díaz et al. (2007) point out, biodiversity in its 'broadest sense' covers not only the number of species, but also the number, abundance and composition of genotypes, populations, functional groups, and even the richness of spatial patterns exhibited by habitats mosaics and landscapes. Once again, we have to look carefully at what is being measured and reported. Conclusions like those of Schwartz et al. (2000) cannot be taken at face value. Others have argued that the evidence suggests there is a clear and direct relationship between key aspects of ecosystem function and various measures of biodiversity besides richness, such as number of functional groups or evenness.

Balvanera et al. (2006), for example, have recently undertaken an extensive meta-analysis of experimental studies involving the manipulation of different components of biodiversity and the assessment of the consequences for ecosystem processes. Their analysis suggests that in general current evidence supports the contention that for various measures of biodiversity there *is* a positive association with a number of different measures of ecosystem functioning. The small number of negative relationships reported in the literature, they suggest, tended to be associated with studies which measured properties at the population (individual species density, cover or biomass), rather than those which looked at community level characteristics (e.g. density, biomass, consumption). The strength of the relationship between biodiversity and the measure of ecosystem function tended to be strongest at the community rather than the whole ecosystem level. A number of mechanisms underpin the relationships observed; we will consider species complementarity and the role of functional groups. The discussion will also flag up the threats that invasions of alien species might have for the output of ecosystems services and the 'insurance value' of diverse ecological systems for human well-being.

Species complementarity

Much of the discussion about the links between components of biodiversity and ecosystem functioning has been focused at what the MA call 'supporting services' or what we have called 'intermediate products'. These are things which are not consumed by people directly but may contribute to some final benefit. Few studies have been able to trace the complete 'production chain' from ecological structure and processes through to human well-being. As Balvanera et al. (2006) note, the majority of studies have focused on the consequences of biodiversity change for ecosystem

productivity, and has tended to be derived from ecosystems that are easily manipulated such as grasslands. Nevertheless while the evidence for the mechanisms linking biodiversity to ecosystem function is indicative rather than conclusive, some insights are possible.

Productivity is in fact an important ecosystem function to consider because while it may not often be a direct service, it underpins many other kinds of output. For example more productive woodlands may support a larger standing crop of timber and hence offer greater flood or climate regulating services. Richmond et al. (2007) suggest, in fact, that terrestrial net primary productivity can be used as a proxy or indicator for a number of other ecosystem services. In support of their argument they cite the work of Gaston (2000) who observed that the output of food, timber and fibre tends to be higher in areas with high net primary production, and that at global scales, patterns of biodiversity and the services associated with it generally increases with net primary production. The accumulation of biomass also has a beneficial 'supporting role' through its contribution to soil formation and the protection of soils from erosion. This kind of view is also supported by Costanza et al. (2007) who have investigated the inter-dependence of net primary productivity and biodiversity at very broad spatial scales, namely for ecoregions in North America. They found that over half the spatial variation in net productivity could be explained by patterns of biodiversity, if the effects of temperature and precipitation were taken into account. Using the relationships they develop, these authors predict that across the temperature ranges in which most of the world's biodiversity is found occur, a 1% change in biodiversity results in a 0.5% change in the value of ecosystem services.

Positive diversity-productivity relationships have been observed in a number of terrestrial systems at local scales. In grassland systems in Europe, for example, there is good experimental evidence that maintaining high levels of plant species diversity increases grassland productivity. Fagan et al. (2008) have observed that for restored grasslands on a range of soil types across southern England, there appears to be positive effects of increased species richness on ecosystem productivity. In contrast to earlier studies which monitored systems over relatively short periods, the conclusions of this study were based on data collected over eight years. Naeem et al., (1995), Tilman et al., (1996, 1997a&b) and Lawton et al. (1998) have also provided evidence to support the existence of a direct positive relationship, and Cardinale et al. (2007) have also emphasised that the productive advantage of mixtures or over monocultures appears to increase over time.

Similarly, a close association between biodiversity and ecosystem functioning is also apparent in many soil ecosystems. Lavelle et al. (2006), for example, reports that many experiments have shown significant enhancements of plant production in the presence of Protoctista, Nematodes and Enchytraeidae, Collembola and combinations of these organisms, as well as termites, ants and earthworms. A number of factors may be responsible for such effects, including: increased release of nutrients in the plant rhizosphere; the enhancement of mutualistic micro-organisms, mycorrhizae and N-fixing micro organisms; greater protection against pests and diseases, both above and below ground; greater protection against pests and diseases; the positive effect of micro-organisms on soil physical structure; and the production of plant-growth promoters.

Hooper et al. (2005) have made an extensive review of many of the issues that have been the focus of recent discussion, and conclude that certain combinations of species are complementary in their patterns of resource use and can increase average rates of productivity and nutrient retention. 'Complementarity' is said to exist when species have niche relationships that allow the species group to capture a

wider range of resources in ways that do not interfere with each other over space or time or when inter-specific interactions between species enhance the ways they collectively capture resources compared to when they grow in isolation (Cardinale et al., 2007; Hooper, 1998). Hooper et al. (2005) argue that the diversity of functional traits in the species making up a community is one of the key controls of ecosystem properties. While there is a potentially large variability across ecosystems in terms of species and functional diversity, there is clear evidence, they suggest, that variations in ecosystem function can “at least in part” be explained by “differences in species or functional *composition*” (italics ours).

It seems that similar conclusions can also be drawn for many marine systems. Worm et al. (2006), for example, have identified a fairly strong positive association between biodiversity and productivity in marine systems, based on their meta-analysis of published experimental data. They found that the evidence suggested that increased biodiversity of both primary producers and consumers appeared to enhance the ecosystem processes examined. By way of explanation they identified a number of factors, including complementary resource use, positive interactions between species and increased selection of highly performing species at high diversity. Moreover, they noted that the restoration of biodiversity in marine systems was also found to substantially increase productivity.

The importance of functional groups and functional traits

While there is evidence that species richness is important for maintaining ecosystem functioning, the existence of potential complementary relationships between species suggests that the presence of particular groups of species with particular properties or capabilities is also significant. As Kremen (2005) notes, although we generally understand ecosystem services to be properties of whole ecosystems or communities, the functions that support them often depend upon particular populations, species, species guilds or habitat types. Thus the analysis of functional traits, that is the particular distinguishing properties of different ecological groupings within an ecosystem, has emerged as an important area of research in relation to understanding how ecosystem services are generated (Diaz et al. 2007; Balvanera et al. 2006).

De Bello et al. (2008, p4) define a functional trait as “a feature of an organism which has demonstrable links to the organism’s function”, that is to its role in the ecosystem or its performance. “As such,” they suggest, “functional traits determine the organism’s effects on ecosystem processes or services (effect traits) and/or its response to pressures (response traits)”. Although the notion of a functional trait is most easily applied at the species level, the concept can also be extended to groups of organisms with similar attributes, all of which may possess (sometimes to different degrees) similar effects or response characteristics. Whether it be at the level of single species or some wider grouping, however, there is growing consensus that ‘functional diversity’, that is the type, range and relative abundance of functional traits in a community can have important consequences for ecosystem processes (De Bello, 2008).

For example, the picture that has emerged from recent work on nutrient cycling is that functionally diverse systems appear to be more effective in retaining nutrients than simpler ones (Hooper and Vitousek, 1997, 1998). Engelhardt and Ritchie (2001) have shown that in wetland systems, not only does increased flowering plant diversity enhance productivity, but it also aids the retention of phosphorus in the system, thereby aiding the water purification service. The ability of vegetation to capture and store nutrients is also widely recognised in the practice of establishing

buffer strips along water courses to protect them from agricultural run-off as part of water purification measures. However, the effect may not simply be additive, but more to do with the presence of particular groups of species, their particular capabilities or functions, and their abundance in relation to the level of nutrient in the system.

