

CHAPTER SIX

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

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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, p. 18

Introduction: 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 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 contribute to our spiritual well-being, through their cultural or religious significance or the opportunities they provide for recreation and the enjoyment of nature.

In this chapter, we will look at the goods and services that ecosystems can provide and the role that biodiversity may play in producing them,¹ specifically 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. We will also explore how these ideas link up with those of the Ecosystem Approach to environmental management and policy, and some of the implications of this for how sustainable development is defined. This does not mean that traditional ideas about the need for conservation are unimportant, rather that those making the case for biodiversity need to set these issues in a broader context, and consider whether nature has utilitarian as well as intrinsic values (see for example, Chan *et al.* 2007).

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

Ecosystems services and the Ecosystem Approach

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 the conservation and sustainable use of those systems and their contribution to human well-being’.² 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 per cent of the ecosystem services evaluated are being degraded or used unsustainably, with 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 2000.³ 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 even earlier, 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

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

³ www.un.org/millenniumgoals/ (accessed 24th July, 2008)

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

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 (Frid and Raffaelli, this volume; see also Hartje *et al.* 2003). A new focus was required to achieve robust and sustainable management and policy outcomes and 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 Approach forms the basis for considering all the services provided to people by biodiversity and ecosystems in a holistic framework (Secretariat of the Convention on 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 in a good understanding of the biophysical limits that constrain ecological processes and the spatial and temporal scales at which they operate. Before we can take the Ecosystem Approach forward, we need to explore the science that underpins these ideas.

Ecosystem service typologies

Although we can define an ecosystem service in fairly simple terms, as ‘the benefits ecosystems provide’ (MA 2005, p.1), difficulties can arise when applying the concept in an operational setting. A number of typologies (categorisation of different types of service) have been proposed. In the typology suggested by the MA, four broad types of service were recognised, namely: those that

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

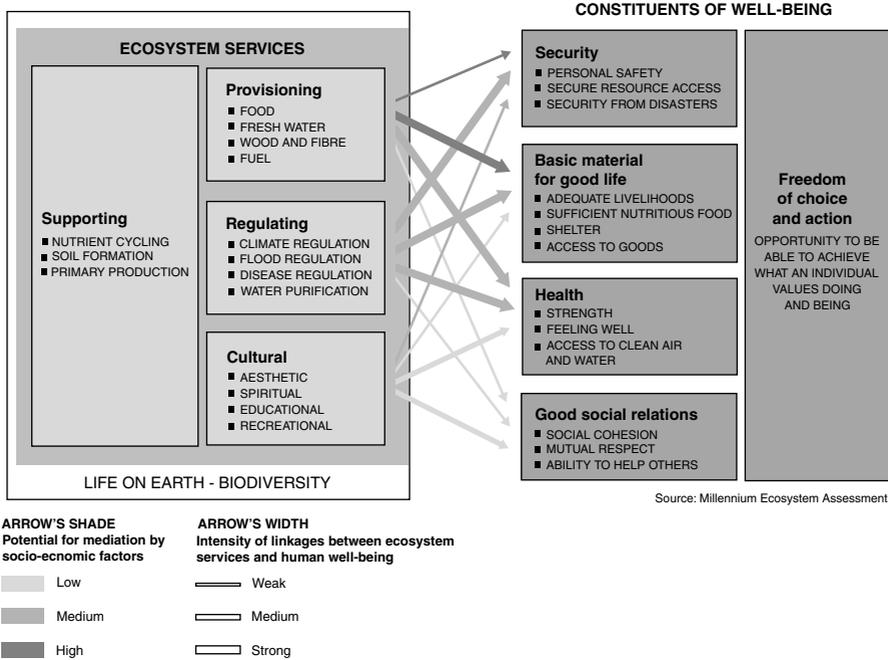


Figure 6.1 The links between ecosystem services and human life well-being (after MA 2005).

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 6.1 and Table 6.1. The typology shown in Table 6.1 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.

It is important to note features of the typology and relationships shown in Figure 6.1. First, ‘biodiversity’ *per se* is not a service; rather, the MA represents 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.

