Chapter 2

Biodiversity, ecosystems and ecosystem services

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March 2010

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Key Messages

- All ecosystems are shaped by people, directly or indirectly and all people, rich or poor, rural or urban, depend on the capacity of ecosystems to generate essential ecosystem services. In this sense, people and ecosystems are interdependent social-ecological systems.

- The ecosystem concept describes the interrelationships between living organisms (people included) and the non-living environment and provides a holistic approach to understanding the generation of services from an environment that both delivers benefits to and imposes costs on people.

- Variation in biological diversity relates to the operations of ecosystems in at least three ways:
    1. increase in diversity often leads to an increase in productivity due to complementary traits among species for resource use, and productivity itself underpins many ecosystem services,
    2. increased diversity leads to an increase in response diversity (range of traits related to how species within the same functional group respond to environmental drivers) resulting in less variability in functioning over time as environment changes,
    3. idiosyncratic effects due to keystone species properties and unique trait-combinations which may result in a disproportional effect of losing one particular species compared to the effect of losing individual species at random.

- Ecosystems produce multiple services and these interact in complex ways, different services being interlinked, both negatively and positively. Delivery of many services will therefore vary in a correlated manner, but when an ecosystem is managed principally for the delivery of a single service (e.g. food production), other services are nearly always affected negatively.

- Ecosystems vary in their ability to buffer and adapt to both natural and anthropogenic changes as well as recover after changes (i.e. resilience). When subjected to severe change, ecosystems may cross thresholds and move into different and often less desirable ecological states or trajectories. A major challenge is how to design ecosystem management in ways that maintain resilience and avoids passing undesirable thresholds.

- There is clear evidence for a central role of biodiversity in the delivery of some – but not all - services, viewed individually. However, ecosystems need to be managed to deliver multiple services to sustain human well-being and also managed at the level of landscapes and seascapes in ways that avoid the passing of dangerous tipping-points. We can state with high certainty that maintaining functioning ecosystems capable of delivering multiple services requires a general approach to sustaining biodiversity, in the long-term also when a single service is the focus.

1 Introduction

This chapter explores current understanding of the relationships between biodiversity, the structure and functioning of ecosystems, and the provision of ecosystem services. It aims specifically to clarify:

- The nature of and evidence for the links between biodiversity, ecosystems, and ecosystem services;
- Ecosystem responses to anthropogenic impacts;
- The risks and uncertainties inherent in management of ecosystems that developed long before the evolution of *Homo sapiens*.

A basic level of understanding is an essential prerequisite to the appropriate application of economic analysis. This chapter highlights the complexities of the concepts of biodiversity and ecosystems, and examines the relationships between biodiversity, ecosystem functioning and ecosystem services. The interactions among the various assemblages of biotic and abiotic components into ecosystems are assessed based on our current scientific knowledge. This evidence is further discussed in the context of how to help inform the policy agenda on the connections between biodiversity and ecosystem services.

The chapter gives a review of the individual ecosystem services themselves with commentary and analysis on the important factors underpinning the services, gaps in knowledge and uncertainties. Recognizing that in reality, ecosystems generate multiple services, this chapter examines the complications arising from ‘bundles’ of ecosystem services, where strategic priorities may result in trade-offs in service provision. The need for practical approaches to the recognition, quantification and mapping of ecosystem services is examined, and a synthesis presented of the alteration of biodiversity and ecosystems and their functioning with increasing known impacts of global change. Analysis of the growing biophysical knowledge base is essential to help economists understand and interpret the dynamics and complex interactions among living organisms, the abiotic environment and diverse cultural and socio-economic contexts.

1 Biodiversity and ecosystems

1.1 Theory and definitions

Biodiversity reflects the hierarchy of increasing levels of organization and complexity in ecological systems; namely at the level of genes, individuals, populations, species, communities, ecosystems and biomes. It is communities of living organisms interacting with the abiotic environment that comprise, and characterize, ecosystems. Ecosystems are varied both in size and, arguably, complexity, and may be nested one within another.

Application of the ecosystem model (Tansley 1935; Odum 1969) implies comprehensive understanding of the interactions responsible for distinctive ecosystem types, but unfortunately this knowledge is rarely available. As a result, the use of the term ecosystem, when describing entities such as forests, grasslands, wetlands or deserts is more intuitive than based on any distinct spatial configuration of interactions.

Where communities of organisms persist in dynamic equilibrium over long periods of time and occupy the same physical space, ecosystems may appear to have discrete physical boundaries, but these boundaries are porous to organisms and materials. Boundaries are, of course, most noticeable when there are major differences in the abiotic environment (for example lakes versus grasslands) and certainly some terrestrial ecosystems still extend over very large areas of the planet, for example savannah and tropical rainforests. Nevertheless, species abundance and species composition within these ecosystems always varies temporally and spatially. The population dynamics of species create temporal heterogeneity, while gradients in abiotic variables lead to spatial heterogeneity (Whittaker 1975) often over orders of magnitude (Ettama and Wardle 2002).

Ecosystem processes (Table 1.a) result from the life-processes of multi-species assemblages of organisms and their interactions with the abiotic environment, as well as the abiotic environment itself. These processes ultimately generate services when they provide utilities to humans (see Table 1.b). Alterations in biodiversity can result in very noticeable changes in ecosystem functioning: for example individual genes may confer stress tolerance in crops and increased productivity in agricultural ecosystems, and invasive species may transform fundamental ecosystem processes such as the nitrogen cycle (see section 3). The dimensions of biodiversity and its relationships to human well-being have been extensively addressed by Levin (2000), including both the services that biodiversity supports and the evolutionary genesis of biodiversity together with the ecological processes underlying patterns and trends.

The relationship between biodiversity and ecosystem functioning cannot be revealed by ecological studies of communities that focus on the structure and behaviour of species and populations at a location. What is needed in addition are studies that address the flux of energy and matter through the ecosystem. The measures used may be different: for example, community studies may employ indices measuring aspects of biodiversity, whereas ecosystem studies utilize measures of standing crop, or flux of nutrients. Both are important in the evaluation of ecosystem services. Services directly linked to primary plant productivity, e.g. provisioning of food, are measured in biomass per unit area, or nutrient content per unit biomass, whereas cultural services may require a measure of complexity of biodiversity at a suitable scale, e.g. species richness in spatial units within the landscape (Srivastava and Vellend 2005). However, this is not to say that such measures are mutually exclusive. For example, the service of biological pest control is best estimated both by measures of biodiversity in terms of insect predator guilds, and their temporal relative abundance.

Table 1.a. Some examples of biological and physical processes and interactions that comprise ecosystems functions important for ecosystem services. (From Virginia and Wall, 2000)

Ecosystem function	Processes
Primary production:	Photosynthesis Plant nutrient uptake
Decomposition:	Microbial respiration Soil and sediment food web dynamics
Nitrogen cycling:	Nitrification Denitrification Nitrogen fixation
Hydrologic cycle:	Plant transpiration Root activity
Soil formation:	Mineral weathering Soil bioturbation Vegetation succession
Biological control:	Predator-prey interactions

Table 1.b: Examples of relationships between biodiversity and ecosystem services.

Component of biodiversity	Example of ecosystem service (see also section 3)	Sources
Genetic variability	Medicinal products	Chai et al. (1989)
Population sizes and biomass	Food from crops and animals	Kontoleon et al. (2008)
Species assemblages, communities and structures	Habitat provision and recreation	Rosenberg et al. (2000)
Interactions between organisms and their abiotic environment	Water purification	Hefting et al. (2003)
Interactions between and among individuals and species	Pollination and biological control	Messelink et al. (2008)

In any community of organisms, some groups make the principal contribution to a particular process, and so contribute to the overall functioning of the ecosystem of which they are a part. Thus, the critical functions of communities of soil organisms are decomposition and nutrient and elemental cycling, whereas plant communities contribute biomass production through photosynthesis. Communities in the soil are intimately interlinked (through root-microbe interrelations) with vegetation, and faunal communities depend not only on primary plant production *per se* but on the composition and physical structure of plant communities for habitat. This linkage between above-ground and below-ground parts of ecosystems is fundamental in all cases, as exemplified by provisioning ecosystem services in low-input agriculture by the role of legumes within cropping cycles.

Box 1 illustrates some of the linkages between different communities of organisms in relation to their major functions. These interactions contribute both to the regulation of biomass in an ecosystem and to the diversity of species assemblages within communities.

Box 1: Biotic communities and their major functions

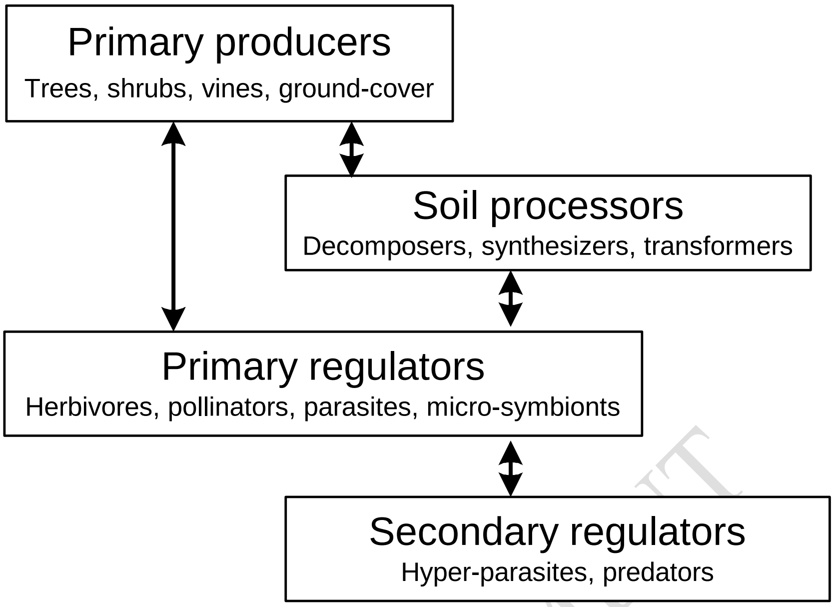

Figure 1: Illustrative relationships between different functional groups in ecosystems. (following Swift et al. 2004).

Primary producers:

Classification of plants into functional groups has an extensive history. Groupings can be based on a variety of reproductive, architectural and physiological criteria, but scale and efficiency of resource capture is often suggested as the main criterion. This will be determined by features of both architecture (e.g. position and shape of the canopy and depth and pattern of the rooting system) and physiological efficiency (see Smith et al. 1997). In some agro-ecosystems photosynthetic microorganisms may constitute a significant group, e.g. lowland rice.

Soil processors:

This is a very diverse community of organisms, involved in decomposition of organic matter (decomposers), soil synthesis (synthesizers) and nutrient cycling (transformers).

Decomposers:

This is a group of enormous diversity that can be subdivided taxonomically into bacteria, fungi, invertebrates, and others) having functional roles in the breakdown and mineralization of organic materials of plant or animal origin.

Synthesizers:

These are species that change the structure of soil and its porosity to water by burrowing, transport of soil particles amongst soil horizons, and formation of aggregate structures. Many of these species also contribute to decomposition.

Transformers:

This includes a range of autotrophic bacteria that utilize sources of energy other than organic matter (and therefore are not classifiable as decomposers) and play key roles in nutrient cycles as transformers of elements (carbon, nitrogen, phosphorus, sulphur etc.). Some heterotrophs that have a decomposer function but also carry out elemental transformations beyond mineralization (e.g. free-living di-nitrogen fixers).

Primary regulators:

Organisms that have a significant regulatory effect on primary production and therefore influence the goods and services provided by plants.

Pollinators:

Pollinators are a taxonomically very disparate group of organisms that includes many insect groups and vertebrates such as birds and bats.

Herbivores:

Vertebrate grazers and browsers are readily distinguished from invertebrate herbivores, although their impacts may be functionally similar and significant at the ecosystem level. The balance of effects of different types of herbivore can influence the structure of plant cover.

Parasites:

Microbial and fungal infections of plants may limit primary production in analogous manner to herbivory. Parasitic associations can also influence the growth pattern of plants and hence their architecture and physiological efficiency.

Micro-symbionts:

Mutualistic plant-microbial associations, e.g. di-nitrogen-fixing bacteria and mycorrhizal fungi.

Secondary regulators:

Hyper-parasites and predators:

This is diverse group of microbial parasites and vertebrate and invertebrate predators that feed on organisms in other groups and at other trophic levels.

Spatial interconnectedness maintains links and genetic interchange between populations of species, and underpins ecosystem functioning directly through physical connections. This is evident when considering energy and nutrient budgets; for example where nutrients ‘spiral’ downstream (Newbold et al. 1981) or move between floodplain wetlands and riverine ecosystems, especially due to flood ‘pulses’ (Junk et al. 1989). In this way, fish populations of African rivers benefit from the organic matter and nutrients deposited by both wild and domesticated herbivores grazing the floodplains during the dry season (Drijver and Marchand 1985). ‘Allochthonous’ organic matter (i.e. dead organic matter produced outside and transported into an ecosystem) may be important to the stability of ecosystems. At local scales dissolved or particulate organic matter may be dispersed by rivers during flooding (Junk et al. 1989). At larger scales, the annual migration of Pacific salmon (*Oncorhynchus* spp.) plays a key role in marine-freshwater nutrient recycling over vast distances (Mitchell and Lamberti 2005) with known dependencies for aquatic insect communities in Alaskan streams (Lessard and Merritt 2006), for brown bears *Ursus arctos* and for predatory birds (Hilderbrand et al 1999; Helfield and Naiman, 2006) and surrounding forest ecosystems. Polis et al. (1997) have highlighted the importance of understanding the impacts of nutrient transfers across ecosystem boundaries to the understanding of the dynamics of these systems.

The interactions within communities of organisms at population and community level play a key role in determining the stability and resilience of the ecosystem as a whole. Communities are structured by multiple biotic processes, and external conditions may strongly influence the outcome. Mouritsen et al. (1998) for example describe the dramatic impact of elevated summer temperatures on parasitic infections (by microphallid trematodes) on the mud snail *Hydrobia uvae* and amphipod *Corophium volutator* in Danish mudflats. High ambient temperatures in 1990 elevated the infection rate, which in turn led to the complete collapse of the amphipod population. The local extinction of this sediment-stabilizing population subsequently led to significant mudflat erosion and changes in topography. The result was substantive community depauperation, especially in macro-invertebrates, resulting in a change to the ecosystem (see also Griffin et al. 2009).

Understanding the role of biodiversity in ecosystem functioning has been considerably advanced by complementary studies of both the flow of energy and matter through trophic networks and the functional diversity of species within ecosystems (see Srivastava et al. 2009; Suding et al. 2008; Diaz et al. 2007a; Diaz and Cabido 2001). Villéger et al. (2008) have recently explored functional diversity indices that seek to encompass findings from both types of study. De Leo and Levin (1997) made a useful distinction between these two approaches. In practice, they are not mutually exclusive, and both underpin the ability of the ecosystem to support services of value to society. However, an increasing body of scientific evidence indicates that functional diversity, rather than species diversity *per se*, enhances ecosystem functions such as productivity (Tilman et al. 1997a; Hooper and Dukes 2004; Petchey et al. 2004), resilience to perturbations or invasion (Dukes 2001; Bellwood et al. 2004) and regulation of the flux of matter (Waldbusser et al. 2004).

Some species have a disproportionate influence on ecosystem functioning relative to their biomass and abundance, and the loss of such a ‘keystone’ species has cascading effects on community diversity and ecosystem functioning (Bond 1993). For example, the removal of the Pacific sea otter (*Enhydra lutris*) from Californian coastal ecosystems has led to the loss of the kelp community and many fish species; removal of fish-eating caiman from some areas of the Amazon resulted in a decline in the fish population and catch because of reduced nutrient cycling in the food chain (Williams and Dodd 1980); large changes in African elephant (*Loxodonta africana*) numbers have substantial effects on plant productivity, soil nutrient cycles and vegetation diversity in savannah woodlands and forests; and the impacts of herbivores on savannah plant communities are altered in ecosystems dominated by tsetse-flies.

A detailed discussion of functional traits, functional groups and functional diversity is provided by Hooper et al. (2005) where they concluded that:

I. Species functional characteristics strongly influence ecosystem properties. An increase in diversity leads to an increase in productivity due to complementary traits among species for resource use.

II. Increased biodiversity leads to an increase in response diversity (range of traits related to how species within the same functional group respond to environmental drivers) resulting in less variability in functioning over time (Elmqvist et al. 2003; Hughes et al. 2002).

III. Idiosyncratic effects due to keystone species properties and unique trait-combinations that may result in a disproportional effect of losing one particular species compared to the effect of losing one ‘average’ species.

1.2 The role of diversity in ecosystem functioning

In this section, we discuss issues of diversity and productivity and the roles of functional diversity before examining factors in ecosystem stability and change and the maintenance and generation of services.