The relationship between plant diversity and the retention of soil nutrients appears to be due to direct uptake of minerals by vegetation and by the effects of plants on the dynamics of soil microbial populations (Hooper and Vitousek 1997, 1998, Niklaus et al., 2001). The importance of diversity in relation to nutrient cycling is, in fact, particularly strong in soil ecosystems. Brussaard et al. (2007), for example report that there is evidence to suggest that increased mycorrhizal diversity positively contributes to nutrient and, possibly, water use efficiency. Barrios (2007) has also recently reviewed the importance of the soil biota for ecosystem services and land productivity, and notes the evidence pointing to the positive impacts of micro-symbionts on crop yield, as a result of increases in plant available nutrients. This is especially due to those functional groups that contribute to fertility through biological nitrogen fixation, such as *Rhizobium*, and phosphorus through arbuscular mycorrhizal fungi (see for example, Giller, 2001 and Smith and Read, 1997, cited by Barrios, 2007).

Using the terminology of response and effect traits outlined above, we can therefore see that by promoting particular functional responses in one group of organisms by appropriate land management, in this case the soil biota, particular effects might be achieved elsewhere by virtue of the way other organism groups react to changed ecosystem functioning. Schimel and Gullledge (1998) have made the distinction between what they call “narrow processes”, like nitrification, which are performed by small number of key species, and other processes, such as decomposition, which tend to be dependent upon a wider range of organisms. Narrow processes, it would seem may be more susceptible to changes in biodiversity or the abundance of particular functional groups, than the broader ones, although generalisations are often difficult to make. In the case of nitrification, for example, this may be a narrow process but the organisms which carry it out are widespread, and so it appears to be a fairly resilient process.

In relation to the processes leading to soil formation and stabilisation it has been suggested that it is not the abundance and diversity of soil organisms that it most important, but rather their functional attributes (e.g. Swift et al., 2004). Thus de Ruiter et al. (2005) have shown, for example, that stability of the soil ecosystem is closely linked to the relative abundance of the different functional groups of organisms. Soil macrofauna (e.g. ants, termites, and earthworms) have also been observed to play an important role in the modification of soil structure through bioturbation, the production of biogenic structures (Brussaard et al., 2007; Lavelle and Spain, 2001), and thus have an important affect soil water and nutrient dynamics through their impact on other soil organisms (Barrios 2007). Earthworms and macro- and micro-invertebrates can increase soil structure via burrows or casts and enhance soil fertility through partial digestion and communitation of soil organic matter (Zhang et al., 2007).

The analysis of functional groups and their associated traits is not, of course, restricted to soil ecosystems but can be applied more generally. A particular issue that has attracted much in the recent literature is the vulnerability of the service provided by pollinators (Losey and Vaughan, 2006; Zhang et al., 2007). It has been estimated that the production of over 75% of the world's most important crops and 35% of the food produced is dependent upon animal pollination (Klein et al., 2007).

Bees are the dominant taxa providing crop pollination services, but birds, bats, moths, flies and other insects can also be important. Pollinator diversity is essential for sustaining this highly valued service, which Costanza et al. (1997) estimated at global scales to be worth about \$14 per ha per year. However, as Hajjar et al. (2008) have argued, the loss of biodiversity in agro-ecosystems through agricultural intensification and habitat decline has adversely affected pollination systems and has caused the loss of pollinators throughout the world (Kearns et al., 1998; Kremen et al., 2002, 2004; Ricketts et al., 2004).

The consequences of such losses of pollinators for ecosystem functioning have been documented by Richards (2001) who has described a number of cases where low fruit or the setting of seeds by crops and the reduction in crop yields has been attributed to a fall in pollinator diversity. There is increasing evidence that conserving wild pollinators in habitats adjacent to agriculture improves both the level and stability of pollination, leading to increased yields and income (Klein et al., 2003). Indeed, several studies from Europe and America have demonstrated that the loss of natural and semi-natural habitat, such as calcareous grassland, can impact upon agricultural crop production through reduced pollination services provided by native insects such as bees (Kremen et al., 2004).

Despite these concerns, little was known until recently about the patterns of change and what implication the loss of pollinators might have. However, an important addition to the literature has been made by Biesmeijer et al. (2006), who looked at the evidence available for the parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands.

Biesmeijer et al. (2006) compiled almost one million records for all native bees and hoverflies in both countries that could provide evidence of changes in abundance. Their analysis, which compared the period up to 1980 with that since, found that there was evidence of declines in bee abundance in Britain and the Netherlands, but that the pattern was more mixed for hoverflies, with declines being more dependent on location and species assemblage. In both countries those functional groups of pollinators with the narrowest habitat requirements were the ones to show the greatest declines. Moreover, in Britain, it was found that those plants which are most dependent on insect pollinators (the functional group represented by obligatory out-crossing plants) were also declining, compared to other plant groups which depended on water and wind for pollination or were self-pollinating. Wind and water pollinated plants were found to be increasing while those that were self-pollinators were broadly stable. As Biesmeijer et al. (2006) note, while it is difficult to determine whether the decline in insect pollinated plants precedes the loss of pollinators or vice versa, taken together, they suggest that in Britain especially, we are seeing a causal connection between local extinctions of functionally linked plant and pollinator species.

Thus while species richness per se may be important in relation to the maintenance of ecosystem functioning, the role of particular 'keystone' species or groups, with particular functional capabilities in communities should not be overlooked. This was the basis of the additional relationship that we recommended in Figure 4 (Curve C), which suggests in certain circumstances, the removal of one or a small component of biodiversity can have a proportionally large effect on ecosystem functioning (cf. Kremen, 2005). There are, in fact, many situations in which particular species have been found to play pivotal roles in maintaining ecosystem processes.

Alien vs. native species

As noted above, Schwartz et al. (2000) argued that along with evidence for a direct relationship between biodiversity and ecosystem functioning, the conservation argument may be strengthened if it can be shown that services are also dependent on the presence of a wide range of *native* species. Complementary functional relationships between species or species groups do not normally arise by chance, but comes about through of some kind of co-evolutionary process. Thus it is hardly surprising that the introduction of alien species might undermine such relationships and potentially disrupt service output.

There are two key issues that have been the focus of recent discussion in relation to the threat posed by alien species to ecosystem functioning. First, the properties of ecosystems that makes them resistant to invasion. Second, the impact that aliens might have on ecosystem functioning or service output.

Balvanera et al. (2006) suggest that the regulation of invasive species by native flora is a service of economic importance. On the basis of their meta-analysis they suggest that when plant diversity was highest, the abundance, survival, fertility of invaders was reduced. Hooper et al. (2005) draw similar conclusions. They suggest that current evidence indicates that susceptibility to invasion by exotic species is strongly influenced by species composition and, under similar environmental conditions, generally decreases with increasing species richness. However, other factors, such as propagule pressure, disturbance regime, and resource availability also strongly influence invasion success. Klironomos (2002) has also shown that the soil microflora may also be important in controlling invisibility of communities. In an experimental study he found that while some plants maintained low densities on 'home soils' as a result of the accumulation of species-specific pathogens, plants alien to these conditions did not, and could become invasive. Thus other factors may override effects of species richness. Hooper et al. (2005) caution that by increasing species richness one may actually increase the chances of invasibility within sites, if these additions result in increased resource availability, as in the case of nitrogen-fixers, or increased opportunities for recruitment through disturbance.