Table 6.1. 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

The second important point to note about the typology shown in Figure 6.1 is that the supporting services have a different relationship to human well-being than the other three types of service: they do not directly benefit people, but are part of the often complex mechanisms and processes that generate other services. As Banzhaf and Boyd (2005), Boyd and Banzhaf (2005, 2006) and Wallace (2007) have noted, the MA and the wider research literature are 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, is 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 6.2. The diagram makes a distinction between ecological structures and processes created or generated by living organisms 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 cascade linking the two ends of a 'production chain'. The idea is best illustrated by an example.

The presence of ecological structures like woodlands and 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 – which is why it is helpful to separate out this capability and call it a function. However, whether this function is regarded as a service or not depends upon whether 'flood control' is considered 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

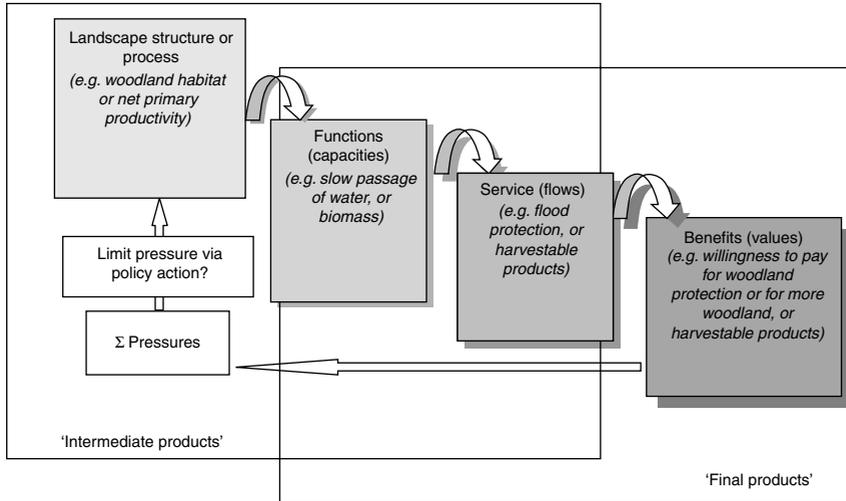


Figure 6.2 The relationship between biodiversity, ecosystem function and human well-being.

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 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. Here, we have included the idea of functions as capabilities in Figure 6.2 to help those less familiar with the field to pick their way through current debates.

The second important idea that the cascade concept highlights 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 that led Banzhaf and Boyd (2005, p. 12) to suggest that service typologies are difficult to construct. They claim that identification of what is an ecosystem service depends on context because they are ‘contingent’ on ‘particular human activities or wants’. The problem, which is also recognised by Wallace (2007), is illustrated by Figure 6.3, showing the different roles that ‘water quality’ can have in the analysis of ecosystem services and

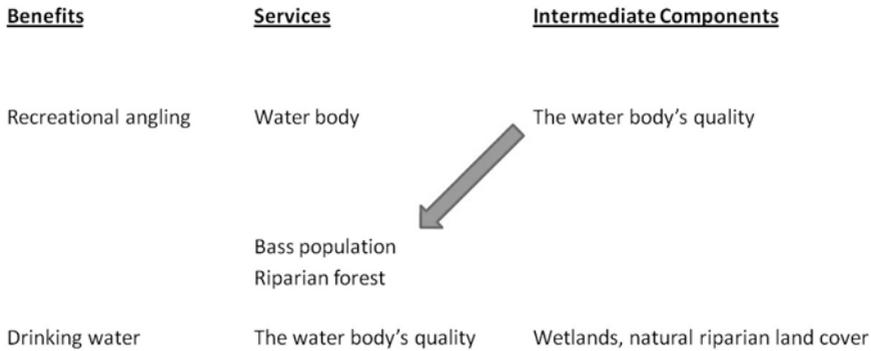


Figure 6.3 The identification of benefits, services and functions in the context of recreational angling and the provision of drinking water (after Banzhaf and Boyd 2005).

societal benefits. The quality of the water body in Figure 6.3 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 elements 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. In this situation the quality of the water is more a function or capability of the ecosystem; it is needed to produce the service. Notice also in Banzhaf and Boyd’s 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, such as 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

The message that emerges from the discussion above is that while the idea of ecosystems producing services may be attractive to the ecosystem ecology community, this is a new and developing field where concepts evolve rapidly. Nevertheless, it is clear that ecosystem services are defined by human activities and needs, an observation which has the following implications:

- 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. Rather, lists of services like those provided by the MA should be treated more as a menu of *service-benefit themes*, within particular contexts. Concepts like ‘processes’, ‘functions’, ‘services’ and ‘benefits’ should be seen more as prompts to help sort out the complexities of a given problem rather than as a set of watertight definitions that ecosystems have to be squeezed into.