1.2.1 Species diversity and productivity – terrestrial systems

Species dominating a community are generally major controllers of system function, yet evidence suggests that less obvious or abundant species have major roles in the functioning of ecosystems. These ‘ecosystem engineers’ (Swift et al. 2004), and ‘keystone species’ (Lyons *et al.*, 2005), may be uncommon species that greatly influence community dynamics, e.g. through enhancing resistance to species invasions (Lyons & Schwartz, 2001) or through their role as pollinators and seed dispersers (Cox et al. 1991). The population of an uncommon species may change dramatically in abundance and importance in response to particular conditions (Hobbs *et al.*, 2007), e.g in temperate lakes, species of plankton respond to seasonal changes in water temperature and mixing, and the associated availability of nutrients, resulting in rapid successional changes of species (Abrantes et al. 2006).

The diversity of functional types in soils is strongly linked to productivity. Many experiments have shown significant enhancements of plant production owing to the presence of soil animals, and specifically their diversity in the case of earthworms (Lavelle et al. 2006). The enhancement of primary production might be the result of increased release of nutrients from decomposition, enhancement of mutualistic micro-organisms (van der Heijden et al. 1998), protection against diseases, and effects on soil physical structure. However, experimentally removing key taxonomic groups from soil food webs may have little impact on rates of processes such as soil respiration and net ecosystem production (Ingham et al. 1985; Liiri et al. 2002; Wertz et al. 2006), possibly because the exceptional diversity of soil organisms and the relatively low degree of specialization in many groups means that many different species can perform similar processes (Bradford et al. 2002; Fitter et al. 2005).

The role of biodiversity in maintaining productivity has been studied in theoretical, controlled-environment and small- and large-scale field studies (see, for example, Naeem et al. 1995; Tilman et al. 1996, 1997b; Lawton et al. 1998), but few data are from “mature” natural ecosystems. Grace et al. (2007) compared a large set of natural ecosystems and suggested that the influence of diversity on productivity was weak when examined at small spatial scales. Nevertheless, a meta-analysis of published studies found clear evidence of a positive effect of biodiversity on productivity at the same trophic level where biodiversity was measured (Balvanera et al. 2006). Furthermore, Balvanera et al (2006) draw the following conclusions based on the review of current data: 1) plant diversity appears to enhance belowground plant and microbial biomass, 2) plant diversity has positive effects on decomposer activity and diversity, and both plant and mycorrhizal diversity increase nutrients stored in the plant compartment of the ecosystem, 3) increasing the diversity of primary producers contributes to a higher diversity of primary consumers, 4) higher plant diversity contributes to lowering plant damage by pest organisms, and 5) abundance, survival, fertility and diversity of invasive species is reduced when plant diversity increases. At large spatial scales, Costanza et al. (2007) showed that over half of the spatial variation in net productivity in North America could be explained by patterns of biodiversity if the effects of temperature and precipitation were taken into account.

In intensively managed and disturbed ecosystems, maximum productivity is typically achieved in systems of very low diversity, for example heavily fertilized monocultures. However, these systems require large inputs of resources, including fertilizers, biocides and water, which generally are not environmentally or economically sustainable (Wright 2008). Sustained high production without anthropogenic resource augmentation is normally associated with high levels of biodiversity in mature ecosystems. In an eight-year study, Bullock et al. (2007) reported positive effects of increased species richness on ecosystem productivity in restored grasslands on a range of soil types across southern England. Similarly, Potvin and Gotelli (2008) reported higher productivity in biologically diverse tree plantations in the tropics, suggesting that increasing diversity in timber plantations may be a viable strategy for both timber yields and biodiversity conservation.

1.2.2 Species diversity and productivity – marine systems

Biodiversity is also associated with enhanced productivity in marine systems (Worm et al. 2006). Arenas et al. (2009) examined how different components of biodiversity influence the performance of macroalgal assemblages in natural communities. They found positive relationships for biomass and species richness with productivity but also relationships of spatial aggregation and species evenness with some of the productivity-related variables analyzed. In a meta-analysis of published experimental data (Balvanera et al. 2006), it was found that increased biodiversity of both primary producers and consumers enhanced the ecosystem processes examined; the restoration of marine ecosystems has also been shown to increase productivity substantially. Overfishing together with climate change and other pressures are producing impacts of unprecedented intensity and frequency on marine ecosystems, causing changes in biodiversity, structure and organization of marine assemblages directly and indirectly (Worm et al. 2006). Numbers and diversity of large pelagic predators have been sharply reduced and the impacts of this loss can cascade through marine communities (Heithause et al. 2008). Predictions about how communities will respond to marine predator declines have to consider the risk effects and behaviorally mediated indirect interactions. In the case of vertebrate predators and long-lived prey species in particular, a sole focus on direct predation might greatly underestimate the community effects of predator loss (Heithause et al. 2008).

Although evidence from numerous experiments has very often shown a positive, but near universal saturating relationship between biodiversity and ecosystem functioning (Loreau 2008), analysis of deep sea ecosystems has shown a very different pattern. A recent global-scale study based on 270 datasets from 116 deep-sea sites, showed that functioning of these ecosystems is not only positively but also exponentially related to biodiversity in all the deep-sea regions investigated (Danovaro et al. 2008). Three independent indicators of ecosystem efficiency were used: 1) the meiofaunal biomass to organic C fluxes ratio, to estimate the system's ability to use the photic's zone primary production, 2) the prokaryote C production to organic C flux ratio, to estimate the system's ability to use and recycle organic matter deposited on the sea floor; and, 3) the total ratio of benthic meiofaunal biomass to sediment's biopolymeric C content, to estimate the system's ability to channel detritus to higher trophic levels. Significant and exponential relationships were found between biodiversity and each of these three independent indicators. Results suggest that higher biodiversity supports higher rates of ecosystem processes and an increased efficiency with which these processes are performed (Danovaro et al. 2008). These exponential relationships support the hypothesis that mutually positive functional interactions (ecological facilitation) are prevalent in these deep-sea ecosystems. Although there is still no full understanding of all the processes regulating deep-sea food webs and the ecological role of each species, it is hypothesized that the increase in bioturbation of the seafloor may increase benthic fluxes and the redistribution of food within the sediment, leading to an increase in ecosystem functioning. These results suggest that biodiversity loss in deep-sea ecosystems might be associated with significant reductions in functioning. Deep-sea sediments cover 65% of the world's surface, and deep-sea ecosystems play a key role in ecological and biogeochemical processes at a global scale. The importance of deep-sea biodiversity in maintaining the sustainable functioning of the worlds' oceans may still be grossly underestimated (Danovaro et al. 2008).

1.3 Functional groups and functional diversity

Functional groups are groups of organisms that perform particular operations in an ecosystem. They might, for example, produce biomass, pollinate, fix nitrogen, disperse seeds, consume other organisms, decompose biomass, mix soils, modify water flows, and facilitate reorganization and colonization. Loss of a major functional group may cause drastic alterations in ecosystem functioning (Chapin et al. 1997; Jackson et al. 2001). Hooper et al. (2005) concluded that certain combinations of species are complementary in their patterns of resource use and can increase average rates of productivity and nutrient retention, making diversity of functional traits one of the key controls on ecosystem properties.

Redundancy (i.e. more than one species performing the same process role) of functional traits and responses in ecosystems may act as an 'insurance' against disturbance and the loss of individual species if the diversity of species in the ecosystem encompasses a variety of functional response types (Hooper et al. 2005; Winfree and Kremen 2009). *Response diversity*, i.e. different responses to environmental change among species that contribute to the same ecosystem function, has been argued to be critical in ecosystem resilience (Elmqvist et al. 2003). Such species may replace each other over time, contributing to the maintenance of ecosystem function over a range of environmental conditions. Regional losses of such species increase the risk of large-scale catastrophic ecosystem shifts because spatial sources for ecosystem reorganization after disturbance are lost (O'Neill and Kahn 2000; Bellwood et al. 2004). This is a poorly understood area, but nonetheless current ecological theory predicts that when an ecosystem service is provided jointly by many species, it will be stabilized against disturbance by a variety of 'stabilizing mechanisms'. Few studies have investigated the occurrence of stabilizing mechanisms in landscapes affected by human disturbance. Winfree and Kremen (2009) used two datasets on crop pollination by wild native bees to assess three potential stabilizing mechanisms: density compensation (negative co-variance among species' abundances); response diversity (differential response to environmental variables among species); and cross-scale resilience (response to the same environmental variable at different scales by different species). They found evidence for response diversity and cross-scale resilience, but not for density compensation, concluding that these mechanisms may contribute to the stability of pollination services, thus emphasizing the insurance value of seemingly ‘redundant’ species.

1.4 The complexity of finding quantitative links between biodiversity and ecosystem services

In principle it should be straightforward to relate biodiversity measures to ecosystem service delivery, but in practice it is complicated by several factors (see also Chapter 3). First, biodiversity is a multidimensional concept and its description and measurement therefore takes many forms. Descriptions of biodiversity include classifications of the various hierarchical levels (communities, species, individuals, genes) but also of other dimensions such as interaction webs (trophic, host-parasite, pollinator), evolutionary diversity based on phylogenetic trees, trait diversity based on species-specific traits, or composite measures that attempt to summarize multiple measures. Some of these measures have been developed with a particular purpose in mind, others are attempts to simplify the complexity.

The second problem relates to the diverse set of purposes for the various measures of biodiversity that have been developed. Most available measures have been developed for specific purposes, so the available measures may not be what are needed for a particular purpose. For example, many available data sets that show large-scale (global, continental, major biome) distributions of biodiversity are measures of species richness, primarily derived for conservation reporting and planning, and tend to be counts of species richness or measures of population trends for large-bodied animals and plants. At smaller spatial and geographical scales, information is more varied, but again it is often information gathered for particular purposes (e.g. national reporting to international bodies for food and agricultural production and trade, conservation reporting, environmental quality monitoring). Therefore, most of the available data have been collected for another purpose, and are not obviously applicable to measures of biodiversity change that can inform analyses of ecosystem service delivery.

The third problem is that, although ecosystem service delivery often increases in quality, quantity or resilience with increasing biodiversity, the strength and the form of the relationship, and the measure of biodiversity that is the best predictor of ecosystem service quality or quantity, varies widely according to the ecosystem service being considered.

The above considerations mean that it is not yet possible to account accurately for the role of biodiversity, nor the probable impact of its decline, on ecosystem service delivery in general. On the one hand, measures of species richness (and subsets such as endemism, rarity, threat etc.), which are available globally for vertebrates and some plant groups, are hard to link directly to ecosystem functions and processes. On the other hand, locally available, ecosystem-specific or taxon-specific measures of functional type or functional diversity may relate well to certain specific ecosystem functions, but may not be generally applicable to other valued services in that ecosystem. Unfortunately, these local measures cannot be scaled-up to larger areas or transferred to other ecosystem types.

The extent to which biodiversity metrics can be used for ecosystem service assessments is therefore a direct consequence of whether the measures are correct for the context. Unfortunately, because the understanding of the role of biodiversity is still incomplete, one can only be confident about a few cases where good data are available that are known to support ecosystem service valuations. For example:

The productivity of terrestrial and aquatic systems for marketed foods, fuels or fibres can be measured using production statistics. The relevant measures of diversity in arable systems, for example, relate to crop genetic diversity, the diversity of land races and wild relatives, and the diversity of pests, pathogens, predators and symbionts. The most relevant biodiversity metric for crops is genetic diversity.

The ecosystem service of food production depends in many cases on pollinators. Here the relationship between the service and biodiversity is strong, and the relevant metric is pollinator species richness. While the form of these relationships may be quite general, it appears that the resistance of different areas to pollinator loss varies quite widely according to the nature of the plant-pollinator interaction web in that ecosystem, and the recent history of pollinator and plant decline.

Many cultural services depend primarily on species diversity, and tend to concentrate on the large-bodied, charismatic plants, birds and mammals. The relationships between the service and biodiversity in these cases are very strongly dominated by diversity measures that never saturate. In fact the values increase with the addition of more, rare forms. For these purposes, the global conservation species datasets are useful and highly relevant. However, the relationships do not scale down simply within countries or local areas.

The ecosystem service of freshwater quality shows a weak but rapidly saturating relationship with biodiversity and is strongly focused on a few functional types that are likely to be generally applicable across both scales and systems.

Some work done on ecosystem processes such as primary productivity or decomposition (referred to as supporting services in the Millennium Ecosystem Assessment (MA 2005)) may also be relevant for many ecosystem services that ultimately depend on them. In studies, plant functional traits such as leaf area or plant size are strong predictors of ecosystem process strength, and measures such as the weighted mean of the plants in the community are the best predictor, though sometimes the presence or absence of particular trait values are also very significant (Diaz et al. 2007b; Suding et al. 2008).

2 The links between biodiversity, ecosystem functions and ecosystem services

The following review of the evidence base for links between biodiversity, ecosystem functions and specific ecosystem services is based on two recent reviews, Balmford et al. (2008) and the EASAC report “Ecosystem services and biodiversity in Europe” (EASAC 2009) and updated with additional studies and reports. Substantial knowledge gaps remain, and understanding of the underlying processes for the generation of several services is limited; the following presentation reflects this variable knowledge. This section follows the general typology of services presented in chapter 1 and treats the services one by one, with the potential linkages among multiple ecosystem services further discussed in section 4. The typology where services are classified as *provisioning, regulating, habitat and cultural* is mainly used as a way of structuring information and does not reflect the inherent complexity where, e.g. a provisioning service, like fish, is not just representing a protein source, but also carries a strong cultural dimension related to harvesting techniques, preparation, symbolism etc. To place cultural values in a separate category is thus underestimating the cultural dimension of many of the services in other categories and this should be an area for further development.

PROVISIONING SERVICES

2.1 Provision of food

Context and importance of service

Agro-ecosystems provide food for human consumption and, together with the associated ecosystems supporting marine and freshwater fisheries, underpin global food security. Today 35% of the Earth’s surface is used for growing crops or rearing livestock (MA 2005). Grazing land alone accounts for 26% of the Earth’s surface, and animal feed crops account for a third of all cultivated land (FAO 1999). Heywood (1999) estimated that well over 6,000 species of plants are known to have been cultivated at some time or another, and many thousands that are grown locally are scarcely or only partly domesticated, whilst as many, if not more, are gathered from the wild. Despite this, only about 30 crop species provide 95% of humanity’s food (Williams and Haq 2002) and it has been argued that the world is currently over-dependent on a few plant species.

Plants and animals derived directly from marine biodiversity provide a significant part of the human diet. Fisheries and aquaculture produced 110 million tonnes of food fish in 2006, a *per capita* supply of 16.7 kg (FAO 2009). Almost half of this (47 %) was produced by aquaculture. For nearly 3 billion people, fish represent at least 15% of their average *per capita* animal protein intake. Whereas official statistics estimate that in low-income food-deficit countries, the contribution of fish to the total animal protein intake was <20%, the true proportion is probably higher in view of the under-recorded contribution of small-scale and subsistence fisheries (FAO 2009).

Sensitivity of service to variation in biodiversity – terrestrial agro-ecosystems

Harlan (1975) argued that the increasing dependence on fewer species for crops was leading to the loss of native genetic resources, and higher yielding modern varieties were displacing ‘landraces’ uniquely adapted to local conditions. In genetic terms, landraces are typically heterozygous at many loci, and this *in-situ* gene pool, together with that in wild crop relatives, remains an essential source of genetic diversity for plant breeders for new varieties. Failure to maintain sufficient genetic diversity in crops can incur high economic and social costs. The potato famine in Ireland in the nineteenth century is generally attributed to the low genetic diversity of the potatoes cultivated there, making the entire crop susceptible to potato blight fungus, a problem resolved by using resistant varieties from original gene pools in South America. Mixtures of varieties may successfully reduce disease incidence and increase yields as for example with the case of barley in Europe (Hajjar et al. 2008; see general review in de Vallavieille-Pope 2004), although there is much variation and often conflicting conclusions are drawn.

Hooper and Chapin (2005) argue that maintenance of high productivity over time in monocultures almost invariably requires heavy and unsustainable subsidies of chemicals, energy, and financial capital (EASAC 2009). They suggest that, from both economic and ecological perspectives, diversity must become increasingly important as a management goal. Organic farming can increase biodiversity (species richness and abundance), but with inconsistent effects among organisms and landscapes (Bengtsson et al. 2005). Even though crop yields may be 20% lower in organic farming systems, inputs of fertilizer and energy may be reduced by 30–50%, and pesticide input by >90%, suggesting that the enhanced soil fertility and higher biodiversity found in organic plots may render these systems less dependent on external inputs (Mader et al. 2002). In addition, they may be as profitable, or more so, than conventional agro-industrial systems. However, reduced yields in organic farming results in a trade-off between land for agriculture and land for maintaining wild biodiversity. Biodiversity could be promoted by using intensive agriculture and devoting spare land to biodiversity or by extending ‘organic’ or integrated farming systems that promote biodiversity (Fischer et al. 2008), but the outcomes of these two approaches would be very different.

The value of biodiversity is evident in permanent grassland and pasture ecosystems, where increased species richness often enhances biomass productivity and ecosystem functioning (Bullock et al. 2007; Tilman et al. 1996, 1997a, b; Naeem et al. 1995). Such gains appear to exploit species complementarity (Cardinale et al. 2007), but may also reflect the ‘sampling effect’ (McNaughton 1993) i.e. the relative higher frequency of the more productive species in a mixture.