There is a long history of people intervening and encouraging or promoting the spread of alien species – often with damaging consequences for ecosystem services. Bosch and Hewlett (1982), for example, reviewed evidence from 94 experimental catchments, and concluded that forests dominated by coniferous trees or *Eucalyptus* spp. caused larger changes than native deciduous hardwoods on water supply following planting. Calder (2002) reports that in South Africa reforestation with exotic species such as *Pinus* spp. and *Eucalyptus* spp. significantly increased the probability of drought by reducing water flows in the dry season. In Europe, Robinson et al. (2003) reported significant changes in flows at the local scale, especially in *Eucalyptus globulus* plantations in Southern Portugal. Elsewhere, in Chile Oyarzun and Huber (1999) showed that *Pinus radiata* and *Eucalyptus* decreased water supply during the summer period.

On the basis of such evidence, Görgens and van Wilgen (2004) have suggested that invasive plants may in some situations have a negative impact on water resources. van Wilgen (in press), for example, makes an assessment of the current and potential impacts of invasive alien plants on selected ecosystem services in South Africa. They estimate reductions in surface water runoff as a result of the current level of invasion was equivalent to about 7% of the national total. Most of this is from the shrublands of the fynbos and grassland biomes. The analysis suggests that the potential reductions in water supply would be significantly higher if the invasive

species occupied their full potential range. Impacts on groundwater recharge would be less severe. As a result of the current level of invasion of alien species it was estimated that in relation to the potential number of livestock that could be supported, there was a reduction in grazing capacity of around 1%. However, they estimate that future impacts could be closer to 71%.

Although the introduction and spread of alien or invasive species may be problematic, their control may also pose difficulties. The recent study by Marrs et al. (2007) has, for example, highlighted just how important it is to understanding the ability of ecosystems to retain nutrients. Their work aimed to develop management strategies for the control of bracken encroachment in semi-natural communities in the UK. They found that bracken has a much greater capacity to store C, N, P, K, Ca and Mg than the other vegetation components associated with semi-natural habitats. As a consequence when bracken control measures are applied, there is a higher risk of the nutrients being released to into the environment through run-off. The authors point out that this effect poses a dilemma for policies designed to control a mid-successional invasive species for conservation purposes. There is, they suggest, "a need to balance conservation goals against potential damage to biogeochemical structure and function" (Marrs et al., 2007, p1045). Understanding the trade-offs between the different types of benefit associated with different management strategies or policy options is one of the key concerns of the ecosystem approach.

The insurance value of biodiversity

A novel finding from the Balvanera et al. (2006) review was that as the number of trophic levels increased between the point where the experimental intervention was made and the measurement of effects were recorded, the change in productivity was less marked. This is an interesting finding, because it suggests that ecosystems may sometimes have the capacity to buffer the effects of disturbance at one level and prevent or minimise impacts elsewhere. Such buffering has in fact been widely recognised in the ecological literature, and has been considered in much wider debates concerning the issue of ecosystem resilience.

Kremen (2005) has pointed out that if we are to manage ecosystem services successfully, then we must understand how changes in community structure collectively affect the level and stability (resilience) of the ecosystem services over space and time. Although the links between diversity and stability have long been the subject of debate in ecology (Pimm, 1984, Tilman, 1996), the recent attention to the role of functional groups in communities throws some light into how resilient systems are constructed.

Walker (1995), for example, has argued that ecosystem stability measured by the probability that all species can persist, is increased if each important functional group is made up of several ecologically equivalent species, each with different responses to environmental pressures. In this sense ecological redundancy is good because it enhances ecosystem resilience. This is not to say that functionally important groups that have only one or very few species are not a priority for conservation, because their functions could be quickly lost with species extinctions (Figure 4, Curve C). Nevertheless, the conservation of functional redundancy may also be an important goal, if we are not to live in an unstable world.

Baumgärtner et al. (2005) and Quaas and Baumgärtner (2007) have made a recent analysis of the 'insurance value' of biodiversity in the provision of ecosystem services, and suggest that redundancy of functional groups is an important property securing the output of ecosystem services. However, as the review of Balvanera et

al. (2006) suggest the buffering effects of biodiversity may be quite specific. They found the evidence suggested that while the buffering effects of biodiversity of nutrient retention and the susceptibility to invasive species was positive, it was not so clear for disturbances related to warming, drought or high environmental variability. In the absence of further work, they conclude that a precautionary approach to the management of biodiversity is required.

Biodiversity and social-ecological ecosystems

The Ecosystem Approach emphasises that decisions about biodiversity and ecosystem services have to be looked at in a wider, social and economic context. Thus ecologists have to find ways of linking their insights about the way ecosystems work to broader understandings of how people benefit from nature's services, and what can be done to help sustain and improve their well-being. As a result many of our most basic concepts may need to be rethought. The notion of an ecosystem is, perhaps, one of these.

As Jax (2007) has shown, the ecosystem concept has been used in a number of different ways, and he argues that there is probably no single "right" definition for the term. People, he observes, have modified the idea for their different purposes. It is interesting to note that the same thing is happening in the context of the debate about ecosystem services. Among other things, the cascade model for ecosystem services that we have presented (Figure 2) seeks to emphasise that as scientists we are in fact dealing with a 'coupled social-ecological system' and that if we are to understand its properties and dynamics traditional disciplinary boundaries might need to be redrawn or dissolved. To what extent should societal processes be included within an 'ecosystem'?

The notion of a social-ecological system, or SES, is one that has increasingly been used in the research literature to emphasise the 'humans-in-the-environment' perspective that the Ecosystems Approach promotes. The term SES is also used to emphasise the fact that ecological and social systems are generally both highly connected and co-evolve at a range of spatial and temporal scales (see for example Folke, 2006; 2007). More particularly, Anderies et al. (2004) has suggested that their structure is best understood in terms of the relationships between resources, resource users and governance systems. If we follow this logic, then in defining the nature of the units that we, as ecologists study, we must combine our scientific understandings of the relationships between biodiversity and ecosystem functioning with insights into wider social and economic structures and processes. We can, in fact, see this kind of development in the recent work surrounding the concept of a 'service providing unit'.

The idea of a service providing unit (SPU) was first introduced by Luck et al. (2003), who argued that instead of defining a population or organisms along geographic, demographic or genetic lines, it could also be specified in terms of the service or benefit it generates at a particular scale. For example, an SPU might comprise all those organisms contributing to the wildlife interest of a site or region, or all those organisms or habitats that have a role in water purification in a catchment. It is a kind of ecological 'foot-print' of the service. As the result of work arising out of the *Rubicode*⁶ Project, Vandewalle et al. (2007) have shown how the idea can be linked into the concept of a social-ecological system. The framework shown in Figure 5 is now being used to try understand the way different pressures and drivers impact upon the socio-ecological systems, and the relationships between the particular

⁶ <http://www.rubicode.net/rubicode/index.html> (Accessed 24th July, 2008)

components of biodiversity that generate the service, ecosystem service providers (ESPs), and ecosystem service beneficiaries (ESBs).

>>>Insert Figure 5 about here

Models such as those shown in Figure 5 will enable ecologists to develop a much richer understanding of the links between biodiversity, ecosystem services and human well being. In particular, it will help us identify the kinds of trade-offs that might have to be considered between services if different development paths are chosen. An illustration of the kinds of analysis that we require is provided by the recent work of Steffan-Dewenter et al. (2007) who have looked at the trade-offs between income, biodiversity and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Their study considered the way that incomes changed along a gradient of increasing land use intensity associated with the gradual removal of forest canopies and the reduction of shade. It appeared that there was a doubling of farmers income associated with the reduction of shade from more than 80% to around 30-50%. However, this was associated with only limited losses of biodiversity and ecosystem function, compared to the initial conversion of forest or the complete conversion of agroforestry systems to intensive agriculture. While farmer's incomes increased further with conversion to unshaded agricultural systems, Steffan-Dewenter et al. (2007, p. 4973) suggested that low-shade agroforestry represents the "best compromise between economic forces and ecological needs".