- While it is important to identify the ‘final product’ consumed or used, 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 that product depends. In fact, as Fisher and Turner (2008) and Costanza (2008) have argued, services do not have to be utilised directly by people. These authors prefer to think of intermediate and final services or products, rather than becoming trapped in arguments about what is and is not a true service (see Figure 6.2). This is a helpful perspective, 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, other ways of categorising are likely to emerge in addition to 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 6.2). Some, like carbon sequestration, are global in nature; since the atmosphere is so well mixed all localities where carbon is fixed are potentially useful. By contrast, others, like waste treatment and pollination, depend on proximity. ‘Local proximal’ services are, according to Costanza, 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 at which they originate (*in situ* services). Finally he identifies services like cultural and aesthetic ones, which depend on the movement of users to specific places.

Costanza (2008) emphasises the need for different classification schemes, highlighting classifications that try to describe the degree to which users can be excluded from accessing services, or the extent to which users may interfere with each other when they enjoy the service (Table 6.3). Those goods and services that are privately owned or 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 goods the other cannot because the service or goods are finite. Most provisioning services fall into this category. A variation on

Table 6.2. *Ecosystem services classified by their spatial characteristics (after Costanza 2008).*

Global non-proximal (does not depend on proximity)
<ul style="list-style-type: none"> • <i>Climate regulation</i> • <i>Carbon sequestration</i> • <i>Carbon storage</i> • <i>Cultural/existence value</i>
Local proximal (depends on proximity)
<ul style="list-style-type: none"> • <i>Disturbance regulation/storm protection</i> • <i>Waste treatment</i> • <i>Pollination</i> • <i>Biological control</i> • <i>Habitat/refugia</i>
Directional flow related: flow from point of production to point of use
<ul style="list-style-type: none"> • <i>Water regulation/flood protection</i> • <i>Water supply</i> • <i>Sediment regulation/erosion control</i> • <i>Nutrient regulation</i>
<i>In situ</i> (point of use)
<ul style="list-style-type: none"> • <i>Soil formation</i> • <i>Food production/non-timber forest products</i> • <i>Raw materials</i>
User movement related: flow of people to unique natural features
<ul style="list-style-type: none"> • <i>Genetic resources</i> • <i>Recreation potential</i> • <i>Cultural/aesthetic</i>

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, which illustrates 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 those services, 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.

A key theme of the Ecosystem Approach is the emphasis it gives to holistic 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 (Jones and Paramor, this volume). Although ecologists and natural resource

Table 6.3. *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)

managers have been actively involved in the debate about ecosystem services, it is important to note that the way the concepts and terminology are developing is also being shaped by geographers, economists and a range of other social and natural scientists. Many disciplines are 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 section of this chapter we will therefore look at what progress has been made in understanding the role of biodiversity in the production of ecosystem services.

Biodiversity, ecosystem function and service output

The assumption that ecosystem service output is sensitive to changes in biodiversity is implicit in many of the arguments made for conserving and restoring ecological systems. Here, we critically examine that proposition.

Schwartz *et al.* (2000) take stock of the evidence linking biodiversity and ecosystem function over the previous decade, 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 kinds of issues experimental and observational studies face in resolving these key questions. They 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 relationship between biodiversity and ecosystem function are possible, for the conservation case to be strengthened a *direct and positive association* needs to be observed.

Figure 6.4 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 is that in A, ecosystem function is highly sensitive to variations in biodiversity, and in B, there is a saturation

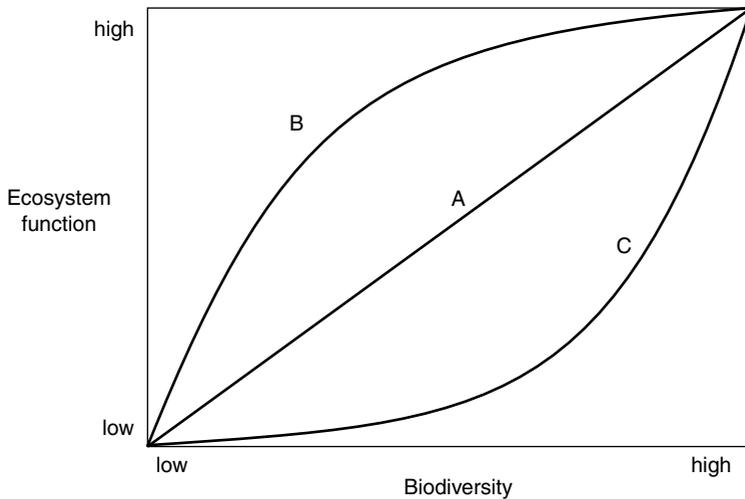


Figure 6.4 Potential relationships between biodiversity and ecosystem functioning (after Schwartz *et al.* 2000, and Kremen 2005).