Sensitivity of service to variation in biodiversity – marine systems and aquaculture

With dwindling marine fish stocks worldwide, aquaculture is thought to be the way to increase fish production necessary to feed an increasing human population. But this activity, which has been growing rapidly and accounts now for half of the global fish production, is still very dependent on wild fish for seed and feed (FAO 2009) and thus on functioning natural ecosystems and biodiversity. Intensively cultured fish and shrimp are fed on fish meal and fish oil that comes mainly from fishing (Deutsch et al. 2007). Furthermore, most aquaculture uses other ecosystem services, especially nutrient recycling and water purification. Since they are concentrated in coastal areas, strong impacts are already being felt in some places (e.g. Chile, Thailand) and this has made the expansion of aquaculture difficult. Although much research has been devoted to the replacement of fish meal and fish oils with land plant-based materials (e.g. soy meal and other cereals), with very good results (Carter and Hauler 2000; Clayton et al. 2008), provision of these foodstuffs themselves has important environmental impacts (Fearnside 2001; Steinfeld et al. 2006; FOE 2008), and their diversion to fish food has nutritional costs for many poor people (Delgado et al. 2003) with high social costs. The use of seaweeds harvested from natural ecosystems or cultivated in seawater (e.g. Valente et al. 2006) may be a way to produce feed for herbivorous fish without burdening fisheries or agricultural land.

Where are services generated?

Food is produced principally in intensively managed agro-ecosystems, but apart from areas devoted to wildlife conservation or recreation, and those used for other production systems (e.g. forestry), most landscapes/seascapes are involved in food production to some extent. Urban and suburban areas have allotment and other forms of gardens that are used for food production, particularly in developing countries. The ubiquity of agricultural production also means that other ecosystems are frequently adjacent to food-producing land and processes and practices of agriculture may therefore have a broader impact. This may involve spray drift of pesticides, nutrient pollution and barriers to the migration and dispersal of organisms among remaining patches of non-agricultural land, with negative consequences for the ability of distributed populations to withstand environmental change.

Uncertainties in delivery of service

At current levels of consumption, global food production will need to increase by 50% within the next four decades to meet the demands of a growing human population (UN 2009) and as consumption levels and world food prices rise, pressure to maximize the area under production will grow. Given the rapidly growing demands on the planetary ecosystems (Rockström et al. 2009), it is becoming critical to understand how a dramatic increase in agricultural production and shifting land use in combination with climate change will affect natural processes of the biosphere and levels of key regulating ecosystem services (e.g., CO_2, nitrogen flow, freshwater consumption). Large uncertainties remain about the outcome of these complex interactions. Increasing offshore aquaculture for the production of fish and seaweeds for food will result in substantial intensification of the use of the sea for food production and since the open sea is usually poor in nutrients, these will have to be added (with deep-sea water or artificial fertilization). The effects of these practices for the open sea ecosystems and processes are poorly understood.

2.2 Water provision (2), including regulation of water flows (10) and water purification (11)

Context and importance of service – water provisioning

Ecosystems play important roles in the global hydrological cycle, contributing to water provision (quantity, defined as total water yield), regulation (timing, the seasonal distribution of flows) and purification (quality, including biological purity as well as sediment load) (Dudley and Stolton 2003; Bruijnzeel 2004; Brauman et al. 2007). Global water use is dominated by agricultural withdrawals (70% of all use and 85% of consumptive use), including livestock production, followed by industrial and domestic applications. Vegetation, particularly forests, significantly influences the quantity of water circulating in a watershed. It is commonly assumed that forests generate rainfall and, in comparison with pasture and agriculture, promote higher rates of evapotranspiration and greater aerodynamic roughness, leading to increased atmospheric humidity and moisture convergence, and thus to higher probabilities of cloud formation and rainfall generation. Although evidence is increasing (Bruijnzeel 2004) that large-scale land use conversions affect cloud formation and rainfall patterns, this effect is highly variable and specific. The hypothesis of a 'biotic pump' has been elaborated by Makarieva et al. (2006) and Makarieva and Gorshkov (2007) as an explanation of high rainfall in continental interiors of the Amazon and Congo river basins. Marengo et al. (2004) discussed the role of the Amazonian 'water pump' (see Chapter 1, Figure 7), assumed to sustain rain-fed agriculture and other ecological systems elsewhere in the continent. Shiel and Murdiyarso (2009) reviewed the mechanisms and proposed that if the 'water pump' hypothesis proves accurate, modest forest loss may transform conditions in continental interiors from moist to arid, and forest biodiversity may be an underestimated factor in regional rain fall regulation.

Context and importance – water regulation and purification

In areas with seasonal rainfall, the distribution of stream flow throughout the year is often of greater importance than total annual water yield. This is particularly important to agricultural production, as irrigation is most important during the dry season. The same conditions that increase water infiltration also result in lower surface run-off. The link between regulation of water supply and water quality is strong because rapid flows of water through soil or ecosystems reduce the time in which transformations can occur; extreme weather events thereby lead to poorer water quality.

Sensitivity of services to variation in biodiversity

Although vegetation is a major determinant of water flows and quality, and micro-organisms play an important role in the quality of groundwater, the relationship of water regulation and purification to biodiversity is poorly understood, except in so far as the states of soil and vegetation determine water flows and storage. The activity of soil organisms has a large and direct impact on soil structure and hence on infiltration and retention rates. Ecosystems such as forest and wetlands with intact groundcover and root systems are considered very effective at regulating water flow and improving water quality. Vegetation, microbes, and soils remove pollutants from overland flow and from groundwater through various means, including: physically trapping water and sediments; adhering to contaminants; reducing water speed to enhance infiltration; biochemical transformation of nutrients; absorbing water and nutrients from the root zone; stabilizing eroding banks; and diluting contaminated water (Brauman et al. 2007). Changes to water quality that occur in soil include the transformations of persistent organic pollutants (POPs), sequestration and conversion of inorganic ions (nitrate, phosphate, metals), and removal of disease-causing microbes such as *Cryptosporidium* (Lake et al. 2007). Similar processes, including nutrient uptake and consumption of pathogens, occur in water bodies, including lakes and rivers of good ecological quality.

Where are services generated?

Water reaches freshwater stores (lakes, rivers, aquifers) by a variety of routes, including direct precipitation, surface and subsurface flows, and human intervention. In all cases, the water quality is altered by the addition and removal of organisms and substances. Ecosystems therefore play a major role in determining water quality. In particular, the passage of water through soil has a profound impact, both through the dissolution of inorganic (for example nitrate, phosphate) and organic (dissolved organic carbon compounds, pesticides) compounds and the modification of many of these by soil organisms. This service is therefore relevant to all terrestrial ecosystems, but may be of particular significance in urban and intensively managed ecosystems.

Uncertainties in delivery of service

Most changes to the capacity of ecosystems to regulate and provide freshwater seem to derive from, and be generally proportional to, land-use change. However, in some situations a relatively small additional change may trigger a disproportionate – and sometimes difficult to reverse – response from ecosystems' hydrological function (Gordon et al. 2008). For example, human-induced eutrophication can lead to sudden shifts in water quality from clear to turbid conditions, due to algal blooms (Scheffer et al. 1993) which affect freshwater fisheries and recreational use of water bodies. Reduction of nutrient concentrations is usually insufficient to restore the original state, with restoration necessitating very substantially lower nutrient levels than those at which the regime shift occurred (see section 5.1 below). Another example is represented by cloud forest loss, which results in a regime shift that may be largely irreversible. In some areas, such forests were established under a wetter rainfall regime, thousands of years previously. Necessary moisture is supplied through condensation of water from clouds intercepted by the canopy. If the trees are cut, this water input stops and the resulting conditions can be too dry for recovery of the forest (cf. Folke et al. 2004). In addition, climate change potentially can trigger sudden changes, particularly in regions where ecosystems are already highly water-stressed.

2.3 Fuels and fibres

Context and importance of service

The provision of fuels and fibres – such as timber, cotton, jute, sisal, sugars and oils - has historically been a highly important ecosystem service. Natural systems provide a great diversity of materials for construction and fuel, notably oils and wood that are derived directly from wild or cultivated plant species. Production of wood and non-wood forest products is the primary commercial function of 34% of the world's forests, while more than half of all forests are used for such production in combination with other functions, such as soil and water protection, biodiversity conservation and recreation. Yet only 3.8% of global forest cover corresponds to forest plantations, indicating that a substantial fraction of natural forests is used for productive uses (FAO 2006).

There is currently intense interest and strong policy direction to increase the proportion of energy derived from renewable sources, of which biological materials are a major part. At present, this is being achieved partly by the cultivation of biomass crops and partly by diversion of materials otherwise useable as food for people or animals, including wheat and maize, to manufacture ethanol as a replacement for petrol and other oil-derived fuels. Recently a big effort has been put into the cultivation of algae for biofuels. Although most attempts at cultivation have selected microalgae known to have high oil content, some studies using macroalgal biomass are also underway (Ross et al. 2008; Adams et al. 2009). This production, which does not need arable land or freshwater, may be a way to produce clean energy without the social costs of terrestrial alternatives. The wider environmental impacts of these cultivations, however, will have to be determined, since they would be very large scale operations. In this context, Hill et al. (2006) have argued that biodiesel, in comparison to bioethanol, returns such significant environmental advantages that it deserves subsidy.

Sensitivity of service to variation in biodiversity

As in the case of food production, the mix of species cultivated in production forests is selected to maximize the rate of return on timber production, and does not generally reflect the range of ecosystem services that are co-produced with timber – watershed protection, habitat provision, climate amelioration and so on. Managed forests, like farms, typically depend upon a small number of species. The question of whether forests are more productive in terms of biomass if they have higher tree species diversity has been addressed by a few studies, with mixed results. For example, tree species diversity was found to have a negative relationship with above-ground biomass in natural forests of Central Europe (Szwagrzyk and Gazda 2007), no relationship with productivity in Aleppo pine and Pyrenean Scots forests of Spain (Vilà et al. 2003), and a positive effect on wood production in early successional Mediterranean type forests (Vilà et al. 2007). Although species diversity might lead to higher productivity in the forest, the proportion of commercial species in more diverse sites is typically lower (FAO 2006). On the other hand, species richness has been found to increase yields in tropical tree plantations, due to increased growth of individual trees (Potvin and Gotelli 2008), and it may reduce the impact of pests on timber species. At present, however, commercial timber production is dominated by a small number of species.

For biofuels, it seems unlikely that biodiversity of the crop will play a direct role in most production systems, although all land-based biofuel production will still rely on the supporting and regulating services, such as nutrient and water cycling, for which biodiversity of soil organisms is important. The exception is the proposal to use mown grassland as a second-generation biofuel. Sustained production in such a system may well be best achieved by a diverse mixture of plant species. Biofuel production with algae is dependent on aquatic biodiversity for the provision of species adapted to the different places where cultivations would be held.

Where are services generated?

Most ecosystems are important, including forests, savannas, grasslands and marine and coastal systems in delivering this service. Ecosystems likely to be used for biofuel production include forests, arable land generally and grasslands. There is likely to be strong pressure to bring land currently regarded as marginal for agriculture into production for biofuel production; because time-to-market issues are less important than for food production systems. Remote and relatively inaccessible areas where land values are low may be targets for biofuel systems, introducing conflicts with recreation and biodiversity conservation.

Uncertainties in delivery of service

It is likely that a decline in the provision of wild timber, plant fibres and fuelwood will take place in proportion to the decline in the forested area. Fragmentation, however, may result in a much quicker decline in forest productivity than what would be expected given the total area of remaining forest (Laurance et al. 2001). Climate change has also been implicated in increasing forest fire risk (e.g. Westerling et al. 2006) and the combined effects of fragmentation and climate change may conspire to prompt an abrupt increase in fire risk, which may be particularly devastating (and less likely to be reversible) in tropical rain forests, as species are not ecologically adapted to fire, and each fire event tends to increase the likelihood that future fires will take place.

2.4 Genetic resources

Context and importance of service

Genetic diversity of crops increases production and decreases susceptibility to pests and climate variation (Ewel 1986; Altieri 1990; Zhu et al. 2000). In low-input systems especially, locally adapted varieties often produce higher yields or are more resistant to pests than varieties bred for high performance under optimal conditions (Joshi et al. 2001). In agriculture, the diversity of genetic resources comprises the traditional resources (wild types and the older domesticated landraces) together with modern cultivars. Genetic resources will be increasingly important in support of improved breeding programs (e.g. for crop plants, farm animals, fisheries and aquaculture), with a wide range of objectives for increasing yield, resistance to disease, optimization of nutritional value, and adaptation to local environment and climate change. Advances in genomics research are opening up a new era in breeding, where the linkage of genes to traits (marker-assisted selection) provides a more efficient and predictable route than conventional breeding programs to improved strains.

Sensitivity of service to variation in biodiversity

This is a service for which biodiversity is of central importance, because genetic diversity is inevitably lost when biodiversity declines. The greatest focus on genetic diversity as a service is in the protection of gene pools for agriculture. The Food and Agriculture Organization of the United Nations (FAO) has done much significant work at the global level to support characterization of genetic resources in the food crop, livestock, fisheries/aquaculture and forestry sectors, but quantifiable data on trend analysis in genetic resources are very limited and have been collected only for relatively brief periods. There are now numerous initiatives to collect, conserve, study and manage genetic resources *in situ* (for example growing crops) and *ex situ* (for example seed and DNA banks) worldwide. New techniques using molecular markers are providing new precision in characterizing biodiversity (at the level of molecular systematics and taxonomy) and the genetic diversity within collections – a significant aid to developing management strategy to identify gaps and redundancy (Fears 2007). Box 2 highlights the fundamental importance (option/insurance value) of this reservoir of genetic diversity to crop improvement for stress tolerance.

Box 2: Biodiversity at the gene level

A success story

In low-lying agricultural regions of the world, in Bangladesh and India for example, farmers suffer annual crop losses because of flooding of up to 4 million tons of rice (*Oryza sativa*) – enough to feed 30 million people – and the costs across the vast rain-fed lowland areas of Asia, as a whole, amount to about a billion dollars. Flood tolerance originally observed in a traditional Indian variety FR13A, and subsequently located with molecular markers and transferred into modern cultivars by conventional plant breeding (Xu et al. 2006), is conferred by a particular gene, the Sub1A-1 gene at the polygenic 'Submergence-1' (Sub1) locus. This gene halts the elongation of rice stems as a response to flooding, ensuring carbohydrate conservation for further growth when flood waters recede, and enhances yield over susceptible varieties (see Figure 2). Phylogenetic analysis has shown that this particular gene is also present in wild relatives *O. rufipogon* and *O. nivara* that persist in the wetlands of south and South East Asia. These wetlands, such as the Plain of Reeds in southern Vietnam, not only provide ecosystem services in regulation of water flow and quality but also act as a habitat for the evolution of genetic variation amongst *Oryza* species.

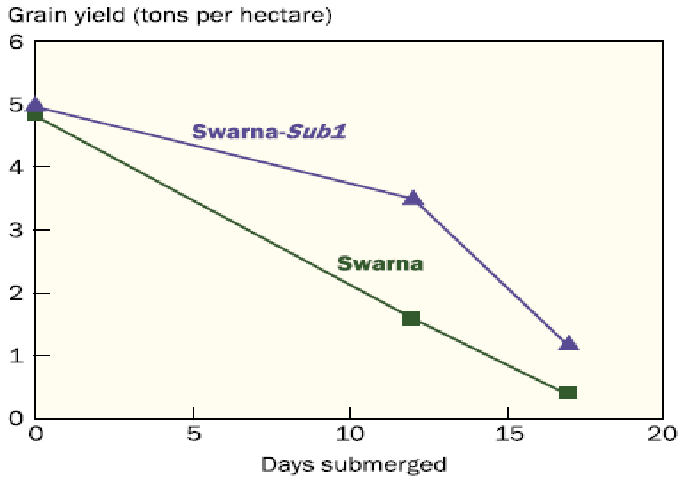

Figure 2: **The impact of insertion of the Sub-1 gene on the yield of the rice cultivar Swarna.** This gene confers tolerance to early submergence in water. Plants were completely submerged 14 days after the transplanting of 14 day-old seedlings in field trials at the International Rice Research Institute (Mackill 2006).

A current threat

The evolution of a new race (Ug99) of wheat stem rust (*Puccinia graminis*) in 1999 in the East African Highlands, and its subsequent range expansion from Kenya to Ethiopia has followed the predominant west-east airflows dispersing spores. It threatens global wheat production because of the absence of resistance in most modern cultivars. The potential migration path from East Africa via the Arabian peninsular, to the Middle East into the rice-wheat belt of the Indo-Gangetic plains represents a major threat to food security in South Asia. Strategies to mitigate the risks of loss of yield in a crop that underpins the livelihoods of millions of people requires the breeding of durable resistance into cultivars locally adapted for yield potential. Incorporating different combinations of race-specific resistance genes into new cultivars is one way forward. Such genetic diversity is present in germ plasm of wild relatives of wheat (e.g. *Triticum speltoides* and *T. monococcum*) and traditional Kenyan landraces (Singh et al. 2006).