Conclusions

Ecologists will increasingly have to work alongside economists, geographers and a range of other social scientists to understand the value that biodiversity and ecosystem services have, to assess the costs and benefits of different conservation and management strategies, and to help design the new governance systems needed for sustainable development. Biodiversity has intrinsic value and should be conserved in its own right. However, the utilitarian arguments which can be made around the concept of ecosystem services and human well-being are likely to become an increasingly central focus of future debates about the need to preserve 'natural capital'. Thus the wider research community needs to engage with them. Although term sustainable development has come to mean many things the concept must include the maintenance of ecosystem services and the elements of human well-being that depend upon them.

If the Ecosystem Approach is to be embedded in decision making then we need to understand of the links between biodiversity and ecosystem services. We need to be aware of the limits of ecological functioning and the how external pressures may impact on ecological structures and processes. Ecosystems can exhibit non-linear responses to such pressures and the possibility of rapid regime shifts as thresholds are crossed can mean that responses, in terms of service outputs, can be difficult to predict (Carpenter et al. 2006). We also need to better understand the appropriate spatial and temporal scales at which ecological systems operate if the ecosystem services are to be managed wisely or restored if they have been damaged. The task of mapping ecosystem services and the construction of atlases of ecosystem services will provide the opportunity for ecologists and others to work together. It will require the development of new types of spatially explicit models that link biodiversity to ecosystem function and the benefits socio-ecological systems provide in a multi-functional context. Although some progress in mapping ecosystem services has been made (see for example, Naidoo et al. 2008; Naidoo and Ricketts, 2006, Troy and Wilson, 2006a&b, and the InVEST toolbox available through the Natural Capital

Project⁷) many challenges remain. These include developing better theories and better sources of data about biodiversity and the range of supporting services that living organisms provide.

The integrity of ecosystems is fundamental to human well-being. As scientists we need to understand the links between biodiversity and the benefits that people enjoy from nature. We also need to describe to the wider community how these links operate, if biodiversity issues are to be taken into account in decision making. The discussion of ecosystem services is, we suggest, one way of demonstrating the relevance of the Ecosystem Approach to the needs of society.

Acknowledgement

The authors acknowledge the support of various organisations, including the Department for Environment, Food and Rural Affairs (Defra), Natural England and the European Academies Science Advisory Council (EASAC) for project work which informed the contents of this review.

⁷ <http://www.naturalcapitalproject.org/toolbox.html#InVEST> (Accessed 24th July, 2008)

References

- Aarssen, L.W. (1997) High productivity in grassland ecosystems: affected by species diversity or productive species? *Oikos*, 80, 1833-184.
- Anderies, J.M., Janssen, M.A. and Ostrom, E. (2004) A Framework to Analyze the Robustness of social-ecological systems from an institutional perspective. *Ecology and Society* 9(18) [online] available at: www.ecologyandsociety.org/vol9/iss1/art18 (Accessed 24th July, 2008)
- Banzhaf, S., and J. Boyd (2005) *The Architecture and Measurement of an Ecosystem Service Index*. Discussion Paper, Resources for the Future DP 05-22, 54 pp.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. and Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, 9, 1146-1156.
- Barrios, E. (2007) Soil biota, ecosystem services and land productivity. *Ecological Economics*, 64, 2, 269-285.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M. Ohlemüller, R. Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R, Thomas, C.D., Settele, J. and W. E. Kunin (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science*, 313, 351-354.
- Binning, C., Cork, S., Parry, R. and Shelton, D. (2001) Natural Assets: An Inventory of Ecosystem Goods and Services in the Goulburn Broken Catchment. CSIRO Sustainable Ecosystems, Canberra. Download; www.ecosystemservicesproject.org/html/publications/index.htm (accessed 24th August, 2008)
- Bosch, J.M. and Hewlett, J.D. (1982) A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology*, 55, 1982, 3-23.
- Boyd, J., and S. Banzhaf (2005) Ecosystem Services and Government Accountability: The need for a new way of judging Nature's Value. *Resources*, Summer 2005, 16-19.
- Boyd, J. and S. Banzhaf (2006) *What are Ecosystem Services?* Discussion Paper Resources for the Future DP 06-02, 26 pp.
- Brussaard, L., P. C. de Ruiter, et al. (2007) Soil biodiversity for agricultural sustainability. *Agriculture, Ecosystems & Environment*, 121, 3, 233-244.
- Baumgärtner, S., (2007) The insurance value of biodiversity in the provision of ecosystem services. *Natural Resource Modeling*, 20, 1, 87-127.
- Calder, I.R. (2002) Forests and Hydrological Services: Reconciling public and science perceptions. *Land Use and Water Resources Research*, 2, 2.1-2.12
- Cardinale, B.J., Wright, J.P., Cadotte, M.C., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M. and Weis, J.J. (2007) Impacts of plants diversity on biomass production increase through time because of species complementarity. *PNAS* 104, 46, 18123-18128.
- Carpenter, S. R., Bennett, E. M., and Peterson, G. D. (2006) Scenarios for ecosystem services: an overview. *Ecology and Society* 11(1): 29. [online] URL: <http://www.ecologyandsociety.org/vol11/iss1/art29/>

- Chan, K.M., Pringle, R.M., Ranganathan, J., Boggs, C.L., Chan, Y.L., Ehrlich, P.R., Haff, P.K., Heller, N.E., Al-Khafaji, K. and Macmynowski, D.P. (2007) When Agendas Collide: Human Welfare and Biological Conservation. *Conservation Biology*, 21, 1, 51-68.
- Cork, S., D. Shelton, C. Binning and R. Parry (2001) *A framework for applying the concept of ecosystem services to natural resource management in Australia*. Third Australian Stream Management Conference, Brisbane. Cooperative Research Centre for Catchment Hydrology.
- Costanza, R. (2008) Ecosystem services: multiple classification systems are needed. *Biological Conservation*, 141, 350-352.
- Costanza, R., D'Arge, R., DeGroot R., Farber, S., Grasso, M., Hannon B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Raskin, R., Sutton, P. and M. van den Belt (1997) The Value of the World's Ecosystem Services and Natural Capital. *Nature*, 387, 253–260.
- Costanza, R., Fisher, B., Mulder, K., Liu, S., Christopher, T. (2007) Biodiversity and ecosystem services: A multi-scale empirical study of the relationship between species richness and net primary production. *Ecological Economics*, 61, 478-491.
- Daily, G. C. (1997) Introduction: What are Ecosystem Services? In: Daily, G.C. (Ed.) *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C., 1-10.
- De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Bardgett, R., Berg, M., Cipriotti, P., Cornelissen, H., Feld, C., Hering, C., Martins da Silva, P., Potts, S., Sandin, L., Sousa, J.S., Storkey, J. and Wardle, D. (2008) Functional traits underlie the delivery of ecosystem services across different trophic levels. Deliverable of the Rubicode Project (download: www.rubicode.net/rubicode/outputs.html)
- De Groot, R.S., (1992) *Functions of Nature: Evaluation of Nature in Environmental Planning, Management and Decision Making*. Wolters-Noordhoff, Groningen.
- De Groot, R.S., Wilson, M.A. and R.M.J. Boumans (2002) A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics*, 41, 393–408.
- de Ruiter, P.C., Neutel, A.M., Moore, J.C., 2005. The balance between productivity and food web structure in soil ecosystems. In: Bardgett, R.D., Usher, M.B., Hopkins, D.W. (Eds.), *Biological Diversity and Function in Soil*. Cambridge University Press, Cambridge, pp. 139–153.
- Díaz, S., Fargione, J., Chapin F.S. III and Tilman, D. (2007) Biodiversity loss threatens human well-being. *PLOS Biology*, 4, 8, e277. DOI: 10.1371/journal.pbio.0040277.
- Engelhardt, K.A.M., Ritchie, M.E. (2001) Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature*, 411, 6838, 687-689.
- European Commission (2008) The economics of ecosystems and biodiversity. Interim report. http://ec.europa.eu/environment/nature/biodiversity/economics/pdf/teeb_report.pdf (Accessed 24th July, 2008)
- Fagan, K.C., Pywell, R.F., Bullock, J.M., Marrs, R.H (2008) Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. *Journal of Applied Ecology*, 45, 4, 1293-1303