effect, so that decline in ecosystem function occurs much more rapidly at low levels of species richness. Schwartz *et al.* 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 significantly affecting their function (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.* concluded that few studies supported the hypothesis that there was a simple, direct linear relationship between species richness and some measure of ecosystem function 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 a 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 sampling effect: by considering a greater number of species one is more likely to include highly productive ones (Huston and McBride 2002, Thompson *et al.* 2005).

In examining these arguments, it is important to note that there is considerable disagreement about what the evidence shows because the problem is so complex. 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) make a similar point in the context of agricultural systems.

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.* (2006) 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 habitat mosaics and landscapes. In addition, the non-science community may have very different mental constructs of 'biodiversity', which can include iconic non-living features of the landscape, such as castles or tractors, as well as concepts such as tranquillity and scenery (Fischer and Young 2007).

Notwithstanding the difficulty of tying down the term 'biodiversity', the evidence suggests that 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 current evidence generally supports the contention that for various measures of biodiversity there is a positive association with a number of different measures of ecosystem functioning. They suggest that the small number of negative relationships reported in the literature tend to be associated with studies which measured properties at the population level (individual species density, cover or biomass), rather than those which looked at community-level characteristics (e.g. density, biomass, consumption). Also, 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 ecosystem 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 on what the MA call 'supporting services' or what we have called 'intermediate products'. These 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 have tended to be derived from

ecosystems that are easily manipulated, such as grasslands. Nevertheless, productivity is an important ecosystem function 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 that terrestrial net primary productivity can be used as a proxy for a number of other ecosystem services, citing 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 associated services generally increase 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 view is supported by Costanza *et al.* (2007), who have investigated the inter-dependence of net primary productivity and biodiversity at the spatial scales of eco-regions 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. On the basis of the relationships they develop, the authors predict that across the temperature ranges in which most of the world's biodiversity occurs, a 1 per cent change in biodiversity would result in a 0.5 per cent 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 appear to be positive effects of increased species richness on ecosystem productivity. In contrast to earlier studies which monitored systems over relatively short periods, their study covered an 8-year period. Naeem *et al.* (1995), Tilman *et al.* (1996, 1997a and 1997b) and Lawton *et al.* (1998) have also provided evidence to support the existence of a direct positive relationship, whilst Cardinale *et al.* (2007) have emphasised that the productive advantage of mixtures over monocultures appears to increase over time.

Similarly, a close association between biodiversity and ecosystem functioning is apparent in many soil ecosystems. Lavelle *et al.* (2006), for example, report many experiments that show 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 microorganisms; greater protection against pests and diseases, both above and below ground; the positive

effect of microorganisms on soil physical structure; and the production of plant-growth promoters.

Hooper *et al.* (2005) extensively review the issues surrounding 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 on ecosystem properties. While there is a potentially large variability across ecosystems in terms of species and functional diversity, there is clear evidence that variations in ecosystem function can ‘at least in part’ be explained by ‘differences in species or functional *composition*’ (our italics).

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 increased biodiversity of both primary producers and consumers appears to enhance the ecosystem processes examined. They identified a number of explanatory 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 complementary relationships between species suggests that the presence of groups of species with particular properties 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, the distinguishing properties of different ecological groupings, has emerged as an important area of research into understanding how ecosystem services are generated (Díaz *et al.* 2006, Balvanera *et al.* 2006).

De Bello *et al.* (2008, p. 4) define a functional trait as ‘a feature of an organism which has demonstrable links to the organism’s function’, that is, 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 (*ibid.*).

For example, recent work on nutrient cycling has shown that functionally diverse systems appear to be more effective in retaining nutrients than simpler systems (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 enhancing 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 diffuse 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 levels of nutrients 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 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 possible 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 in the case of phosphorus through arbuscular mycorrhizal fungi (see for example, Giller *et al.* 2005 and Smith and Read 1997, cited by Barrios 2007).