Where are services generated?

All ecosystems are important for their genetic resources. Agricultural biodiversity can be considered to have a special status because of previous human efforts to improve varieties, hence the specific focus of the International Treaty on Plant Genetics Resources to conserve resources for food and agriculture. The replacement of landraces by high-yielding food crop varieties, taken together with other changes in agricultural practice has accelerated the erosion of genetic variation in cultivated material. The loss of genetic diversity associated with more intensive agriculture may also have deleterious impacts on the non-domesticated plants and animals (and micro-organisms) in the ecosystem. A decline in crop genetic diversity has consequences for their genetic vulnerability and their plasticity, for example to respond to biotic and abiotic stress.

Uncertainties in delivery of service

Given the likely non-linear relationship between area and genetic diversity, in some cases a small change in area (of natural habitat, or of traditional agricultural lands) may result in a disproportionate loss in genetic diversity of crops or livestock. This is probably more likely in areas that have already suffered extensive habitat loss and land conversion where the remaining populations of particular varieties and breeds are quite small. Climate change may also have non-linear effects on genetic diversity of crops and livestock.

2.5 Medicinal and other biochemical resources

Context and importance of service

Biochemicals encompass a broad range of chemicals of high value, for example metabolites, pharmaceuticals, nutrients, crop protection chemicals, cosmetics and other natural products for industrial use (for example enzymes, gums, essential oils, resins, dyes, waxes) and as a basis for biomimetics that may become increasingly important in nanotechnology applications as well as in wider contexts (Ninan 2009). Some of the best-characterized examples are pharmaceuticals, the value of which has been long recognized in indigenous knowledge. It has been estimated that “of the top 150 prescription drugs used in the U.S., 118 originate from natural sources: 74% from plants, 18% from fungi, 5% from bacteria, and 3% from one vertebrate (snake species)” (ESA 2000). In addition to these high-value biochemical products, there is an important related consideration in the use of biomass for chemical feedstocks in addition to bioenergy, where development of integrated biorefineries will generate the building blocks (platform chemicals) for industrial chemistry. A report from the US Environmental Protection Agency (2007) concludes that economically competitive products (compared with oil-derived) are within reach, for example for celluloses, proteins, polylactides, plant oil-based plastics and polyhydroxyalkanoates (Ahmann and Dorgan 2007). The high-value products may make use of biomass economically viable, leading to significant land-use conflicts.

Sensitivity of service to variation in biodiversity

Biodiversity is the fundamental resource for bioprospecting, but it is rarely possible to predict which species or ecosystem will become an important source. A wide variety of species – microbial, plant and animal – have been valuable sources of biochemicals, but the achievements so far are assumed to be only a very small proportion of what could be possible by more systematic screening. The impact of the current global decline in biodiversity on the discovery of novel biochemicals and applications is probably grossly underestimated. Biodiversity loss resulting from relatively low-value activities such as logging may compromise future high-value activities (as yet undiscovered) associated with the search for novel biochemicals and chemicals.

Where are services generated?

All ecosystems are potential sources of biochemicals. Numerous examples can be cited from the oceans and shoreline, freshwater systems, forests, grasslands and agricultural land. Species-rich environments such as tropical forests have often been assumed to supply the majority of products. However, the problem of the general lack of a robust and reliable measure to assess the commercial or other value of an ecosystem is compounded by the expectation that most biochemical resources have yet to be discovered and exploited. Microbes seem likely to be especially rich in undiscovered metabolic capacities, and the complexity of soil ecosystems indicates the potential in searching for novel biochemicals there.

Uncertainties in delivery of service

Species richness may be quickly reduced as habitat destruction progresses in highly diverse regions (e.g. Forest et al. 2007), and the sources of biochemicals may change abruptly e.g. in coral reefs going through a phase shift.

2.6 Ornamental resources

Context and importance of service

Biodiversity has played an iconic, ornamental role throughout the development of human society. Uses of plant and animal parts, especially plumage of birds, have been important in conferring individual status, position and influence. Ornamental plants are typically grown for the display of their flowers but other common ornamental features include leaves, scent, fruit, stem and bark. Considerable exploration effort, and some of the rationale of the voyages of discovery, was underpinned by the search for and transfer of species to be enjoyed in parks, gardens, private greenhouses and zoos by wealthy members of societies less endowed with biodiversity.

A modern example is provided by the statement by the Zoological Society of London that aquarium fish are the most popular pets in the world, representing an industry which in 1999 was worth $3 billion in annual retail sales. About 10% of the species are caught from the wild, causing concerns over the viability of stocks (ZSL 2006). Over 20 million freshwater fish are exported each year from the Brazilian Amazon and this generated $3 million in 2006 (Prang 2007). Birds are another focus of the ornamental value of biodiversity. In 1992, the trade in CITES (Convention on International Trade in Endangered Species)-listed wild birds was banned in the U.S., “leaving the EU responsible for 87% of the trade” (RSPB 2007). Because of fears for animal and human health, the EU issued a trade ban from July 2007, saving probably up to 2 million wild birds annually from the pet trade. Following the ban, the Royal Society for the Protection of Birds estimated that trade in CITES-listed threatened birds may drop from ca. 800,000 per year to a few hundred, because “import of small numbers of wild birds into the EU by zoos and some pet owners will still be allowed” (RSPB 2007).

Sensitivity of service to variation in biodiversity

The service is related completely to individual species and is highly sensitive to maintenance of viable populations.

Where are services generated?

The same applies as for service 3.5.

Uncertainties in delivery of service

The same applies as for service 3.5.

REGULATING SERVICES

2.7 Air quality regulation and other urban environmental quality regulation

Context and importance of service

Ecosystems contribute to several environmental regulation services of importance for human well-being, particularly in urban areas where vegetation may significantly reduce air pollution and noise, mitigate the ‘urban heat island’ effect (e.g. Santomouris 2001), and reduce impacts related to climate change (Bolund and Hunhammar 1999). This potential is often substantial (e.g. Pickett et al. 2008). For example, in the Chicago region, trees were found to remove some 5,500 tonnes of air pollutants per year, providing a substantial improvement in air quality (McPherson et al. 1997). Vegetation reduces noise levels, and dense shrubs (at least 5 m wide) can reduce noise levels by 2 dB(A), while a 50-m wide plantation can lower noise levels by 3–6 dB(A) (Bolund and Hunhammar 1999). Evergreen trees are preferred because they contribute to noise reduction year round (Ozer et al. 2008). Urban parks and vegetation reduce the urban heat island effect and have an important potential for lowering urban temperatures when the building envelope is covered with vegetation, such as green roofs and green walls, with the largest effect in a hot and dry climate (Alexandri and Jones 2007). In relation to overall climate change mitigation, urban ecosystems may assimilate non-negligable quantities of carbon, e.g. in Stockholm County, ecosystems assimilate about 17% of total anthropogenic CO_2 (Jansson and Nohrstedt 2001), and residential trees in the continental United States may sequester 20 to 40 teragrams C per year (Jenkins and Riemann 2003).

Green areas, vegetation and trees, also have direct health benefits, e.g. in a study from New York, presence of street trees was associated with a significantly lower prevalence of early childhood asthma (Lovasi et al. 2008). Green area accessibility has also been linked to reduced mortality (Mitchell and Popham 2008) and improved perception of general health (e.g. Maas et al 2006). In a review by Bird (2007), links were noted between access to green spaces and a large number of health indicators, e.g. coping with anxiety and stress, treatment for children with poor self-discipline, hyperactivity and Attention Deficit Hyperactivity Disorder (ADHD), benefiting elderly care and treatment for dementia, concentration ability in children and office workers, healthy cognitive development of children, strategies to reduce crime and aggression, strengthened communities, and increased sense of well-being and mental health. The distribution and accessibility of green space to different socio-economic groups, however, often reveals large inequities in cities (e.g. Pickett et al. 2008), contributing to inequity in health among socio-economic groups, although confounding effects are not always possible to separate (Bird 2007).

Sensitivity of service to variation in biodiversity

To what extent biodiversity and variation in species composition plays a role in the generation of environmental quality services is still poorly investigated (Elmqvist et al. 2008). For air quality, filtering capacity increases with leaf area, and is thus higher for trees than for bushes or grassland (Givoni 1991). Coniferous trees have a larger filtering capacity than trees with deciduous leaves (Givoni 1991). Figure 3 illustrates a hypothesized distribution of species richness in relation to degree of anthropogenic impact. The urban core has fewer species and often very different species involved in generation of ecosystem services than in more rural areas. Interestingly, the number of plant species in urban areas often correlates with human population size, and plant diversity may correlate positively with measures of economic wealth as shown for example, in Phoenix, USA (Kinzig et al. 2005).

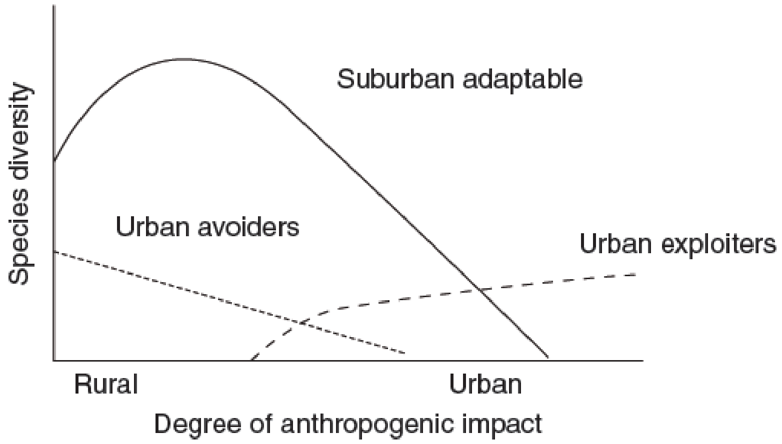

Figure 3: **Organisms may respond differently to increasing human impact.** Urban avoiders are large-bodied species or species linked to late successional stages. These species might be very sensitive and show a decline already at moderate human impacts. Suburban adaptable species may, to various degrees, utilize human modifications of the landscape; a large number of plant and animal species are likely to belong to this group. Urban exploiters directly benefit from human presence for food, reproduction or protection, and may often be cosmopolitan, generalist species. Source: Elmqvist et al. (2008).

Where are services generated?

Urban ecosystem services may be generated in a diverse set of habitats, including parks, cemeteries, vacant lots, streams, lakes, gardens and yards, campus areas, golf courses, bridges, airports and landfills. To what extent exotic species contribute to reduced or enhanced flow of ecosystem services is virtually unknown for any urban area, but since introduced species make up a large proportion of the urban biota, it is important to know not only to what extent introduced species are detrimental, but also to what degree some of the introduced species may enhance local diversity and maintain important functional roles.

Uncertainties in delivery of service

Considerable knowledge gaps remain about uncertainties and dynamics of urban ecosystem services. The Millennium Ecosystem Assessment (MA 2005), which covered almost every other ecosystem in the world, largely neglected urban systems, while on the other hand, the World Development Report (World Bank 2009), the world's largest assessment of urbanization, has left out ecosystems. Considerable uncertainties relate to the extent that isolation and fragmentation in the urban landscape influence the sustained generation of environmental quality services, and to the effects of climate change and rapid turnover of species on ecological functions of importance for these services.

2.8 Climate regulation

Context and importance of service

Climate is regulated on Earth by a natural ‘greenhouse effect’ that keeps the surface of the planet at a temperature conducive to the development and maintenance of life. Numerous factors interact in the regulation of climate, including the reflection of solar radiation by clouds, dust and aerosols in the atmosphere. In recent years the climate has been changing and the Earth is becoming warmer. Current change is driven largely by increases in the concentrations of trace gases in the atmosphere, principally as a result of changes in land use and rapidly rising rates of combustion of fossil fuels. The major greenhouse gas (CO_2) is absorbed directly by water and indirectly (through photosynthesis) by vegetation, leading to storage in biomass and in soils as organic matter; the ability of soils to store carbon is a major regulator of climate. Other greenhouse gases, notably methane (CH_4) and nitrous oxide (N_2O) are regulated by soil microbes. Organisms in the marine environment play a significant role in climate control through their regulation of carbon fluxes, by acting as a reserve or sink for CO_2 in living tissue and by facilitating burial of carbon in sea bed sediments (Beaumont et al. 2007). The capacity of the marine environment to act as gas and climate regulator is very dependent on its biodiversity.

An additional issue is the impact of vegetation on albedo: the reflection of incident radiation by land surfaces. Dark surfaces, especially those covered by evergreen forest, absorb more radiation than light surfaces, especially snow. Consequently, afforestation of boreal zones may lead to greater levels of warming, potentially outweighing the reduction expected from enhanced carbon sequestration by new trees.

Aerosols have a profound effect on climate, by intercepting and scattering radiation, and by acting as cloud condensation nuclei, thus reducing the amount of solar radiation reaching the Earth’s surface. The production of aerosols by marine systems is well understood and has been taken into account in climate models. However, evidence is increasing that forests emit substantial amounts of biogenic volatile organic compounds, which can form aerosol particles. Forests are therefore simultaneously sinks for CO_2, sources of aerosol particles and determinants of albedo (Kulmala et al. 2004).

Sensitivity of service to variation in biodiversity

The interplay between biodiversity and climate regulation is poorly understood. The largest single store of carbon in terrestrial ecosystems globally is in the peat soils of the boreal and cool temperate zones of the northern hemisphere. The response of peatlands to climate change is crucial to predicting potential feedbacks on the global carbon cycle (Belyea and Malmer 2004). The climate-regulating function of peatlands also depends on land use because intensification of land use is likely to have profound impacts on soil carbon storage and on the emission of trace gases. Considering the area of drained and mined peatlands, restoration on abandoned mined peatlands may represent an important biotic offset through enhanced carbon sequestration (Waddington et al. 2001). However, mires are also major sources of potent greenhouse gases and the biodiversity of soil microbes is likely to play an important role in trace gas (methane) production (Roulet 2000). Current evidence for the role played by soil biodiversity in key processes leading either to carbon sequestration or to the release of trace gases is weak.

The exchange of CO_2 between atmosphere and ocean is larger than that between atmosphere and terrestrial ecosystems. Some of this occurs by physical processes, involving the equilibrium between CO_2 and carbonate, but a significant proportion is accounted for by biological processes. Although oceanic macrophytes account for less than 1% of global biomass carbon, the net primary productivity of the oceans is roughly equal to that of all terrestrial systems.

Where are services generated?

All soils store carbon, but to widely varying extents. The largest stores are in peatlands, but soils rich in organic matter occur in many ecosystems, especially where low temperature, low pH or waterlogging inhibit decomposition. Forests are the only major ecosystems where the amount of carbon stored in biomass of the plants exceeds that in the soil; deforestation therefore also affects climate regulation. Agricultural ecosystems currently have low soil carbon stores owing to intensive production methods, and there is scope for enhancing those stores. Marine ecosystems also play a major role in climate regulation through carbon sequestration and aerosol emission.

Uncertainties in delivery of service

Many uncertainties are associated with this service, particularly related to large time lags in the feedbacks between changes in ecosystem processes and the atmosphere. The global carbon cycle is strongly buffered, in that much of the CO_2 discharged by human activities into the atmosphere is absorbed by oceans and terrestrial ecosystems (Janzen 2004). However, the rate of emissions increasingly exceeds absorption capacity, and this capacity is at the same time reduced still further by anthropogenic damage to ecosystems. The complex interactions and long time lags make it very difficult to forecast eventual outcomes or if and when important thresholds will be passed.

2.9 Moderation of extreme events

Context and importance of service

Extreme events or 'natural hazards' are defined here as infrequent phenomena that may pose a high level of threat to life, health or property. Living organisms can form and create natural barriers or buffers, such as forests (including mangroves), coral reefs, seagrasses, kelp forests, wetlands, and dunes, and these can mitigate the effects of some natural hazards such as coastal storms (Wells et al.

2006), hurricanes (Costanza et al. 2006), catchment-borne floods (Bradshaw et al. 2007), tsunamis (Kathiresan and Rajendran 2005), avalanches (Gruber and Bartelt 2007), wild fires (Guenni et al. 2005) and landslides (Sidle et al. 2006). The available evidence for some of these effects is still scarce, and in some cases controversial. Many hazards arise from human interaction with the natural environment and are sensitive to environmental change. Examples include:

- flash floods due to extreme rainfall events on heavily managed ecosystems that cannot retain rainwater;
- landslides and avalanches;
- storm surges due to sea-level rise and the increasing use of hard coastal margins;
- air pollution due to intensive use of fossil fuels combined with extreme summer temperatures;
- fires caused by prolonged drought, with or without human intervention.