- Fisher, B. and Turner, K. (2008) Ecosystem services: Classification for valuation. *Biological Conservation*, 141, 1167-1169.
- Folke, C. (2006) Resilience: the emerging of a perspective for socio-ecological system analysis. *Global Environmental Change*, 16, 253-267.
- Folke, C. (2007) Social-ecological systems and adaptive governance of the commons. *Ecological Research*, 22, 14-15.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, 405, 220-227.
- Giller, K.E., Bignell, D., Lavelle, P., Swift, M.J., Barrios, E., Moreira, F., van Noordwijk, M., Barois, I., Karanja, N., Huising, J., (2005) Soil biodiversity in rapidly changing tropical landscapes: scaling down and scaling up. In: Bardgett, R., Usher, M.B., Hopkins, D.W. (Eds.), *Biological Diversity and Function in Soils*. Cambridge University Press, Cambridge, pp. 295–318.
- Görgens, A.H.M., van Wilgen, B.W., (2004) Invasive alien plants and water resources: an assessment of current understanding, predictive ability and research challenges. *South African Journal of Science*, 100, 27–34.
- Grime, J.P. (1997) Biodiversity and ecosystem function: the debate deepens. *Science*, 277, 1260-1261.
- Grumbine, R.E (1998) Seeds of Ecosystem Management in Leopold's A Sand County Almanac. Commemorative Issue Celebrating the 50th Anniversary of "A Sand County Almanac" and the Legacy of Aldo Leopold Wildlife Society Bulletin, Vol. 26, No. 4, 757-760
- Hardin, G. (1968) The Tragedy of the Commons. *Science*, 162, 1243-1248.
- Hajjar, R., D. I. Jarvis, et al. (2008) The utility of crop genetic diversity in maintaining ecosystem services. *Agriculture, Ecosystems & Environment*, 123, 4, 261-270.
- Hartje, V., Klaphake, A. and R. Schliep (2003) *The international debate on the ecosystem approach: Critical Review, international actors, obstacles and challenges*. BfN Skripten 80.
- Holdren, J. P. and Ehrlich, P. R. (1974) Human population and the global environment. *American Scientist*, 62, 282-292.
- Hooper, D.U. (1998) The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology*, 79, 704–719
- 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.
- Hooper, D. and Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, 277, 1302-1305.
- Hooper, D. U. and Vitousek, P. M. (1998) Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs*, 68, 121-149.
- Huston, M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110, 449-460.
- Huston, M.A. and McBride, A.C. (2002) Evaluating the relative strengths of biotic versus abiotic controls on ecosystem processes. In: Loreau, M. Naeem, S. and Inchausti, P. (eds.) *Biodiversity of Ecosystem Functioning: Synthesis and Perspectives*, Oxford, UK, Oxford University Press, pp. 47-60.

- Jax, K. (2005) Function and “functioning” in ecology: what does it mean? *Oikos* 111, 3, 641-648.
- Jax, K. (2007) Can we define Ecosystems? On the confusion between definition and description of ecological concepts. *Acta Biotheoretica*, 55, 4, 341-355
- Kearns, C., Inouye, D., Waser, N. (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology, Evolution and Systematics*, 29, 83–112.
- Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, 417, 67-69.
- Klein, A-M., Steffan-Dewenter, I., and Tscharntke, T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 270, 955-961.
- Klein, A-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London. B, Biological Sciences*, 274 (1608), 303–313.
- Kremen, C. (2005) Managing ecosystem services: what do we need to know about their ecology? *Ecological Letters*, 8, 468-479.
- Kremen C., Williams, N.M, Bugg, R.L., Fay, J.P. and Thorp, R.W. (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters*, 7, 1109-1119.
- Kremen C., Williams, N.M and Thorp, R.W. (2002) Crop Pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 16812-16816.
- Lavelle, P., T. Decaens, M. Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., and Rossi, J-P. (2006) Soil invertebrates and ecosystem services. *European Journal of Soil Biology*, 42(Supplement 1) S3-S15.
- Lavelle, P. and Spain, A.V., (2001) *Soil Ecology*. Kluwer Academic Publishers, The Netherlands.
- Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A. et al. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*, 391, 72-76.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hetcor, A., Hooper, D.U., Huston M.A., Raffaelli, D., Schmid, B., Timan, D. and Wardle, D.A. (2001) Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science*, 294, 804-808
- Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. *Bioscience*, 56, 4, 331–323.
- Luck, G.W., Daily, G.C. and Ehrlich, P.R. (2003) Population diversity and ecosystem services. *Trends in Ecology and Evolution*, 18, 331-336.
- MA [Millennium Ecosystem Assessment] (2005) *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC.
- Marrs, R. H., K. Galtress, Tong, C., Cox, E. S., Blackbird S. J., Heyes T. J., Pakeman, R. J., Le Duc, M. G. (2007) Competing conservation goals, biodiversity or ecosystem services: Element losses and species recruitment in a

- managed moorland-bracken model system. *Journal of Environmental Management*, 85, 4, 1034-1047.
- Mooney, H. A. and Ehrlich, P. R. (1997) Ecosystem Services: a fragmentary history. In: Daily, G. C. (Ed) *Nature's Services: Societal Dependence on Natural Ecosystems*. Washington, D.C., Island Press, 11-19.
- Naeem, S., Thompson, L.J, Lawler, S.P, Lawton, J.H. and Woodfin, R.M. (1995) Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. *Philosophical Transactions of Royal Society of London*, B347, 249-262.
- Naidoo, R., Balmford, A. Costanza, R., Fisher, B, Green, B., Lehner, B., Malcolm, T.R. and Ricketts, T.H. (2008) Global mapping of ecosystem services and conservation priorities. *PNAS*, 105, 28, 9495-9500.
- Naidoo, R. and Ricketts, T.H. (2006) Mapping the Economic Costs and Benefits of Conservation. *PLOS Biology*, 4, 11, 2153-2164.
- Niklaus, P.A, Kandeler, E, Leadley, P.W, Schmid, B, Tscherko, D. and Körner, C. (2001) A link between plant diversity, elevated CO₂ and soil nitrate. *Oecologia* 127, 540-548.
- Oyarzún, C. and Huber, A. (1999) Water balance in young plantations of *Eucalyptus globulus* and *Pinus radiata* in southern Chile. *Terra*, 17, 35-44.
- Pimm, S. (1984) The complexity and stability of ecosystems. *Nature*, 307, 321 - 326
- Potschin, M, Haines-Young, R. H. (2006) Rio + 10, sustainability science and Landscape Ecology. *Landscape and Urban Planning*, 75, 3-4, 162-174.
- Quaas, M.F. and Baumgärtner, S. (2008) Natural vs. financial insurance in the management of public-good ecosystems. *Ecological Economics*, 65, 397 – 406
- Richards, A. (2001) Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? *Annals of Botany*, 88, 165–172.
- Richmond, A., Kaufmann, R.K., Mynenib, R.B. (2007) Valuing ecosystem services: A shadow price for net primary production. *Ecological Economics*, 64, 454-462.
- Ricketts, T.H, Daily, G.C, Ehrlich, P.R, Michener, C.D. (2004) Economic value of tropical forest to coffee production. *Proceedings of the National Academy Sciences USA*, 101, 12579-12582.
- Robinson, M., Cognard-Plancq, A-L, Cosandey, C., David, J., Durand, P., Führer, H-W., Hall, R., Hendriques, M.O., Marc, V., McCarthy, R., McDonnell, M., Martin, C., Nisbet, T., O'Dea, P., Rodgers, M, and Zollner, A. (2003) Studies of the impact of forests on peak flows and baseflows: a European perspective. *Forest Ecology and Management*, 186, 1-3, 85-97.
- Rounsevell, M.D.A.; Dawson, T.P. and P.A. Harrison (submitted): A conceptual framework to assess the effects of environmental change on ecosystem services. *Biodiversity and Conservation*.
- SCEP [Study of Critical Environmental Problems] (1970) *Man's impact on the global environment*. Cambridge, Massachusetts: MIT Press.
- Schimel J.P. and Gulledege, J. (1998) Microbial community structure and global trace gases. *Global Change Biology*, 4, 7, 745–758.
- Schwartz, M.W, Bringham, C.A, Hoeksema, J.D, Lyons, K.G, Mills, M.H. and van Mantgem, P.J. (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* 122, 297-305.