From the above, it is clear that by promoting particular functional responses in one group of organisms by appropriate land management, in this case the soil biota, effects may occur 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 a small number of key species, and other processes, such as decomposition, which tend to be dependent upon a wider range of organisms. Narrow processes may be more susceptible to changes in

biodiversity or the abundance of particular functional groups, although generalisations are difficult. 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 are most important, but rather their functional attributes (e.g. Swift *et al.* 2004). Thus, de Ruiter *et al.* (2005) have shown 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) can also 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 effect on soil water and nutrient dynamics through their impact on other soil organisms (Barrios 2007). Earthworms and macro- and micro-invertebrates can improve soil structure via burrows or casts and enhance soil fertility through partial digestion and comminution 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 attention 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 per cent of the world's most important crops and 35 per cent 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 pollinator losses for ecosystem functioning have been documented by Richards (2001), who described cases where low fruit set or the setting of seeds by crops and 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 implications 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. They compiled almost one million records for all native bees and hoverflies 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 both 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 showed the greatest declines. Moreover, in Britain, those plants most dependent on insect pollinators (the functional group represented by obligatory out-crossing plants) were also in decline, compared to other plant groups dependent on water and wind for pollination or that were self-pollinating. Wind- and water-pollinated plants were increasing while those that were self-pollinated were broadly stable. As Biesmeijer *et al.* note, it is difficult to determine whether the decline in insect-pollinated plants precedes the loss of pollinators or vice versa, but taken together, there is strong evidence of a causal connection between local extinctions of functionally linked plant and pollinator species.

Whilst species richness per se may be important in relation to the maintenance of ecosystem functioning, the role of particular keystone species or groups with specific functional capabilities should not be overlooked. This is the basis of the additional relationship that we recommend in Figure 6.4 (Curve C), which suggests that in certain circumstances, the removal of one or a small component of biodiversity can have a disproportionately 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

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 rather through co-evolutionary processes. Thus it is likely that the introduction of alien species might undermine such relationships and potentially disrupt service output.

The focus of recent discussion of the threat posed by alien species to ecosystem functioning has been on two key issues. 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 and fertility of invaders were reduced. Hooper *et al.* (2005) draw similar conclusions, suggesting 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 be important in controlling invasibility 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 the 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 promoting the spread of alien species, often with damaging consequences for ecosystem services. Bosch and Hewlett (1982), for example, reviewed evidence from ninety-four experimental catchments, and concluded that forests dominated by introduced 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. In Chile, Oyarzún 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 *et al.* (2008), for example, make an assessment of the current and potential impacts of invasive alien plants on selected ecosystem services in South Africa. They estimate that the reduction in surface water run-off 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. Given

the current level of invasion of alien species, they estimated that in relation to the potential number of livestock that could be supported, there was a reduction in grazing capacity of around 1%, although 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 understand 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. Consequently, when bracken control measures are applied, there is a higher risk of the nutrients being released 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, and that there is 'a need to balance conservation goals against potential damage to biogeochemical structure and function' (Marrs *et al.* 2007, p. 1045). 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 of Balvanera *et al.* (2006) was that as the number of trophic levels increased between the point where the experimental intervention was made and the measurement of effects was 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 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 onto 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 6.4, 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.* (2007) 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) suggests, the buffering effects of biodiversity may be quite specific. They found that while the buffering effects of biodiversity on 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 a broader understanding of how people benefit from nature's services, and what can be done to help sustain and improve their well-being (see also Jones and Paramor, this volume). 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 (see also Raffaelli and Frid, this volume). 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 framework for ecosystem services that we have presented (Figure 6.2) 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 (see also Jones and Paramor, this volume; Raffaelli and Frid, this volume). 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 facts 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) have 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 ecologists study, we must combine our scientific understanding of the relationships between biodiversity and ecosystem functioning with insights into wider social and economic structures and processes. Development of these ideas can be seen in the recent work surrounding the concept of a 'service providing unit' (SPU).

The idea of an SPU was first introduced by Luck *et al.* (2003), who argued that instead of defining a population of 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 can be seen as an ecological 'footprint' of the service. As a 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 6.5 is now being used to try to understand the way different pressures and drivers impact upon social-ecological systems, and the relationships between the particular components of biodiversity that generate the service, ecosystem service providers (ESPs), and ecosystem service beneficiaries (ESBs).