Sensitivity of service to variation in biodiversity

The role of biodiversity in delivering protection from natural hazards is generally small, but it has a role in facilitating recovery from such perturbations. In some particular cases, the ecological integrity of the affected ecosystem is of central importance, and it is likely that loss of biodiversity reduces resilience. Biodiversity plays a key role in the preservation of wetlands and coastal systems such as mangroves that deliver significant ecosystem services. For example, sea-level rise places intense selective pressures on halophytic vegetation whose fate is critical to the survival of salt marshes and other transition ecosystems (Marani et al. 2004). In mountain forests, increasing tree diversity is believed to enhance the protection value against, for example, rock fall (see, for example, Dorren et al. 2004).

Where are services generated?

Flooding is a problem in a wide range of ecosystems, including steep deforested catchments, flat alluvial plains and urban ecosystems with constrained water flows. Flooding can also occur because of exceptionally high tides and storm surges, a problem that will be exacerbated by rising sea levels; coastal wetlands are known to play a major part in defence against tidal flooding. Wind breaks from managed woods or from the use of natural forest features are a traditional means of protecting crops and habitations against both violent storms and general damage from exposure to high winds. In all these cases the role of vegetation is structural, and the part played by species composition will normally be indirect, in controlling the stability and resilience of the system.

Living marine flora and fauna can play a valuable role in the defence of coastal regions, and dampen and prevent the impact of tidal surges, storms and floods. This disturbance alleviation service is provided mainly by a diverse range of species which bind and stabilize sediments and create natural sea defences, for example salt marshes, mangrove forests, kelp forests and sea grass beds (Rönnbäck et al. 2007). Natural hazard regulation services show a declining trend due to loss of natural buffers such as wetlands and mangroves. For example, 20% or 3.6 million ha have been lost from the 18.8 million ha of mangrove forests covering the planet in 1980 (FAO 2007); 20% of coral reefs have been seriously degraded in only the past two decades (Wilkinson 2006); coastal wetland loss is extremely rapid, reaching 20% annually in some areas. On the other hand, the value of the regulation that is provided by these ecosystems is likely to be escalating, given an increase in human vulnerability to natural hazards.

Uncertainties in delivery of service

The effect of ecosystems on natural hazard mitigation is still poorly understood and it is uncertain to what extent abrupt changes in this service may be associated with abrupt changes in ecosystem extension and condition, for example the degradation of coral reefs or forests due to climate change. If the relationship between hazard regulation and ecosystem extension is an inverse asymptotic relationship, then regions where past ecosystem loss has been extensive may suffer a disproportionate future decline in the provision of this service.

2.10 Erosion prevention

Context and importance of service

Vegetation cover is the key factor preventing soil erosion, as classic historical examples such as the American dust bowl of the 1930s demonstrate, where lack of vegetation cover combined with drought resulted in unprecedented wind erosion, destroying farmland and livelihoods (Cooke et al. 1936). Landslide frequency seems to be increasing, and it has been suggested that land-use change, particularly deforestation, is one of the causes. In steep terrain, forests protect against landslides by modifying the soil moisture regime (Sidle et al. 2006).

Sensitivity of service to variation in biodiversity

This ecosystem service is generally not species specific or dependent on biodiversity in general, though in areas of high rainfall or extreme runoff events, forests may be more effective than grassland or herb-dominated communities.

Uncertainties in delivery of service

The same apply as for service 3.9.

2.11 Maintenance of soil quality

Context and importance of service

The process of soil formation is governed by the nature of the parent materials, biological processes, topography and climate. It involves the conversion of a mineral matrix, which has limited capacity to support nutrient cycles, into a complex medium with both inorganic and organic components, and solid, liquid and gas phases in which chemical and biological transformations take place. The progressive accumulation of organic materials is characteristic of the development of most soils, and depends on the activity of a wide range of microbes, plants and associated organisms (Brussaard et al. 1997; Lavelle and Spain 2001). Soil quality is underpinned by nutrient cycling, which occurs in all ecosystems and is strongly linked to productivity. A key element is nitrogen, which occurs in enormous quantities in the atmosphere and is converted to a biologically useable form (ammonium) by bacteria. Nitrogen fertilizer is increasingly expensive (about 90% of the cost is energy, typically from gas) and supplies are therefore not sustainable. Nitrogen fixation by organisms accounts for around half of all nitrogen fixation worldwide, and sustainable agricultural systems will have to rely on this process increasingly in future.

Sensitivity of service to variation in biodiversity

A large part of the organic material in many soils derives from the faeces of soil animals, and both the gross and fine structure of the soil is determined by biological activity. At a fine scale, structure may depend on fungal mycelia and the activities of mycorrhizal fungi, symbiotic with plant roots, which are the most abundant fungi in most soils (Miller and Jastrow 2000).

Many different species are implicated in nutrient cycling, which includes numerous transformations of elements often involving complex biochemistry. Nitrogen cycling may depend on diversity of plant communities and particularly on the presence of particular functional groups. Soil biodiversity has a particularly strong impact on nutrient cycling. Barrios (2007), in reviewing the importance of the soil biota for ecosystem services and land productivity, emphasized positive impacts of microbial symbionts on crop yields, as a result of increases in plant available nutrients, especially nitrogen, through biological nitrogen fixation by soil bacteria such as *Rhizobium*, and phosphorus through arbuscular mycorrhizal fungi.

Only 5–10% of added phosphate is recovered in crops, owing to its strong fixation by soils. In natural ecosystems, symbiotic mycorrhizal fungi are the main route of phosphorus transfer from soil to plant, and the diversity of mycorrhizal fungi can regulate both plant diversity and nutrient efficiency, and possibly water use efficiency (Brussaard et al. 2007). Sustainable agricultural systems will need to make greater use of mycorrhizal fungi, whose diversity is currently very low in arable systems (Helgason et al. 1998). It seems that functional diversity (and its influence on trophic interactions) rather than species diversity, is key to the decomposition, nutrient cycling, and stability of soil processes.

Where are services generated?

Soil formation is a continuous process in all terrestrial ecosystems, but is particularly important and active in the early stages after land surfaces are exposed (e.g. after glaciation).

Uncertainties in delivery of service

Agricultural expansion into new areas often occupies terrains that are not particularly suitable for agriculture, and soil fertility may decline very quickly as crops effectively mine the soil nutrients (Carr et al. 2006).

2.12 Pollination services

Context and importance of service

In some estimates, over 75% of the world's crop plants, as well as many plants that are source species for pharmaceuticals, rely on pollination by animal vectors (Nabhan and Buchman 1997). While the extent to which staple food crops depend on pollinator services has been questioned (e.g. Ghazoul 2005), Klein et al. (2007) found that, for 87 out of 115 leading global crops (representing up to 35% of the global food supply), fruit or seed numbers or quality were increased through animal pollination. In many agricultural systems, pollination is actively managed through the establishment of populations of domesticated pollinators, particularly the honeybee (*Apis mellifera*). However, the importance of wild pollinators for agricultural production is being increasingly recognized (e.g. Westerkamp and Gottsberger 2000; Kremen et al. 2007) and wild pollinators may also interact synergistically with managed bees to increase crop yields (Greenleaf and Kremen 2006).

Sensitivity of service to variation in biodiversity

Bees are the dominant taxon providing crop pollination services, but birds, bats, moths, flies and other insects can also be important. Studies in agricultural landscapes commonly show that increasing distances from forest fragments result in a decrease in both abundance and species-richness of flower-visiting bees (e.g. Steffan-Dewenter and Tscharntke 1999) and a recent quantitative review of 23 studies (Ricketts et al. 2008) found an exponential decay in pollinator richness and native pollinator visitation rate with distance to natural or semi-natural habitats. Hajjar et al. (2008) argue that the loss of biodiversity in agro-ecosystems through agricultural intensification and habitat loss negatively affects the maintenance of pollination systems, and causes the loss of pollinators worldwide (Kearns et al. 1998; Kremen and Ricketts 2000; Kremen et al. 2004; Richards 2001). Richards (2001) reviewed well-documented cases where low fruit or seed set by crop species, and the resulting reduction in crop yields, has been attributed to the impoverishment of pollinator diversity. Increasing evidence indicates that conserving wild pollinators in habitats adjacent to agriculture improves both the level and the stability of pollination services, leading to increased yields and income (Klein et al. 2003). Furthermore, a diverse assemblage of native pollinators provides insurance against year-to-year population variability or loss of specific pollinator species (Ricketts 2004; Tscharntke et al. 2005; Hoehn et al. 2008), and might better serve flowers because of pollinator-specific spatial preferences to a flowering plant or crop field (Klein et al. 2007). Given current declines in populations of managed honeybees (Johnson 2007), and abandonment of beekeeping in regions affected by 'Africanization' of honeybees (Brosi et al. 2007), the importance of wild pollination is likely to increase.

Where are services generated?

This service is important in all ecosystems, though possibly least important in species-poor boreal and arctic systems, where most species are wind-pollinated. Pollinator species often depend on natural or semi-natural habitats for the provisioning of nesting (e.g. tree cavities, suitable soil substrates) and floral resources that cannot be found within crop fields (Kremen et al. 2004). Consequently, the available area of natural habitat has a significant influence on pollinator species richness (Steffan-Dewenter 2003), abundance (Heard et al. 2007; Morandin et al. 2007), and pollinator community composition (Steffan-Dewenter et al. 2002; Brosi et al. 2007). Loss of suitable habitat is a key driver of declines in pollination services by wild pollinators, and habitat degradation through agricultural intensification leads to scarcity in critical floral and nesting resources for many species. In southern China, large areas of fruit orchards now need to be pollinated by hand since wild pollinators have disappeared, with approximately 10 people needed to do the work previously done by one bee colony.

Uncertainties in delivery of service

It is possible that a threshold in pollinator species functional diversity exists, below which pollination services become too scarce or too unstable to persist (Klein et al. 2007). Such a tipping point might occur when, at a landscape context, sufficient habitat is destroyed that the next marginal change causes a population crash in multiple pollinators. Alternatively, a threshold in habitat loss may lead to the collapse of particularly important pollinators, leading to a broader collapse in pollination services. Supporting this prediction, Larsen et al. (2005) found that large-bodied pollinators tended to be both most extinction-prone and most functionally efficient, contributing to rapid functional loss with habitat loss. Increased uncertainty is also represented by climate change, as phenological shifts may result in asynchrony and disruption of plant-pollinator interactions (Memmott et al. 2007).

2.13 Biological control

Context and importance of service

Pests and diseases are regulated in ecosystems through the actions of predators and parasites as well as by the defence mechanisms of their prey. Natural control of plant pests is provided by generalist and specialist predators and parasitoids, including birds, bats, spiders, beetles, mantises, flies, and wasps, as well as entomopathogenic fungi (Way and Heong 1994; Naylor and Ehrlich 1997; Zhang et al. 2007). In the short-term, this process suppresses pest damage and improves yields, while in the long-term it maintains an ecological equilibrium that prevents herbivorous insects from reaching pest status (Zhang et al. 2007, Heong et al. 2007). Agricultural pests cause significant economic losses worldwide. Globally, more than 40% of food production is being lost to insect pests, plant pathogens, and weeds, despite the application of more than 3 billion kilograms of pesticides to crops, plus other means of control (Pimentel 2008). The services of regulation are expected to be more in demand in future as climate change brings new pests and increases susceptibility of species to parasites and predators.

Sensitivity of service to variation in biodiversity

The diversity of natural enemies seems to improve biological control through a variety of mechanisms, including: i) species complementarity, when more than one type of predator or parasitoid adds to the control of a pest species; ii) the sampling effect, whereby a particularly effective natural enemy is more likely by chance alone to occur when more species are present; iii) redundancy, where more species will buffer against disturbance or ecosystem change; and iv) idiosyncrasy, when the whole is greater than the sum of the parts owing to interactions among species (Tscharntke et al. 2005; Kremen and Chaplin-Kramer 2007).

A diverse soil community will not only help prevent losses due to soil-borne pests and diseases but also promote other key biological functions of the soil (Wall and Virginia 2000). Soil-borne pests and diseases such as root-rot fungi cause enormous annual crop losses globally (Haas and Défago 2005), but bacteria in the rhizosphere (the soil surrounding roots) can protect plant roots from diseases caused by root-rot fungi (Haas and Keel 2003); similarly, symbiotic mycorrhizal fungi can protect roots from pathogenic fungi (Newsham et al. 1995). Plant-parasitic nematodes represent a major problem in agricultural soils because they reduce the yield and quality of many crops and thus cause great economic losses. However, nematodes have a variety of microbial antagonists that include nematophagous and endophytic fungi, actinomycetes and bacteria (Dong and Zhang 2006).

Where are services generated?

The natural control of diseases and invasions occurs in all ecosystems. Those heavily influenced by human activity incur the greatest risk of both disease outbreaks and invasion. Data on populations of biological control agents are scarce but the trends are presumed to be negative owing to habitat transformation associated with agricultural intensification (agricultural expansion, enlargement of field size, and removal of non-crop habitat, which results in a loss of the natural landscape features required for maintaining their populations) and increasing pesticide use. On the other hand, the increase in organic farming worldwide may help to reverse this trend (Bengtsson et al. 2005; Willer et al. 2008).

Uncertainties in delivery of service

The relationship between densities of natural enemies and the biological control services they provide is unlikely to be linear (Losey and Vaughan 2006) and biological control functions may decline disproportionately when a tipping point in natural enemy diversity is passed. Empirical evidence in support of this logic is scarce, but the importance of natural enemy assemblage composition in some instances of biological control (Shennan 2008) indicates that changes in composition can lead to disproportionately large, irreversible and often negative shifts in ecosystem services (Díaz et al. 2006).

HABITAT SERVICES

The habitat 'service' was identified in chapter 1 as a distinct category to highlight a) the interconnectedness of ecosystems in the sense that different ecosystems provide unique and crucial habitats for particular life-cycle stages of migratory species; and b) that certain ecosystems have been identified that are of unique importance in that they have been found to exhibit particularly high levels of genetic diversity of major importance to maintain life (genetic diversity) on Earth, and natural adaptation processes. Both of these features underpin all, or most, provisioning, regulating and cultural services (which is why they are often called "supporting services") but they are distinct services in their own right, as explained below, and depend on particular spatial conditions within ecosystems.

2.14 Maintenance of life cycles of migratory species

Context and importance of service

The life cycle of any species is supported in its entirety or in part by the products and behaviour of many others as well as by the nature of the abiotic environment. Products of ecosystems (e.g. nutrients, seeds) may be exported by wind, water or animals (including humans) to support life cycles of species elsewhere. These interactions between ecosystems should be taken into account when assessing the ecological or economic importance of a given area.

Migratory species, e.g. some species of fish, birds, mammals and insects, might use an ecosystem for just part of their life cycle. For example, salmonid fish use clean, aerated, shallow areas of flowing water for courtship and egg-laying, and are dependent on these ecosystems to supply clean water and food for juvenile fish (e.g. Kunz 2004). The adult salmon supports other predatory species, including humans and, on death, contribute significant quantities of organic matter to the river ecosystem. Migrating birds such as geese rely on ecosystems for availability of grazing on their migration ‘flyways’, and can shape vegetation community composition, affecting competitive interactions and potentially increasing spatial heterogeneity by means of selective feeding (van den Wyngaert and Bobbink 2009). Some of the migratory species have commercial value, in which case the ecosystem providing the reproduction habitat provides an important so-called ‘nursery-service’ which is (economically) valued in its own right (e.g. mangroves, providing reproduction habitat to many species of fish and crustaceans, which are harvested as adults far away from their spawning areas). When economically valuing mangrove-ecosystems, this nursery service should be taken into account.

Sensitivity of service to variation in biodiversity

A high level of interdependency exists among species, and any species loss has consequences, some of which remain unnoticed by human observers, while some will be significant for functioning and provision of ecosystem services for migrating species. Loss of biodiversity will inevitably result in loss of functioning, and consequently, loss or degradation of these ecosystem services (Naeem et al. 1995).

2.15 Maintenance of genetic diversity

Context and importance of service

Genetic diversity, both within and between species populations, is characteristic of all ecosystems and, through natural selection, results in evolution and adaptive radiation of species to particular habitats. The degree of genetic diversity present within a species (which can be expressed in a variety of ways (Nei 1987) will depend on both individual species breeding behaviour, the extent to which gene flow occurs between populations, and the biotic and abiotic forces driving selection, in addition to mutation events. Micro-evolution (for example of metals tolerance in grasses) can occur over remarkably short distances of a few metres and within a few generations (Antonovics and Bradshaw 1970). On the other hand, certain species are endemic to particular ecosystems and regions of the world (Morrone 1994), reflecting macro-evolution. Ecosystems that exhibit particularly high levels of biodiversity (biodiversity hotspots) with exceptional concentrations of endemic species, are undergoing dramatic habitat loss. “As many as 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to 25 hotspots comprising only 1.4% of the land surface of the Earth” (Myers et al. 2000). In addition to the overall importance of these ‘hotspots’ in maintaining genetic diversity, this service is of particular and immediate importance in preserving the gene-pool of most of our commercial crops and livestock species. Gene banks, which represent a mechanism of conservation, do not include the processes that generate new genetic diversity and adaptations to environmental change through natural selection.