- Secretariat of the Convention for Biological Diversity (2004) *How the Convention on Biological Diversity promotes nature and human well-being*. Secretariat of the Convention on Biological Diversity with the support of the United Nations Environment Programme (UNEP) and the Government of the United Kingdom.
- Smith, K. R. (2006) Public Payments for Environmental Services from Agriculture: Precedents and Possibilities. *American Journal of Agricultural Economics*, 88, 5, 1167-1173.
- Smith, S.E. and Read, D.J., (1997) *Mycorrhizal Symbiosis*, 2nd Edn. Academic Press, New York.
- Steffan-Dewenter, I, Kessler, M, Barkmann, J, Boss, M.M, Buchori, D, Erasmi, S, Faust, H, Gerold, G, Glenk, K, Gradstein, S.R, Guhardja, E, Harteveld, M, Hertel, D, Hohn, P, Kappas, M, Kohler, S, Leuschner, C, Maertens, M, Marggraf, R, Migge-Kleian, S, Mogeia, J, Pitopang, R, Schaefer, M, Schwarze, S, Sporn, S.G, Steingrebe, A, Tjitrosoedirdjo, S.S, Tjitrosoedirdjo, S, Twele, A, Weber, R, Woltmann, L, Zeller, M. and Tschardtke, T. (2007) Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. *PNAS*, 104, 12, 4973-4978.
- Swallow, B., Kallesoe, M., Iftikhar, U., Van Noordwijk, M., Bracer, C., Scherr, S., Raju, K. V., Poats, S., Duraiappah, A., Ochieng, B., Mallee, H. and Rumley, R. (2007) *Compensation and Rewards for Environmental Services in the Developing World: Framing Pan-Tropical Analysis and Comparison*. W. A. Centre.
- Swift, M.J, Izac, A.-M.N. and van Noordwijk, M. (2004) Biodiversity and ecosystem services in agricultural landscapes – are we asking the right questions? *Agriculture, Ecosystems and Environment*, 104, 113-134.
- Thompson, K., Askew, A.P, Grime, J.P., Dunnett, N.P. and Willis, A.J. (2005) Biodiversity, ecosystem function and plant traits in mature and immature plant communities. *Functional Ecology*, 19, 2, 355-358.
- Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350–363.
- Tilman D, Wedin D. and Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720
- Tilman D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E. (1997a) The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300–1302
- Tilman D., Lehman C.L. and Thomson, K.T. (1997b) Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences*, 94, 1857–1861.
- Troy, A. and Wilson, M.A. (2006a) Mapping ecosystem services: Practical challenges and opportunities in linking GIS and value transfer. *Ecological Economics*, 60, 2, 435-449
- Troy, A. and Wilson, M.A. (2006b) Erratum to “Mapping ecosystem services: Practical challenges and opportunities in linking GIS and value transfer” *Ecological Economics* 60,4, 435–449
- van Wilgen, B.W, Reyers, B. Le Maitre, D.C., Richardson, D.M. and Schonegevel, L. (in press) A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of Environmental Management*, on-

line August 2007. doi:10.1016/j.jenvman.2007.06.015 (accessed 24th August, 2008)

- Vandewalle, M., Sykes, M.T., Harrison, P.A., Luck, G.W., Berry, P., Bugter, R., Dawson, T.P., Feld, C.K, Harrington, R., Haslett, J.R., Hering, D., Jones, K.B., Jongman, R., Lavorel, S., Martins da Silva, P., Moora, M., Paterson, J., Rounsevell, M.D.A., Sandin, L., Settele, J., Sousa, J.P and Zobel, M (2008) Review paper on concepts of dynamic ecosystems and their services. http://www.rubicode.net/rubicode/RUBICODE_Review_on_Ecosystem_Services.pdf (Accessed 24th July, 2008)
- Walker, B. (1995) Conserving Biological Diversity through Ecosystem Resilience. *Conservation Biology*, 9, 4, 747-752
- Wallace, K.J. (2007) Classification of ecosystem services: problems and solutions. *Biological Conservation* 139, 235-246.
- Wallace, K. (2008) Ecosystem services: Multiple classifications or confusion? *Biological Conservation*, 141, 353-354.
- Wardle, D.A, Zackrisson, O, Hörnberg, G. and Gallet, C. (1997) The Influence of Island Area on Ecosystem Properties. *Science*, 277, 1296-1299.
- Wardle, D., R. Bardgett, et al. (2004) Ecological Linkages between aboveground and belowground biota. *Science* 304, 1629-1633.
- Westman, W. E. (1977) How much are Nature's services worth? *Science*, 197, 960-64.
- Worm, B., Barbier, E.B., Beaumont, N., Emmett Duffy, J., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., Watson, R. (2006) Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, 314, 787-790.
- Zhang, W., Ricketts, T. H., Kremen, C., Carney, K., Swinton, S.M. (2007) Ecosystem services and dis-services to agriculture. *Ecological Economics*, 64, 2, 253-260.