Models such as those shown in Figure 6.5 will enable ecologists to develop a much richer understanding of the links between biodiversity, ecosystem services and human well-being. In particular, they will help identify the kinds of trade-offs that might have to be considered between services if different development paths are chosen. An illustration of the kind of analysis required is provided by the recent work of Steffan-Dewenter *et al.* (2007), who examined 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' incomes associated with the reduction of shade from more than 80 per cent to around 30–50 per cent. 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 farmers' incomes increased further with conversion to unshaded agricultural systems, Steffan-Dewenter *et al.* (p. 4973) suggested that low-shade agroforestry represents the 'best compromise between economic forces and ecological needs'.

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

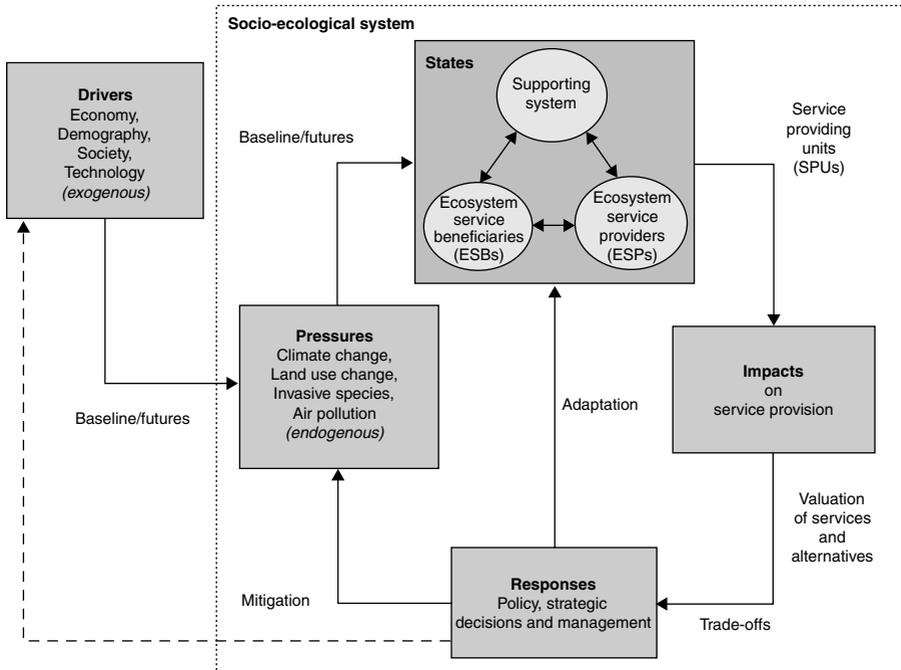


Figure 6.5 A framework for linking direct and indirect drivers, pressures and responses in a coupled socio-ecological system for assessment of the effects of environmental change drivers on ecosystem services (after Rounsevell *et al.* 2009 [in press]). Used with permission from Mark Rounsevell.

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'. The wider research community needs to engage in such debates. Although long-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 healthy ecosystems.

If the Ecosystem Approach is to be embedded in decision making then we need to understand the links between biodiversity and ecosystem services. We need to be aware of the limits of ecological functioning and 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 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 social-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, 2006b; 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.

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References

- Aarssen, L. W. (1997) High productivity in grassland ecosystems: affected by species diversity or productive species? *Oikos*, **80**, 183–4.
- 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 24 July 2008).
- 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**, 1146–56.
- Banzhaf, S., and Boyd, J. (2005) *The Architecture, and Measurement of an Ecosystem Service Index*. Discussion Paper, Resources for the Future DP 05–22.