Sensitivity of service to variation in biodiversity

Preservation of this (remaining) genetic diversity in these hotspots is of strategic value to the provision of ecosystem services, since the hotspots themselves contain not only species richness and genetic diversity within species, but represent the natural laboratory in which evolution can occur. The relationships between biodiversity hotspots, endemism and extinction threat, however, remain a continuing debate in conservation biology (see Prendergast et al. 1993; Orme et al. 2005). The debate about *in-situ* versus *ex-situ* conservation of genetic resources has equivalent prominence in the preservation of sources of both crop and animal germplasm for breeding purposes (see earlier sections). Vavilov (1992) originally promoted the concept of centres of origin of cultivated plants, which recognized that particular temperate and tropical ecosystems were the source of genetic diversity from which crop domestication occurred. The loss of the genetic diversity within habitats within these ecosystems can only be partially balanced by *ex-situ* conservation in gene banks (Nevo 1998), which by their very nature prohibit the continued evolution among wild, feral and domesticated species in the field.

CULTURAL AND AMENITY SERVICES

2.16 3.18-22 Cultural services: aesthetic information, opportunities for recreation and tourism, inspiration for culture, art and design, spiritual experience, information for cognitive development

Context and importance of service

Cultural and amenity services refer to the aesthetic, spiritual, psychological, and other benefits that humans obtain from contact with ecosystems. Such contact need not be direct, as illustrated by the popularity of the virtual experience of distant ecosystems through books, art, cinema, and television. Nor need such contact be of a wild or exotic nature, as shown by the ubiquity of e.g. urban gardens (Butler and Oluoch-Kosura 2006). The classification here largely follows the one in the Millennium Ecosystem Assessment (MA 2005) although considerable debate remains about how the wide range of benefits derived from these services should be classified. It has been proposed that many of these services should more appropriately be placed under provisional services, being of similar importance as food, water, etc. for human well-being (K.Tidball pers. comm.). For convenience, these services are here considered as falling into two main groups: i) spiritual, religious, aesthetic, inspirational and sense of place; and ii) recreation, ecotourism, cultural heritage and educational services.

An economic value is hard to apply to those in the first group, while the second group is more amenable to traditional valuation approaches. Although all societies value the spiritual and aesthetic ‘services’ that ecosystems provide, these may have different significance in affluent, stable and democratic societies. Nevertheless, biodiversity plays an important role in fostering a sense of place in most societies and has considerable intrinsic cultural value. Although recent high-profile research suggests that nature recreation is declining *per capita* in US and Japan (Pergams and Zaradic 2008), this trend is not mirrored in much of the rest of the world, where growth in visitation to protected areas is growing at least as fast as international tourism as a whole. Fewer data are available for other types of outdoor activity, though it has been estimated that each year over half the population of the

UK makes over 2.5 billion visits to urban green spaces (Woolley and Rose 2004), and 87 million Americans participated in wildlife-related recreation in 2006, an increase of 13% over the decade (USFWS 2007). Wildlife-based marine tourism, as whale and dolphin watching, is also a profitable activity that is highly dependent on a functioning ecosystem (Wilson and Tisdell 2003).

Many cultural services are associated with urban areas, and strong evidence demonstrates that biodiversity in urban areas plays a positive role in enhancing human well-being (see section 3. 7). For example, Fuller et al. (2007) have shown that the psychological benefits of green space increase with biodiversity, whereas a green view from a window increases job satisfaction and reduces job stress (Lee et al. 2009). This may have a strongly positive effect on economic productivity and hence regional prosperity. Several studies have shown an increased value of properties (as measured by hedonic pricing) with proximity to green areas (Tyrväinen 1997; Cho et al. 2008). Nihan (2009) and Shu Yang et al (2004) have also pointed to the role of ecosystems in providing design features that can be utilized in the context of eco-design in architecture and urban and community planning

Sensitivity of service to variation in biodiversity

The role of biodiversity varies greatly among these services but is likely to be particularly large for ecotourism and educational uses of ecosystems. However, in many cases biodiversity may not be the typical identifier of the value being placed on the ecosystem, but nevertheless underlies the character recognized by the visitor.

Where are services generated?

Cultural and recreational services based on biodiversity are most strongly associated with less intensively managed areas, where semi-natural biotopes dominate, although in urban areas this may vary. Low-input agricultural systems are also likely to support cultural services, with many local traditions based on the management of land and its associated biological resources. Newly created or restored green spaces are becoming an increasingly important component of the urban environment providing this service.

Uncertainties in delivery of service

Uncertainty may be assessed for tourism, where abrupt changes in the provision of tourism benefits can occur for a range of reasons. Some of these may be ecological, as systems reach tipping points. Key wildlife populations may collapse through disease or other factors, fire may destroy picturesque landscapes, corals may bleach with sudden temperature shifts, ecosystems may suddenly change from one (attractive) to another (less desirable) stable state. Some of these will be reversible, others will be permanent. Abrupt shifts may also (and perhaps more often) be socially instigated. War, terrorism, socio-political disruption, natural disasters and health crises all tend to rapidly and negatively affect international tourism demand. Likewise, events such as the foot and mouth disease outbreak in the UK in 2001 had dramatic impacts as people were prevented from visiting the countryside for recreation. The current volability in oil prices (and thus aviation fuel costs) and potential carbon taxes may have similar impacts on international tourism if such changes are too sudden and result in an increase in recreational visits in areas closer to urban centres (for urban recreational services see section 3.7).

3 Managing multiple ecosystem services

3.1 Bundles of ecosystem services

Functioning ecosystems produce multiple services and these interact in complex ways, different services being interlinked or 'bundled' together, and therefore affected negatively or positively as one service (e.g. food) increases (e.g. Bennet et al. 2009). Most studies so far have focused on one or a few services such as pollination, or food versus water quality and quantity. Characterizing multiple ecosystem services as well as biodiversity across the same region has only recently emerged as a field of study (e.g. Schroter et al. 2005), and the little quantitative evidence available to date has led to mixed conclusions (e.g. Bohensky et al. 2006). Scientists have tended to use land use ⁄ land cover as a proxy for the provision of services (Nelson et al. 2009) even though the relationships between land use, land cover and service provision are largely untested for most services in most regions of the world (Naidoo et al. 2008). Finding ways of assessing how multiple ecosystem services are interconnected and coupled to each other in 'bundles' is one of the major research gaps on ecosystem services identified by the MA (Carpenter et al. 2009). Furthermore, finding ways to target and implement payments for biodiversity conservation with 'bundles' of ecosystem services, e.g. carbon and water services, also is a major priority (Wendland et al. 2009) that will be discussed in section 5.2 below.

3.2 Trade-offs

Some ecosystem services co-vary positively (more of one means more of another) e.g. maintaining soil quality may promote nutrient cycling and primary production, enhance carbon storage and hence climate regulation, help regulate water flows and water quality and improve most provisioning services, notably food, fibre and other chemicals. Other services co-vary negatively (more of one means less of another) such as when increasing provisioning services may reduce many regulating services e.g. provision of agricultural crops may reduce carbon storage in soil, water regulation, cultural services, etc.

Provisioning and regulating ecosystem services can have a range of possible trade-offs. Depending on the type of trade-off (A, B or C in Figure 4), the supply of regulating services can be low, intermediate or high for similar levels of provisioning services. This will have very different implications for the design and management of landscapes. For example, it has been suggested that major ecosystem degradation tends to occur as simultaneous failures in multiple ecosystem services (Carpenter et al. 2006). The dry lands of sub-Saharan Africa provide one of the clearest examples of these multiple failures, causing a combination of failing crops and grazing, declining quality and quantity of fresh water, and loss of tree cover. However, a synthesis of over 250 cases of investments in organic agriculture in developing countries around the world (both dry lands and non-dry lands) showed that the implementation of various novel agricultural techniques and practices could result in a reduction of ecosystem service trade-offs, and increased levels of regulating services, even as crop yields were maintained (Pretty et al. 2005) (corresponding to B or even C in Figure 4).

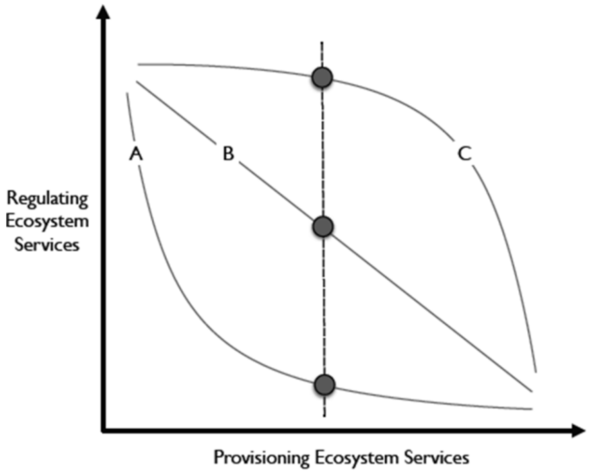

Figure 4: **Potential trade-offs between provisioning services and regulating ecosystem services.** A) Shifting an ecosystem to an increase in provisioning services produces a rapid loss of regulating services, B) regulating services linearly decrease with increases in provisioning services, and C) provisioning services can increase to quite high levels before regulating services decline. Source: Elmqvist et al. (2010).

The generation of some services may also result in other less desired effects, sometimes referred to as disservices, for example, the foods, fuels and fibres grown to satisfy basic human needs for nutrition and shelter may be highly valued, but the pests and pathogens deriving from the same ecosystems have a negative value. Both are products of the way in which the underlying ecosystems are managed, with the result that trade-off decisions have to be made (see Box 3). Knowledge of these relationships is essential to ensure that policy decisions translate into operationally effective and predictable outcomes.

Box 3: Trade-offs among ecosystem services

Several different types of trade-off can be identified, and are not mutually exclusive:

1. Temporal trade-offs: benefits now – costs later

Temporal trade-offs represent the central tenet of sustainable development "... that meets the needs of the present generation without compromising the needs of future generations….." (WCED 1987).

2. Spatial trade-offs: benefits here – costs there

Spatial trade-offs are behind much deliberation between communities and countries (especially water) and also occur between ecosystems and production landscapes. An example of a landscape level trade off is between improved water productivity (evapotranspiration used per tonne of grain) up stream and consequential down stream problems with deteriorating water quality associated with the use of agricultural inputs.

3. Beneficiary trade-offs: some win – others lose

These trade-offs are real but it is possible to move towards "winning more and losing less" by improving access to information on ecosystem services and their valuation, framing and using appropriate incentives and/or markets, and clarifying and strengthening rights of local people over their resources.

4. Service trade-offs: manage for one service – lose another

Manipulation of an ecosystem to maximize one particular service risks reducing others, e.g. maintaining monocultures of a single species (for production of food, fibre and energy), will reduce the delivery of services dependent on the maintenance of biodiversity, including pollination and disease regulation (see Figure 4 and 5 below).

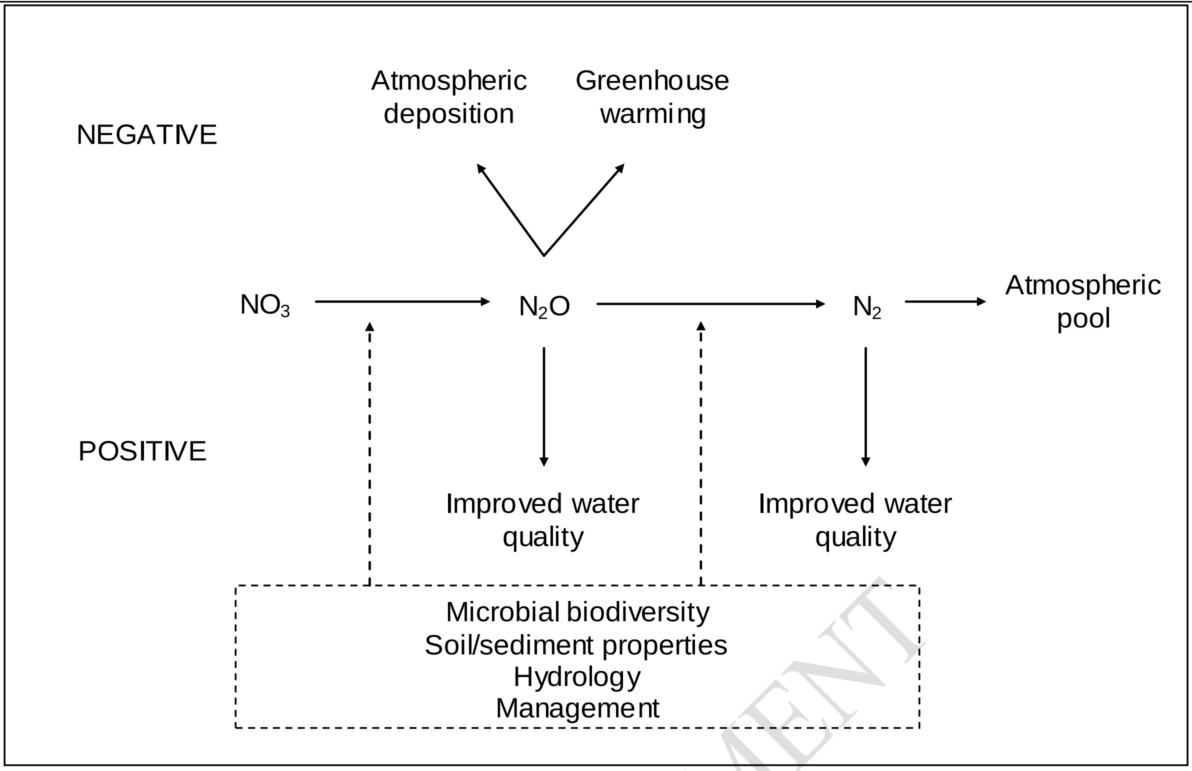

Figure 5: **Wetland trade-off dilemma – water quality versus climate control**

Many wetland soils support denitrifier microorganisms which convert nitrate to di-nitrogen gas in a two stage process with nitrous oxide as the intermediary product. This may result in a major service of water purification, protecting the biodiversity of adjacent waters (Barker et al. 2008). However the balance of N_2O or N_2 production, which is controlled by soil ecosystem properties, may generate a major disservice though release of a potent greenhouse gas (N_2O) as well as a potential source of atmospheric N deposition if full denitrification is not achieved.

3.3 Scales of provision

A number of key requirements need to be satisfied if knowledge of ecosystem services is to be effectively translated into operational practice. The need for a verifiable evidence base and understanding of the trade-offs resulting from interactions requires knowledge of the scale, and the temporal and spatial dynamics and distribution, of ecosystem service delivery. This will enable key questions to be addressed, such as ‘Where and to what extent are services being provided?’ and ‘How much of a particular ecosystem or individual component is necessary to deliver a particular service or combination of services?’

While some services may be realized on the same temporal or spatial scale as the system that generates them, notwithstanding the importance for ecosystem resilience of ecological connections with other ecosystems, others may be realized on completely different scales. These include pollination, which operates at a local scale and can be managed by ensuring that there are areas of land that maintain populations of pollinators in a mosaic of land-use types; hydrological services, which function at a catchment or river basin scale and which require co-operation among land managers at that scale; and carbon sequestration in soil organic matter, which operates at regional and global scales and necessitates policy decisions by governments and international bodies to ensure that appropriate incentives are in place to ensure necessary behaviour by local land managers.

Attempts at quantifying spatial aspects of multiple services include that of the service-providing unit (SPU), defined by Luck et al. (2003) as ‘ecosystem structures and processes that provide specific services at a particular spatial scale’. For example, an SPU might comprise all those organisms contributing to pollination of a single orchard, or all those organisms contributing to water purification in a given catchment area (Luck et al. 2003; 2009). This is a parallel approach to that of the prediction of functioning and service provision in wetland ecosystems using a hydrogeomorphic unit (HGMU) approach (Maltby et al. 1994; Maltby 2009). The HGMU concept uses spatially-defined units to assess functioning at a range of landscape scales, and this method could feasibly be extended for assessment of other ecosystems. One of the major challenges in applying the SPU concept is to translate the unit into tangible and ideally mappable units of ecosystems and landscape/seascape, but the concept potentially offers an approach that focuses on multiple services and where changes to key species or population characteristics have direct implications for service provision.

4 Management of ecosystem services: dealing with uncertainty and change

In an increasingly globalized world, social conditions, health, culture, democracy, and matters of security, survival and the environment are interwoven and subject to accelerating change. Although change is inevitable, it is essential to understand the nature of change, especially the existence of thresholds and the potential for undesirable and, in practice, irreversible regime shifts. It is impossible to know where these potentially dangerous thresholds lie, and current efforts of adapting to climate change and other stressors will require a precautionary approach and a much deeper understanding of resilience and the combined capacity in both social and ecological systems if society is to cope with and benefit from change, i.e. social-ecological resilience (Folke et al. 2004). As the UN Secretary General has observed: “Building ‘resilience thinking’ into policy and practice will be a major task for all of the world’s citizens throughout the new century” (UN Climate summit September 24, 2007).