Figure 1: The Links between Ecosystem Services and Human Well-being (after MA, 2005)

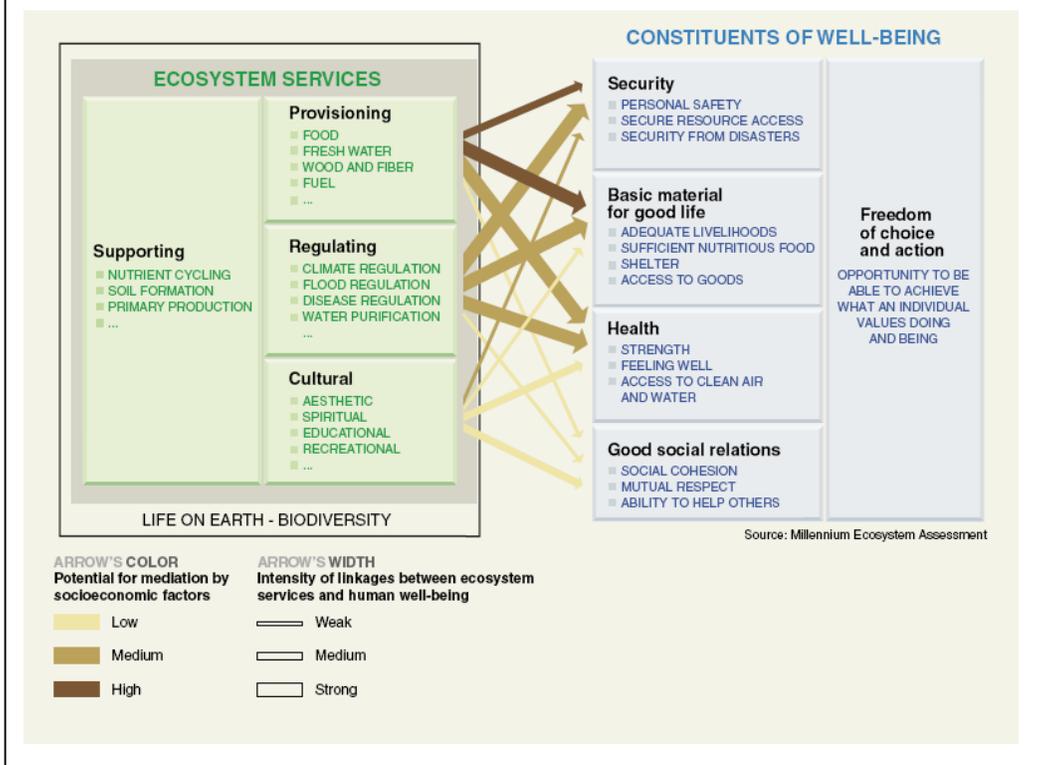


Figure 2: The relationship between biodiversity, ecosystem function and human well being.

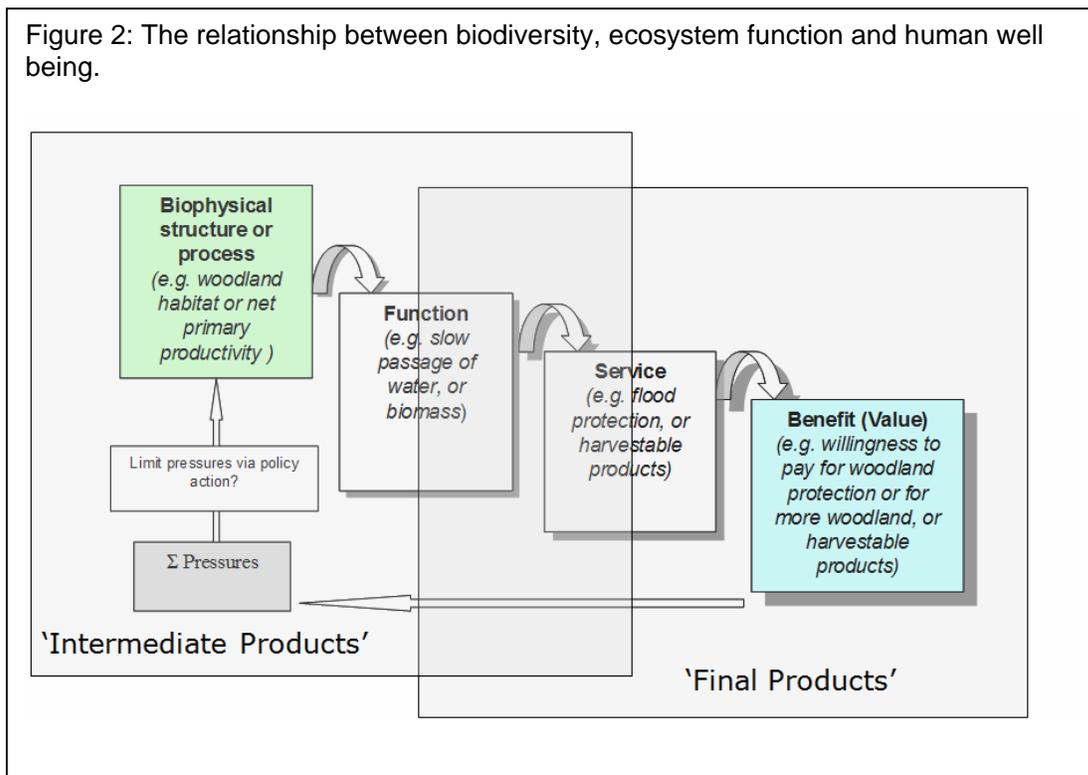
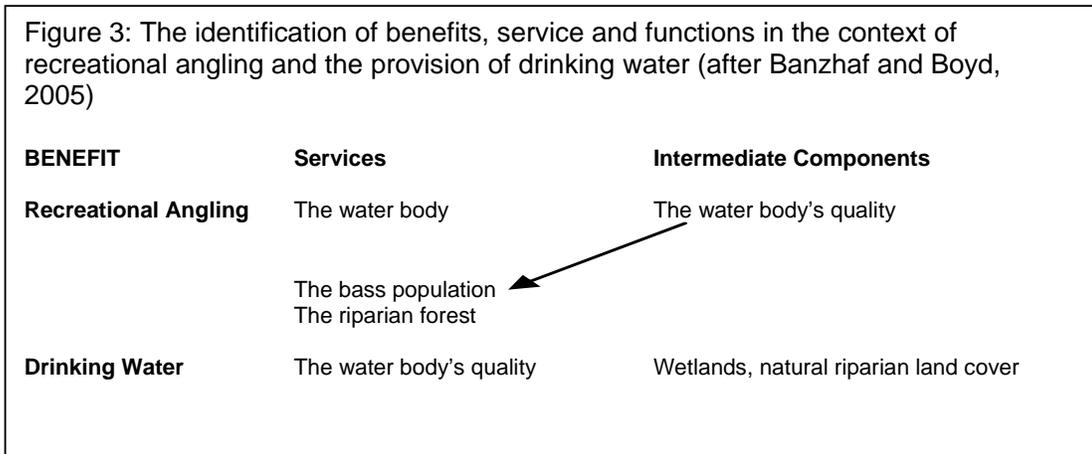


Figure 3: The identification of benefits, service and functions in the context of recreational angling and the provision of drinking water (after Banzhaf and Boyd, 2005)