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

- Barrios, E. (2007) Soil biota, ecosystem services and land productivity. *Ecological Economics*, **64**(2), 269–85.
- Baumgärtner, S. (2007) The insurance value of biodiversity in the provision of ecosystem services. *Natural Resource Modeling*, **20**(1), 87–127.
- 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 Kunin, W. E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, **313**, 351–4.
- 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 24 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**, 3–23.
- Boyd, J., and Banzhaf, S. (2005) Ecosystem services and government accountability: the need for a new way of judging Nature's Value. *Resources*, Summer, 16–19.
- Boyd, J. and Banzhaf, S. (2006) *What are Ecosystem Services?* Discussion Paper Resources for the Future DP 06–02.
- Brussaard, L., de Ruiter, P. C. and Brown, G. G. (2007) Soil biodiversity for agricultural sustainability. *Agriculture, Ecosystems & Environment*, **121**(3), 233–44.
- 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 plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy Sciences*, **104**(46), 18123–8.
- 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: 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., Shelton, D., Binning, C. and Parry, R. (2001) A framework for applying the concept of ecosystem services to natural resource management in Australia. *Third Australian Stream Management Conference*, August 27–29, 2001, Brisbane. Cooperative Research Centre for Catchment Hydrology.
- Costanza, R. (2008) Ecosystem services: multiple classification systems are needed. *Biological Conservation*, **141**, 350–2.
- 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 van den Belt M. (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253–60.
- Costanza, R., Fisher, B., Mulder, K., Liu, S. and 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**, 478–91.
- 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, DC, 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 Boumans, R.M.J. (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. and Moore, J.C. (2005). The balance between productivity and food web structure in soil ecosystems. In: Bardgett, R. D., Usher, M.B. and Hopkins, D. W. (Eds.), *Biological Diversity and Function in Soil*. Cambridge University Press, Cambridge, 139–53.
- Díaz, S., Fargione, J., Chapin F.S. III and Tilman, D. (2006) Biodiversity loss threatens human well-being. *PLoS Biology*, **4**(8), e277. DOI: 10.1371/journal.pbio.0040277.
- Engelhardt, K.A.M. and Ritchie, M.E. (2001) Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature*, **411**, 687–9.
- European Commission (2008) The economics of ecosystems and biodiversity. Interim report. http://ec.europa.eu/environment/nature/biodiversity/economics/pdf/teeb_report.pdf (Accessed 24 July 2008).
- Fagan, K.C., Pywell, R.F., Bullock, J.M. and Marris, 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), 1293–303.
- Fischer, A. and Young, J.C. (2007) Understanding mental constructs of biodiversity: Implications for biodiversity management and conservation. *Biological Conservation*, **136**, 271–82.
- Fisher, B. and Turner, K. (2008) Ecosystem services: Classification for valuation. *Biological Conservation*, **141**, 1167–9.
- Folke, C. (2006) Resilience: the emerging of a perspective for socio-ecological system analysis. *Global Environmental Change*, **16**, 253–67.
- 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**, 220–7.
- Giller, K.E., Bignell, D., Lavelle, P., Swift, M.J., Barrios, E., Moreira, F., van Noordwijk, M., Barois, I., Karanja, N. and 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, 295–318.
- Görgens, A.H.M. and 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**, 1260–1.
- 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*, **26**(4), 757–60.
- Hajjar, R., Jarvis, D.I. and Gemmill-Herren, B. (2008) The utility of crop genetic diversity