4.1 Ecosystems, services and resilience

Physical influences on ecosystems include geology, climate, topography, hydrology, connectivity with other ecosystems, and the results of human activities. Frequent minor disturbances are characteristic of ecosystem functioning. Typically, these may be seasonal influxes of nutrients or organisms, variations in temperature or hydrology, or weather or age damage to structuring organisms e.g. trees, to which the resident species are adapted (e.g. Titlyanova 2009). Large and less frequent disturbances may follow geological disturbances, anthropogenic eutrophication (increased nutrient loading) or toxic pollution, habitat loss, disconnection from adjacent ecosystems, species invasions, climate change and other external drivers of ecosystem change (see later). These larger disturbances can drive permanent or long-term ecosystem change by altering the physical structure of the ecosystem, and through removal of species and alteration of species interactions. Grazing pressure from elephants, for example, can result in the long-term replacement of woodland by grassland (de Knegt et al. 2008). Human activities such as atmospheric deposition of chemicals (Vitousek et al. 1997; Phoenix et al. 2006) have ensured that no pristine environments remain on Earth (Lawton 1997).

Ecosystem responses to changes in key variables such as temperature, nutrient loading, hydrology or grazing may, for example, lead to an increase in productivity (e.g. Aberle et al. 2007), or alter competition between species (Rahlao et al. 2008) by tipping the balance in favour of one species over another as a function of the response diversity. This type of change may be reversible and in proportion to the degree of change in either direction. For example, eutrophication of a normally nutrient-poor ecosystem typically leads to increased production and greater species diversity until a point is reached of high nutrient loading, when fewer, robust species come to dominate (Grime 1988; Badia et al. 2008). Over-grazing or cultivation of a forested ecosystem might alter the vegetation by halting recruitment of new trees and by favouring herbaceous species tolerant of grazing and trampling (Mysterud 2006). If the eutrophication or grazing driver is removed, the site may revert to its former state, unless key species have been eliminated.

A given ecosystem state may be maintained during moderate environmental changes by means of buffering mechanisms. These are negative feedbacks, which maintain the prevailing ecosystem state by containing the potentially exponential growth of some species. For example, in shallow lowland lakes, the increase of fast-growing phytoplanktonic algae is controlled by competition from macrophytes (plants and large algae), which store nutrients, making them unavailable to the algae, and also by invertebrate zooplankton, which grazes the algae. These zooplpankters hide from predators in the macrophytes, while predatory fish such as pike (*Esox lucius*) lurk in the macrophyte beds to ambush the smaller fish that consume zooplankton. Together, these buffering mechanisms serve to reinforce the clear-water status of the lake (Scheffer et al. 1993).

The capacity of an ecosystem to withstand perturbations without losing any of its functional properties is often referred to as *ecosystem resilience*. In practice, minor disturbances to ecosystem stability can serve to increase resilience overall because they impose the necessity for flexibility on species interactions (Gunderson 2000), hence Holling’s original (1973) definition of the term as “the capacity of a system to absorb and utilize or even benefit from perturbations and changes that attain it, and so to persist without a qualitative change in the system". Westman (1978) described resilience as the ability of an ecosystem to recover from disturbance without human intervention. Today the most common interpretation of resilience is that it represents the capacity of a system (e.g. a community, society or ecosystem) to cope with disturbances (e.g. financial crises, floods or fire) without shifting into a qualitatively different state (Gunderson and Holling 2002). A resilient system has the capacity to withstand shocks and surprises and, if damaged, to rebuild itself. Hence, resilience is both the capacity of a system to deal with change and continue to develop (see also Brand 2005; Brand and Jax 2007).

Where environmental drivers are persistent or strong, ecosystems may pass a threshold and undergo sudden and catastrophic structural change (Thom 1969; Loehle 1989; Walker and Meyers 2004). This can shift the ecosystem to an alternative state (Holling 1973; May 1977; Scheffer et al. 2001), which is also sometimes termed a '*regime shift*' (Folke et al. 2004). Such regime shifts can produce large, unexpected, changes in ecosystem services. Examples at local and regional levels include eutrophication of lakes, degradation of rangelands, shifts in fish stocks, breakdown of coral reefs, and extinctions due to persistent drought (Folke et al. 2004). Environmental drivers may not instigate the regime shift directly, but may increase the susceptibility of the ecosystem to change following some disturbance. This has been elaborated particularly in shallow lake ecology (Irvine et al. 1989; Scheffer et al. 1993; Moss 2001). Continuing the lake example above, once an ecosystem is placed under stress from eutrophication, the loss of its macrophytes (perhaps through physical or chemical damage) paves the way for algal dominance, resulting in turbidity, because it removes the refuge of zooplankton from predation and the shelter needed by predatory fish that formerly kept zooplanktivorous fish numbers low. In addition, plant loss increases mixing and re-suspension, and removes competition for nutrients, leaving phytoplankton to dominate the ecosystem (Ibelings et al. 2007). Once these buffering feedbacks of the clear-water state are removed, the ecosystem is subject to the prevailing eutrophication driver, and new buffering feedback mechanisms reinforce the degraded ecosystem state**.**

Crucially, the clear and turbid states are alternatives under similar nutrient regimes. Each is held in place by its own buffering feedback mechanisms (Jeppesen et al. 2007). This means that a simple reduction in nutrient loading to the lake will not result in a reversion to its former clear water status. The change is thus said to be non-linear. Overcoming the buffering mechanisms is neither easy nor cheap nor often possible (see e.g. Phillips et al. 1999). Similar examples have been recorded in coastal systems (Palumbi et al. 2008) and in terrestrial field ecosystems (Schmitz et al. 2006) and woodlands (Walker et al. 1981) among others.

A hypothetical example is provided by a farm that uses most of its land for agriculture, providing a basic provisioning service. Assume that insectivorous birds provide a regulating service in preventing insect pest outbreaks. As long as bird abundances are high, a good crop is produced every year, given schematically as the upper line in Figure 6. If insufficient bird predation on insects occurs there will be a pest outbreak and crop production will be largely reduced (lower line). Since insect abundance is then too high for bird predation capacity (due to a non-convex feeding response function) there is an hysteresis effect, that is, there is a response delay, making it non-linear. The year to year abundance of all bird species that eat insects varies over time, yielding a certain probability distribution for total bird predation every year. The probabilities of crossing from one state into the other are given in Figure 6 as **a** and **b** respectively.

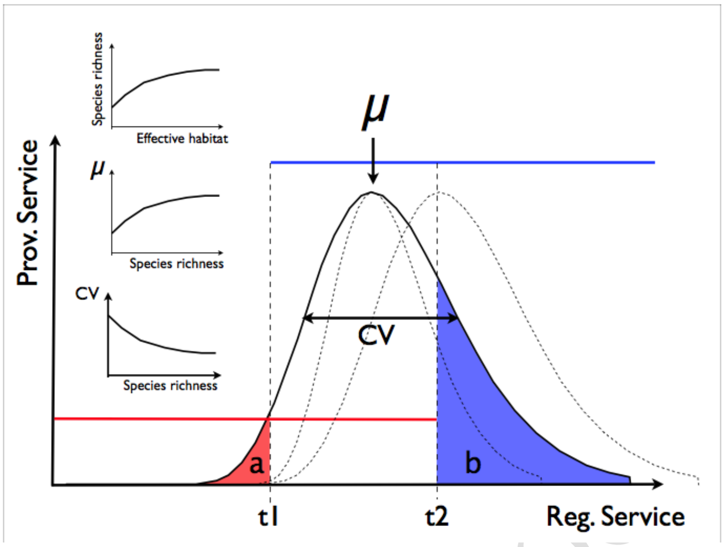

Figure 6: **Interactions between provisioning (crops) and regulating services (biological control).** Upper line –high generation of a biological control (insectivorous birds) leads to a high yield of crops. Lower line –decreased supply of biological control means a decline in crop yield. The characteristics of the larger landscape (inserted graphs) may give rise to non-linearities and thresholds (a and b) and the dynamics of the provisioning service being determined by management in the surrounding landscape (for details see text).

An important characteristic of this system is the shape of the probability function for the regulating service. Since this service is provided by a functional group of species, insectivorous birds, it is useful to examine how the species richness of this group of species would influence its performance. First, number of species may depend on the area of suitable habitat for birds, according to standard species-area relationships (upper inset graph). Species richness is generally positively correlated to total abundance due to complementary resource use among different bird species as shown in the middle inset graph. Higher species richness also results in lower coefficient of variation (CV) in the total bird abundance if there is some degree of negative autocorrelation between different species (Hughes et al. 2002). This negative autocorrelation can be thought of as species having different response functions and the effect on total bird abundance CV is shown in the lowest inset graph. The result of these effects is a change in the probability distribution of the regulating service, insect predation as shown as dashed lines. A consequence of increasing land available for natural bird populations is that the probability of falling into the undesired state with insect outbreaks (lower line) is largely reduced. At the same time the probability of recovering if this should happen increases. One consequence of such relationships is that the expected long-term value of the provisioning service largely depends on the management actions in the surrounding area.

4.1.1 Thresholds, recovery and ecological restoration

Although in many cases it may be possible to restore 'mildly' degraded ecosystems back to some defined earlier state, ecosystems can be so altered that restoration in the strict sense of the term is no longer possible. Given the extent of human impacts on the biosphere, the notions of restoration and restorability need to be expressed with many caveats.

The Society for Ecological Restoration International's *Primer on Ecological Restoration* (SER 2002) defines ecological restoration as 'the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed'. The target is a resilient ecosystem that is self-sustaining with respect to structure, species composition and function, while integrated into a larger landscape and congenial to 'low impact' human activities. However, if an ecosystem has been so disturbed that it crosses one or more thresholds, then restoration, if possible at all, may be achieved only with great difficulty and expense. Furthermore, subjective choices and trade-offs are inevitable and will be based on non-financial or marketable values as well as money and ecological science. For the restoration manager, the awareness of past threshold crossings in these cases should help guide the restoration programs (Clewell and Aronson 2007). Ease and cost will also vary among ecosystems, which impose the need for pragmatism. For example, in the Area de Conservación Guanacaste, in north-western Costa Rica, one of the longest running and largest scale restorations in the world, Janzen and co-workers have found that tropical dry forest recovers much more readily than nearby tropical moist forest (Janzen 2002). Budgeting of investment in labour and other expenses is allocated accordingly.

This example also highlights the fact that ecosystem resilience should not be interpreted in a normative way. Undesirable ecosystem states, such as cow pastures seeded with exotic grasses, may become very resilient to change, and restoration will need an understanding of how to erode undesirable resilient states. Managers should also not always seek to restore in terms of an original or 'pre-disturbance' ecosystem state or trajectory. Recovery of ecosystem *services* through revitalization of ecosystem *processes* may be better options. Placing emphasis on restoring *process* – and thus, ultimately, on ecosystem services – rather than on restoring a specific species inventory (Falk et al. 2006) also facilitates valuation and financing (De Groot et al. 2007; Holmes et al. 2007; see section 5.2 below). This is consistent with the first principle in applying the 'ecosystem approach' under the Convention on Biological Diversity (CBD 2000-2008).

4.2 Resilience thinking in policy and practice

In order to develop a deeper resilience thinking of relevance for policy and practice, there are at least three factors that need to be understood:

Depletion of non-renewable resources. A historic or geological legacy of environmental conditions may be supporting current patterns of use, but these are not being renewed on human time scales. Aside from minerals and fossil fuels, examples include groundwater resources and aquifers effectively containing 'fossil' water built up under different climatic conditions in previous millennia (Foster and Loucks 2006), and carbon storage in peat-based ecosystems developed since the end of the last glacial period, where net accumulation of peat no longer occurs. These represent resources that may be exhausted through use.

The changing environmental 'envelope'. The environmental envelope within which organisms evolve and patterns and processes of biodiversity and ecosystems develop, is changing because of human activity. This raises far-reaching questions of reliance on biodiversity and ecosystems and their viability when their base-line of environmental support and pressure of use is shifting. Coined by Pauly (1995) the related term "shifting baselines" highlights the fact that successive generations adjust to the state of the environment they find themselves in, i.e.an ecosystem state which is already degraded may be accepted as 'normal'. Jackson et al. (2001) collated worldwide data to demonstrate that in marine systems, humans have had such a prominent impact of successively reducing species richness for so long that previous levels of biodiversity are today difficult to imagine. Shifting baselines have major implications for the sustainability of resource use.

The effects of environmental shocks and disturbances. Both natural (e.g. climate, flood, fire, landslide) and human-induced (e.g. climate, sea-level change, deforestation, overgrazing, over-fishing, river-regulation, impoundment, pollution) impacts may be unpredictable and uncertain, producing major step changes, surprises and regime shifts. When faced with change through environmental stress, ecosystems may pass a critical threshold where the existing ecosystem structure collapses (Folke et al. 2004). Erosion of resilience may be an effect of variables such as human-induced environmental changes and loss of biodiversity.

A simple process-response schema is used to represent these relationships (Figure 7). It represents an ecosystem as a functional entity and a result of interactions between its structure and biological composition and processes.

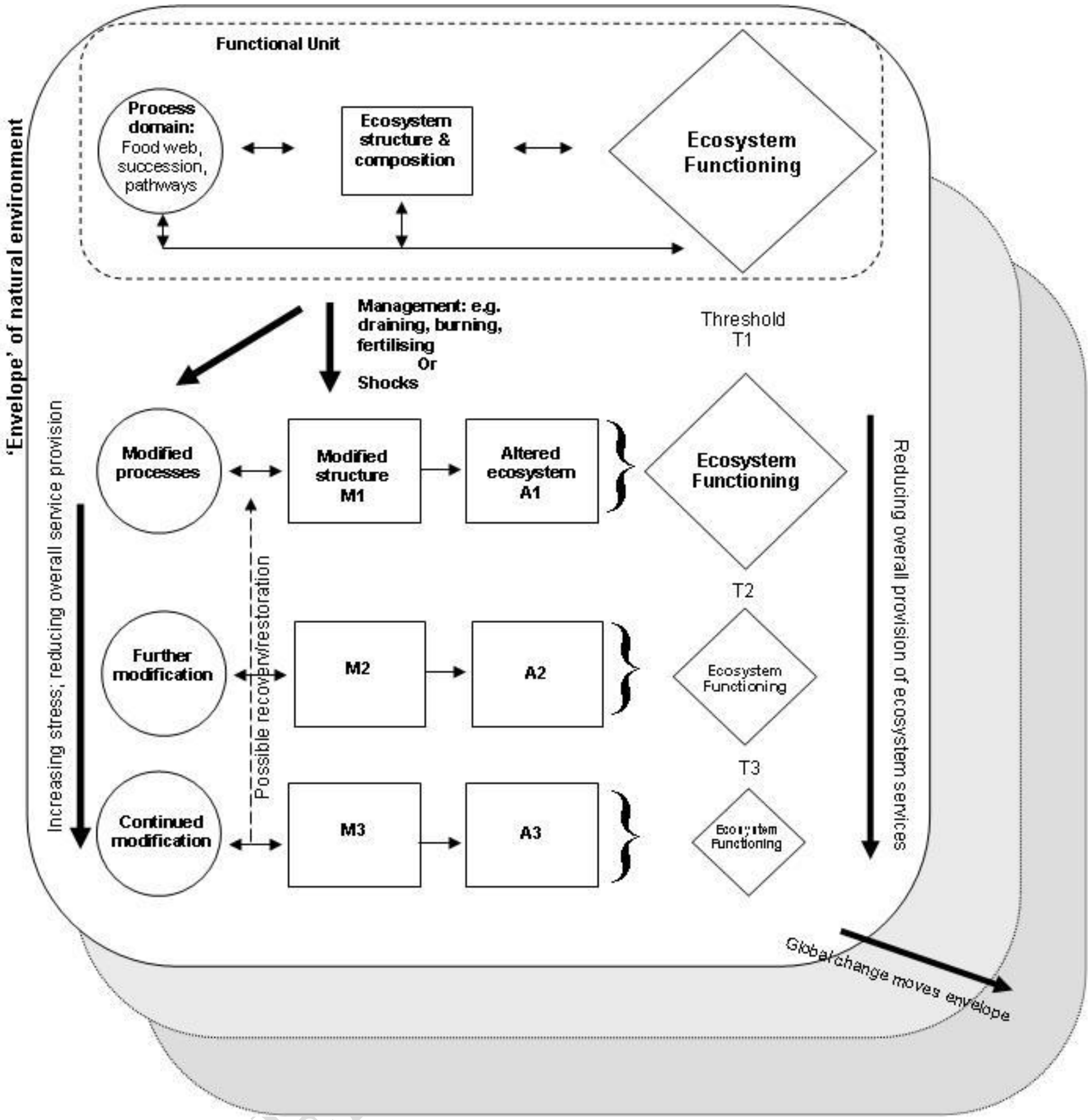

Figure 7: **A process-response model of ecosystem functioning and effects of impacts.** The changing environmental envelope of global environmental conditions alters the predictability of ecosystem responses to perturbations.

Source: Adapted from Maltby et al. (1994).