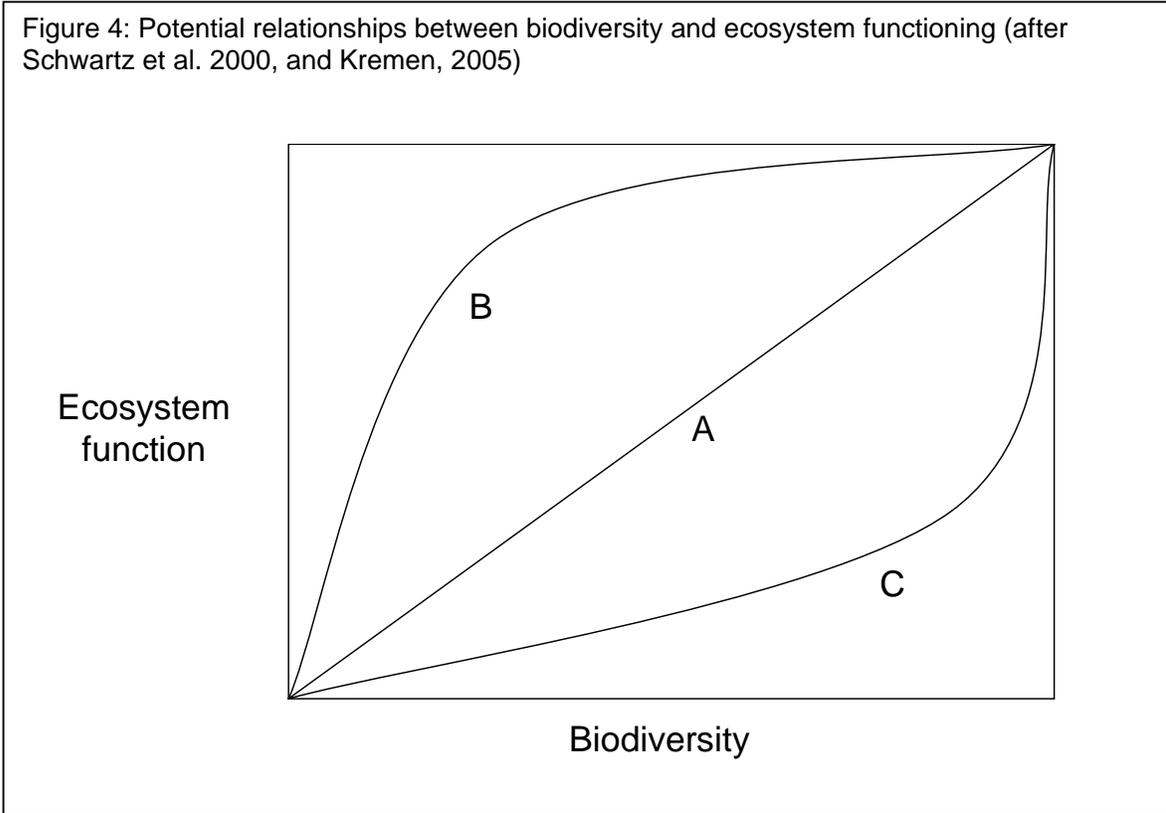


Figure 5: A framework for linking direct and indirect drivers, pressures and responses in a coupled socio-ecological system for assessment of the effects of environmental change drivers on ecosystem services (after Rounsevell et al., submitted).

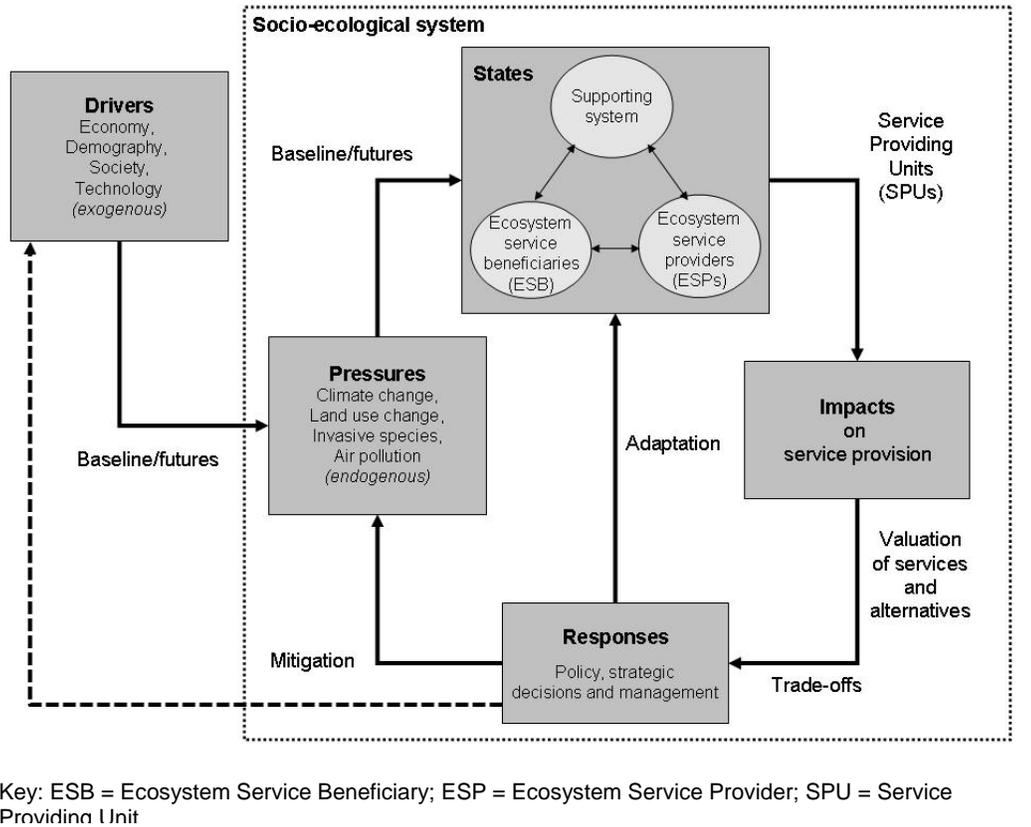


Table 1: A Typology of ecosystem services and their ecological characteristics (after Kremen, 2005)

Service	Ecosystem service providers/ trophic level	Functional units	Spatial scale	Potential to apply this conceptual framework for ecological study
Aesthetic, cultural	All biodiversity	Populations, species, communities, ecosystems	Local–global	Low
Ecosystem goods	Diverse species	Populations, species, communities, ecosystems	Local–global	Medium
UV protection	Biogeochemical cycles, micro-organisms, plants	Biogeochemical cycles, functional groups	Global	Low
Purification of air	Micro-organisms, plants	Biogeochemical cycles, populations, species, functional groups	Regional–global	Medium (plants)
Flood mitigation	Vegetation	Communities, habitats	Local–regional	Medium
Drought mitigation	Vegetation	Communities, habitats	Local–regional	Medium
Climate stability	Vegetation	Communities, habitats	Local–global	Medium
Pollination	Insects, birds, mammals	Populations, species, functional groups	Local	High
Pest control	Invertebrate parasitoids and predators and vertebrate predators	Populations, species, functional groups	Local	High
Purification of water	Vegetation, soil micro-organisms, aquatic micro-organisms, aquatic invertebrates	Populations, species, functional groups, communities, habitats	Local–regional	Medium to high
Detoxification and decomposition of wastes	Leaf litter and soil invertebrates; soil micro-organisms; aquatic micro-organisms	Populations, species, functional groups, communities, habitats	Local–regional	Medium
Soil generation and soil fertility	Leaf litter and soil invertebrates; soil micro-organisms; nitrogen-fixing plants; plant and animal production of waste products	Populations, species, functional groups	Local	Medium
Seed dispersal	Ants, birds, mammals	Populations, species, functional groups	Local	High

Table 2: Ecosystem services classified by their spatial characteristics (after Costanza, 2008)

Global non-proximal (does not depend on proximity)

- *Climate regulation*
- *Carbon sequestration (NEP)*
- *Carbon storage*
- *Cultural/existence value*

Local proximal (depends on proximity)

- *Disturbance regulation/ storm protection*
- *Waste treatment*
- *Pollination*
- *Biological control*
- *Habitat/refugia*

Directional flow related: flow from point of production to point of use

- *Water regulation/flood protection*
- *Water supply*
- *Sediment regulation/erosion control*
- *Nutrient regulation*

In situ (point of use)

- *Soil formation*
- *Food production/non-timber forest products*
- *Raw materials*

User movement related: flow of people to unique natural features

- *Genetic resources*
- *Recreation potential*
- *Cultural/aesthetic*

Table 3: Ecosystem services classified according to their excludability and rivalness (after Costanza, 2008).

	Excludable	Non-excludable
Rival	Rival Market goods and services (most provisioning services)	Open access resources (some provisioning services)
Non-rival	Non-rival Club goods (some recreation services)	Public goods and services (most regulatory and cultural services)