- in maintaining ecosystem services. *Agriculture, Ecosystems & Environment*, **123**(4), 261–70.
- Hardin, G. (1968) The tragedy of the commons. *Science*, **162**, 1243–8.
- Hartje, V., Klaphake, A. and Schliep, R. (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**, 282–92.
- Hooper, D.U. (1998) The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology*, **79**, 704–19.
- Hooper, D.U., Chapin, F.S. III, 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**, 1302–5.
- Hooper, D.U. and Vitousek, P.M. (1998) Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs*, **68**, 121–49.
- Huston, M.A. (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–60.
- 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 University Press, Oxford, UK, 47–60.
- Jax, K. (2005) Function and ‘functioning’ in ecology: what does it mean? *Oikos*, **111**(3), 641–8.
- Jax, K. (2007) Can we define Ecosystems? On the confusion between definition and description of ecological concepts. *Acta Biotheoretica*, **55**(4), 341–55.
- Kearns, C., Inouye, D. and Waser, N. (1998) Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology, Evolution and Systematics*, **29**, 83–112.
- Klein, A-M., Steffan-Dewenter, I. and Tschardtke, 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**, 955–61.
- Klein, A-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. and Tschardtke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **274**(1608), 303–13.
- Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67–9.
- Kremen, C. (2005) Managing ecosystem services: what do we need to know about their ecology? *Ecological Letters*, **8**, 468–79.
- 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**, 1109–19.
- 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**, 16812–16.
- Lavelle, P., Decaens, T., 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**, 72-6.
- 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**, 804-8.
- Losey, J. E. and Vaughan, M. (2006) The economic value of ecological services provided by insects. *Bioscience*, **56**(4), 311-23.
- Luck, G. W., Daily, G. C. and Ehrlich, P. R. (2003) Population diversity and ecosystem services. *Trends in Ecology and Evolution*, **18**, 331-6.
- MA [Millennium Ecosystem Assessment]. (2005) *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC.
- Marrs, R. H., Galtress, K., Tong, C., Cox, E. S., Blackbird S. J., Heyes T. J., Pakeman, R. J. and 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), 1034-47.
- 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*. Island Press, Washington, DC, 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 the Royal Society of London*, **B347**, 249-62.
- 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. *Proceedings of the National Academy Sciences*, **105**(28), 9495-500.
- Naidoo, R. and Ricketts, T. H. (2006) Mapping the economic costs and benefits of conservation. *PLOS Biology*, **4**(11), 2153-64.
- 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**, 540-8.
- 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**, 321-6.
- Potschin, M. and Haines-Young, R. H. (2006) Rio + 10, sustainability science and Landscape Ecology. *Landscape and Urban Planning*, **75**, 3-4, 162-74.
- Quaas, M. F. and Baumgärtner, S. (2007) 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**, 165-72.
- Richmond, A., Kaufmann, R. K. and Mynenib, R. B. (2007) Valuing ecosystem services: A shadow price for net primary production. *Ecological Economics*, **64**, 454-62.
- Ricketts, T. H., Daily, G. C., Ehrlich, P. R., and Michener, C. D. (2004) Economic value of tropical forest to coffee production.

- Proceedings of the National Academy Sciences of the United States of America*, **101**, 12579–82.
- 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 Harrison, P.A. (in press) A conceptual framework to assess the effects of environmental change on ecosystem services. Submitted to *Biodiversity and Conservation* (June 2009).
- SCEP [Study of Critical Environmental Problems]. (1970) *Man’s impact on the global environment*. MIT Press, Cambridge, Massachusetts.
- Schimel, J.P. and Gulledege, J. (1998) Microbial community structure and global trace gases. *Global Change Biology*, **4**(7), 745–58.
- Schwartz, M.W., Bringham, C., 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), 1167–73.
- 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., Hartevelde, 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. *Proceedings of the National Academy Sciences*, **104**, (12), 4973–8.
- 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*. ICRAF Working Paper no. 32. Nairobi: World Agroforestry 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**, 113–34.
- 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), 355–8.
- Tilman, D. (1996) Biodiversity: population versus ecosystem stability. *Ecology*, **77**, 350–63.
- Tilman, D., Wedin, D. and Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718–20.
- 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**, 1300–2.
- Tilman, D., Lehman, C.L. and Thomson, K.T. (1997b) Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 1857–61.
- Troy, A. and Wilson, M.A. (2006a) Mapping ecosystem services: Practical challenges and opportunities in linking GIS and value transfer. *Ecological Economics*, **60**(2), 435–49.
- 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), 435–49.
- van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M. and Schonegevel, L. (2008) A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of Environmental Management*, **89**(4), 336–49, on-line August 2007. doi:10.1016/j.jenvman.2007.06.015 (accessed 24 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. (2007) Review paper on concepts of dynamic ecosystems and their services. www.rubicode.net/rubicode/RUBICODE_Review_on_Ecosystem_Services.pdf (Accessed 24 July 2008).
- Walker, B. (1995) Conserving biological diversity through ecosystem resilience. *Conservation Biology*, **9**(4), 747–52.
- Wallace, K.J. (2007) Classification of ecosystem services: problems and solutions. *Biological Conservation*, **139**, 235–46.
- Wallace, K. (2008) Ecosystem services: Multiple classifications or confusion? *Biological Conservation*, **141**, 353–4.
- Wardle, D.A., Zackrisson, O., Hörnberg, G. and Gallet, C. (1997) The influence of island area on ecosystem properties. *Science*, **277**, 1296–9.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. and Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629–33.
- Westman, W.E. (1977) How much are Nature’s services worth? *Science*, **197**, 960–4.
- 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. and Watson, R. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science*, **314**, 787–90.
- Zhang, W., Ricketts, T.H., Kremen, C., Carney, K. and Swinton, S.M. (2007) Ecosystem services and dis-services to agriculture. *Ecological Economics*, **64**(2), 253–60.