The ecosystem includes biological components representing particular genetic, species and community scale elements, all within a particular 'envelope' of prevailing environmental conditions. Both direct and indirect human influences as well as natural environmental shocks can modify ecosystem structure or the process domain, so altering ecosystem functioning. A sequence of increased modification resulting from increasing intensity of impact is shown as reducing the total combination of functions (although an individual function may actually increase, such as in the case of agricultural productivity). More or less distinct 'tipping points' may indicate the transition or shift from one state to another. The possibilities for recovery to previous ecosystem conditions will depend partly on external drivers discussed above, but mostly on the intrinsic properties and ecological integrity of the ecosystem, as well as time scale. However, erosion of resilience may make it impossible to recover a particular condition of functioning, structure or process because it no longer can occur within the boundary of the new envelope (i.e. due to changes in ecosystem dynamics).

This framework contests models and policies that are based on assumptions of linear dynamics, with a focus on optimal solutions. Applications of such theory and world views tend to develop governance systems that invest in controlling a few selected ecosystem processes, causing loss of key ecological support functions, in the urge to produce particular resources to fulfil economic or social goals (Holling and Meffe 1996). An alternative approach is based on ecosystems viewed as complex and adaptive, characterized by historical (path) dependency, non-linear regime shifts, and limited predictability. A dynamic view of nature and society has major implications for valuations of nature. If a system is discontinuous, the basic theorems of welfare economics are not valid and the result of resource allocation may be very far from the optimum, even if there are well-defined property rights (Mäler 2000). This has major implications for production, consumption and international trade, and also major implications for economic policy. Optimal management will often, because of the complex dynamics, be extremely difficult to implement.

5 Biodiversity, ecosystem services and human well-being

Since ecosystem services are the benefits that people get from ecosystems, it follows that changes in ecosystem services associated with changes in biodiversity will have implications for human well-being. Subsequent chapters explore the methods economists use to estimate the value of non-marketed ecosystem services, and summarize the results of existing valuation studies. Here we consider not how ecosystem services are valued, but how the production of ecosystem services confers value on all components of the biosphere, including biodiversity. The value of biodiversity derives from its role in the provision of ecosystem services, and from peoples' demand for those services. Economists have typically sought to value the individual components of ecosystems or specific services yielded by ecosystems, rather than ecosystems themselves. In some cases – where well-functioning markets exist – the valuation of specific services is straightforward. In most cases it is not. And even where markets for specific services do exist, derivation of the value of individual components of ecosystems is hard. The 'bundling' of services (4.1), and the fact that particular species may contribute to the production of many different services, mean that their marginal contribution to a particular service will be, at best, a partial measure of their value. In addition, the precise role of individual species in the ecological functioning that produces human benefits are typically known only for the well studied and highly controlled processes that yield marketed foods, fuels and fibres. Yet without this knowledge it is not possible to derive the value of either the basic building blocks of individual ecosystem services (however they might be defined) or of the functioning ecosystems that support an array of services. There may be numerous different pathways by which a particular function is generated and a resulting service delivered. Only exceptionally are all these pathways known – a challenge epitomized in the whole question of species ‘redundancy’.

In principle, the value of ecosystems derives from the set of services – the discounted stream of benefits – they produce (Barbier et al. 2009; Barbier 2007). So if we define B_t to be the social benefits from the set of all services provided by an ecosystem at time t, then the present (discounted) social value of that system is:

$$V_0 = \int_0^\infty e^{-\delta t} B_t dt$$

where δ is the social rate of discount. For each time period, B_t is the sum of all benefits deriving from the ecosystem. That is, $B_t = \sum_i B_{it}$. Since those benefits depend upon sets of ecosystem services that, in turn, depend upon biodiversity, the value of of biodiversity can be derived from them. For example, if $B_t = f\left(S_t\left(X_t\right)\right)$ where S_t is the set of services produced, and X_t is the set of species, then the marginal value of the ith species is given by the derivative; $\frac{\partial B_t}{\partial S_t}\frac{\partial S_t}{\partial x_{it}}$. The main challenge for the calculation of the stream of benefits from ecosystems is that while a number of the services in an economy are marketed, many ecosystem services supported by biodiversity are not. Some benefits that contribute to human well-being do not have a price attached to them, and are therefore neglected in normal market transactions (Freeman 2003; Heal et al. 2005). Ecosystems are invariably multifunctional. Except in the case of managed systems (such as agro-ecosystems) their structure and function may be consistent with environmental conditions and historic patterns, but not the purposeful delivery of services. But even managed systems typically yield a range of benefits, and the value of the system depends not only on the value of the benefits that are the primary goal of management, but also on the ancillary services delivered as by-products of the primary services (Perrings et al. 2009).

How bundles of ecosystem services are configured matters. The beneficiaries of services may be spread among quite different stakeholder interests, and be distributed both off-site as well as on-site. Thus the value of freshwater quality improvement may be realized at various points downstream from the ecosystem performing the work and may be particularly significant even for the estuarine, coastal, and more distant marine waters and the services they, in turn, support.

Uncovering the value of ecosystem components requires an understanding of the ways in which they contribute to the production of ecosystem services. Neither individual species nor the ecosystems of which they are a part are exactly comparable or identical. The spectrum from microbial to charismatic top carnivore species encompasses a wide range of processes and functioning. The most charismatic species may be excellent indicators of ecosystem condition but not necessarily be of greatest functional importance. Ecosystem properties vary in detail according to both spatial and temporal factors. To derive the value of ecosystem components from their marginal impact on the production of valued goods and services, we need to know the shape of the ecological production functions that define the relationship between environmental inputs and outputs of goods and services. Ecological production functions thus capture the biophysical relationships between ecological systems and the services they provide, as well as inter-related processes and functions such as sequestration, predation, and nutrient cycling. They accordingly include both well-understood inputs over which humans have direct control, and poorly understood inputs over which humans have variable and often limited control. Identification of ecological production functions requires: i) specification of the ecosystem services of interest, and ii) development of a complete mapping from the structure and function of the ecological system to the provision of the relevant ecosystem services. Although we are making progress in understanding and defining ecological production functions for certain ecosystem services, such as carbon sequestration, the specification of production functions for many important ecosystem services is still rudimentary (Perrings et al. 2009).

Nevertheless, certain things are well understood. Conversion of ecosystems for the production of particular services generally reduces their capacity to provide other services. Whether specialization of this kind enhances the value of the ecosystem depends on the value of the forgone services (Balmford et al. 2002). Converted lands may gain value in terms of provisioning services, but lose value in terms of other types of services, such as water regulation, erosion control, habitat provision, fire regulation and so on. Conversion of natural forest to rice paddies and mangrove forest to shrimp ponds in many parts of South East Asia has led to a reduction in a range of regulatory functions, from storm buffering to silt entrapment (Barbier 2007). In the Mekong Delta, for example, acidification of potential acid sulphate soil materials, resulting from lowering of the water table and oxidation of the marine sediments, reduces the crop yield and harvest after just a few years, and often results in abandonment (Maltby et al. 1996). Such ecosystem alteration yields no obvious compensating gains. In such cases, the cost of reduced water quality, storm and flood protection, wildlife habitat and shrimp or fish recruitment from wild populations have still not been factored in to the decisions that lead to ecosystem change (Barbier 2007). Understanding and valuing the changes in the regulating ecosystem services involved is probably the biggest challenge to the economics of biodiversity at the moment.

The valuation of the contribution of biodiversity to regulating services poses particular challenges. The regulating services provide value through their role in assuring the reliability of service supply over space or time; sometimes expressed in terms of the resilience of the system to environmental shocks. That is, they moderate the variability or uncertainty of the supply of provisioning and cultural services. Estimation of the contribution of individual species to this service is, however, problematic. A small subset of species and their accompanying symbionts, mutualists, or commensalists supply the ecosystem services required for human survival. While an increase in biodiversity may increase production, experimental data indicate that for given environmental conditions this effect is small. The productivity of some biologically diverse communities, for example, has been found to be about 10% higher than the productivity of monocultures, but the effect often saturates at fewer than ten species. If environmental conditions are not constant, however, the effect may increase with the number of species providing that they have different niches and hence different responses to disturbances or changes in environmental conditions. For instance, the regulation of pest and disease outbreaks is affected by foodweb complexity. Simple predator-prey systems are prone to 'boom-and-bust' epidemiology, whereas the presence of multiple predators and prey operating at several trophic levels, and including prey-switching, involves much more stable dynamics (Thebault and Loreau 2006).

The value of biodiversity in regulating the provisioning and cultural services is illustrated in Figure 8. Since people care about the reliability (or variability) in the supply of these services (people are generally risk averse), anything that increases reliability (reduces variability) will be valued. The value of regulating services accordingly lies in their impact on the variability in the supply of the provisioning and cultural services. An important factor in this is the diversity of the functional groups responsible for the services involved. The greater the specialization or niche differentiation of the species within a functional group, the wider the range of environmental conditions that group is able to tolerate. In some cases greater diversity with a functional group both increases the mean level and reduces the variability of the services that group supports. Indeed, this portfolio effect turns out to be one of the strongest reasons for maintaining the diversity of functional groups.

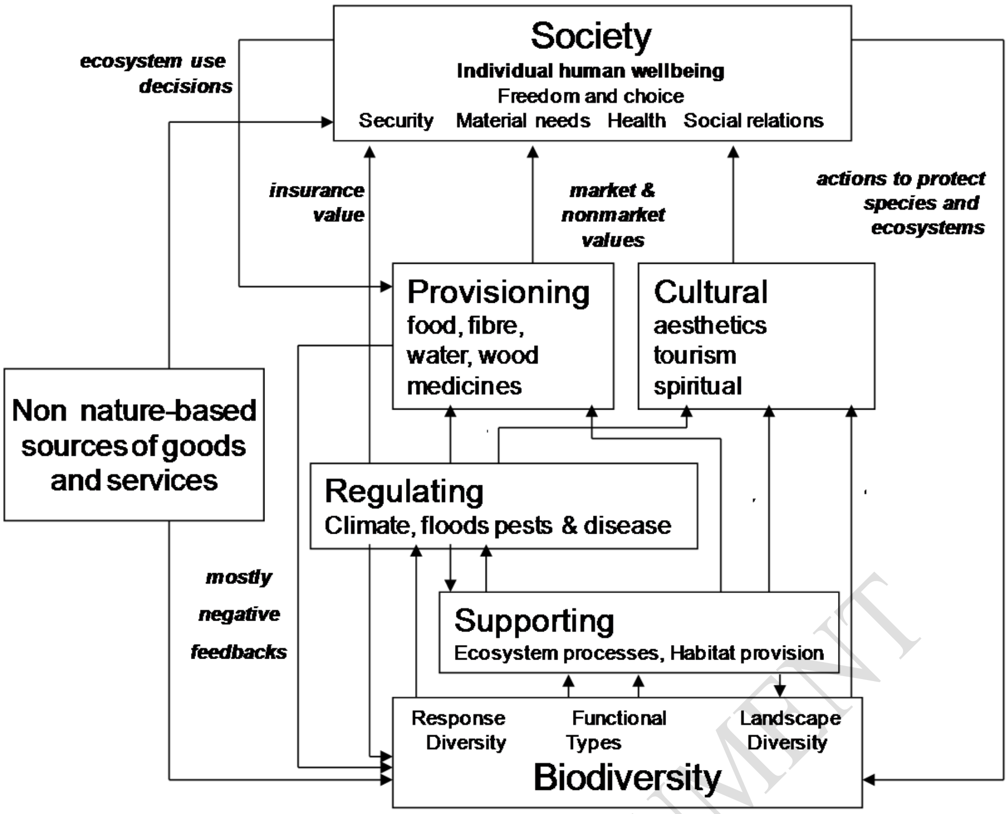

Figure 8: **Deriving the value of biodiversity and the regulating services.** Source: Kinzig et al. (2009).

The general point here is that the value of ecosystem components, including the diversity of the biota, derives from the value of the goods and services they produce. For each of the ecosystem services described in this chapter we have identified its sensitivity to changes in biodiversity. If greater diversity enhances mean yields of valued services it is transparent that diversity will have value. However, it is also true that if greater diversity reduces the variance in the yield of valued services that will also be a source of value. Since people prefer reliability over unreliability, certainty over uncertainty, and stability over variability, they typically choose wider rather than narrower portfolios of assets. Biodiversity can be thought of as a portfolio of biotic resources, the value of which depends on its impact on both mean yields and the variance in yields.

It follows that there is a close connection between the value of biodiversity in securing the regulating services, and its value in securing the resilience of ecosystems. Since resilience is a measure of the capacity of ecosystems to function over a range of environmental conditions, a system that is more resilient is also likely to deliver more effective regulating services. The economics of resilience are considered in more detail in Chapter 5.

The various forms of natural capital (see MA 2005) provide and regulate flows of ecosystem services essential to life and economic production (de Groot et al. 2002). However, with the exception of agricultural land, it is currently undervalued, and sometimes even invisible, both in our national and international systems of economic analysis, and in indicators like Gross Domestic Product (GDP) (Arrow et al. 1995; Dasgupta et al. 2000; TEEB 2008; TEEB 2009). Furthermore, global society is making withdrawals of natural capital stocks far in excess of its yield in interest (ecosystem services, e.g. carbon sequestration) and societal re-investments in natural capital are, to date, limited. Yet increasing evidence shows that investing in the restoration and replenishment of renewable and cultivated natural capital 'pays' in economic and political terms (e.g. Goldstein et al. 2008).

As shown in chapter 1, the concept of restoring natural capital is a relevant concept defined as all investments in renewable and cultivated natural capital stocks and their maintenance in ways that improve the functions of both natural and human-managed ecosystems, while contributing to the socio-economic well-being of people (Aronson et al. 2007). It is thus a broader concept than ecological restoration (section 5.1.1), can be applied at landscape or regional scales, and can generate significant economic savings. For example, integrated programs seeking to restore degraded natural systems and rehabilitate production systems in the Drakensberg Mountain Range Project (Blignaut et al. 2008).

6 Conclusions and further research

We now have a good understanding of the intricacies and outcomes of ecological dynamics as well as the expressions of these processes in the provision of goods and services to human society. Significant gaps in our knowledge remain, but there is an emerging scientific consensus on the need to sustain biological diversity to protect the delivery of ecosystem services. Nevertheless, if we wish, for example, to predict the impact of biodiversity change on variability in the supply of ecosystem services, we need to measure the impact of biodiversity conservation over a range of environmental conditions. In the same way, we need to be able to identify the effect of biodiversity change on the capacity of social-ecological systems to absorb anthropogenic and environmental stresses and shocks without loss of value (Kinzig et al. 2006; Scheffer et al. 2000; see Figures 8 and 9). To do so, requires analysis of the linkages among biodiversity change, ecological functioning, ecosystem processes, and the provision of valued goods and services. To understand and even enhance the resilience of such complex, coupled systems, therefore, we need robust models of the linkages between biodiversity and ecosystem services, and between biodiversity change and human well-being (Perrings 2007).

A major gap in knowledge is how different ecosystems interact in the delivery of services. Ecosystems are rarely homogeneous. Extensive forest ecosystems often contain rivers, lakes and wetlands as well as patches of land which may be farmed or managed as open habitat for wildlife. It is important to know how the various combinations of ecosystems operate together to generate services, which may be enhanced or impeded by interactions. Equally we need urgently to develop evidence-based management practices that maximize the delivery of a broad range of services from individual ecosystems, especially where these are managed intensively for food or fuel production.

Existing knowledge is also sufficient to develop more effective instruments for ecosystem service-based biodiversity conservation, including the payments for ecosystem service (PES) systems discussed elsewhere in this report (TEEB 2009). These instruments offer a mechanism to translate external, non-market values of ecosystem services into real financial incentives for local actors to provide such services (Ferraro and Kiss 2002; Engel et al. 2008). Similarly, existing knowledge is sufficient to develop more effective governance institutions, including property rights regimes and regulatory structures. Once such mechanisms are established, their effectiveness can be increased by improving the quality of available information on the effect of conservation on ecosystem service provision.

Major questions that future research needs to address include:

1. Understanding links between biodiversity, ecosystems and resilience:

- What are the roles of species interactions and functional diversity for ecosystem resilience?
- What are the drivers behind loss of resilience and how do they interact across scales?
- What are the impacts of climate and related environmental changes on ecosystem functioning through effects on species (re)distribution, numbers and process rates?

2. Understanding the dynamics of ecosystem services:

- How can we better analyze effects on regulating ecosystem services of an increase in provisioning services?
- What tools can contribute to accurate mapping of land and seascape units in terms of functioning and service support / provision?
- What specific tools could contribute to better assessment of spatial and temporal dynamics of service provision, especially in relation to defining who benefits, where and to what extent?

3. Understanding the dynamics of governance and management of ecosystems and ecosystem services:

- If all ecosystem services are taken into account, what is the appropriate balance between ‘more diverse landscapes generating bundles of ecosystems services’ and more intensively managed ecosystems like monocultures for food production?
- What are the trade-offs and complementarities involved in the provision of bundles of ecosystem services, and how do changes in the configuration of ecosystems affect their value?
- What are the most effective mechanisms for the governance of non-marketed ecosystem services, and how can these be designed so as to exploit future improvements in our understanding of the relationships between biodiversity, ecosystem functioning and ecosystem services?

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