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The Sustainable Delivery of Goods and Services Provided by Soil Biota

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Soil systems provide numerous goods and services that are critical for human society (Daily et al. 1997; Wall et al. 2001; Millennium Ecosystem Assessment 2003). Many of these goods (e.g., food production, construction materials) and services (e.g., renewal of fertility, carbon sequestration, storage and purification of water, suppression of disease outbreaks) are in part mediated by soil organisms. The reduction of soil services as a consequence of improper management is rarely considered when evaluating consequences of management strategies and decisions. The consequence of such impropriety has been estimated to be in excess of US$1 trillion per year world-wide (Pimentel et al. 1997; Table 2.1), but the local financial consequences will vary according to how dependent the local economy is on ecosystem services. The role of soil organisms depends not only on the type of organisms present and their activity, but probably also on their diversity (Wardle 2002) and on a range of abiotic factors, some of which act locally (soil fertility), while others are more global (climate).

The management of soil systems requires an understanding of the underlying ecosystem processes and how these are influenced by the environment. This sets the borders for the ecology of the species involved. In this chapter, we provide a framework for assessing the role of soil organisms in the delivery of ecosystem goods and services. We use examples from grasslands, forests, and agriculture to illustrate how the consequences of management may be evaluated for the soil system in different environ-

Table 2.1. Total estimated economic benefits of biodiversity with special attention to the services that soil organism activities provide worldwide (modified from Pimentel et al. 1997).

Activity	*Soil biodiversity involved in the activity*	*World economic benefits of biodiversity (× US\$$10^9$/year)*
Waste recycling	Various saprophytic and litter feeding invertebrates (detritivores), fungi, bacteria, actinobacteria, and other microorganisms	760
Soil formation	Diverse soil organisms, e.g., earthworms, termites, fungi, eaubacteria, etc.	25
Nitrogen transformations	Biological nitrogen fixation by diazotroph bacteria, conversion of NH_4 to NO_3 by nitrifying bacteria, conversion of NO_3 to N_2 by denitrifying bacteria	90
Bioremediation of chemicals	Maintaining biodiversity in soils and water is imperative to the continued and improved effectiveness of bioremediation and biotreatment	121
Biotechnology	Nearly half of the current economic benefit of biotechnology related to agriculture involves nitrogen-fixing bacteria, pharmaceutical industry, etc.	6
Biocontrol of pests	Soil provides microhabitats for natural enemies of pests, soil organisms (e.g., mycorrhizae) that contribute to host plant resistance and plant pathogen control	160
Pollination	Many pollinators may have edaphic phase in their life cycle	200
Wild food	For example mushrooms, earthworms, small arthropods, etc.	180
Total		**1,542**

ments. We compare unmanaged with managed grassland and forest ecosystems, and non-tilled with tilled agricultural systems. We discuss which soil systems, habitats, ecological soil functions, soil taxa, and underlying processes are critical to the sustainability of delivering goods and services, and how human activities may affect these by land management and by inducing global change. We work along a gradient, where plant-soil feedbacks in unmanaged systems may resemble those in low-input agriculture or forestry. We discuss whether these continua do indeed exist and what may be learned from unmanaged ecosystems when attempting to manage or enhance the sustainability of managed systems.

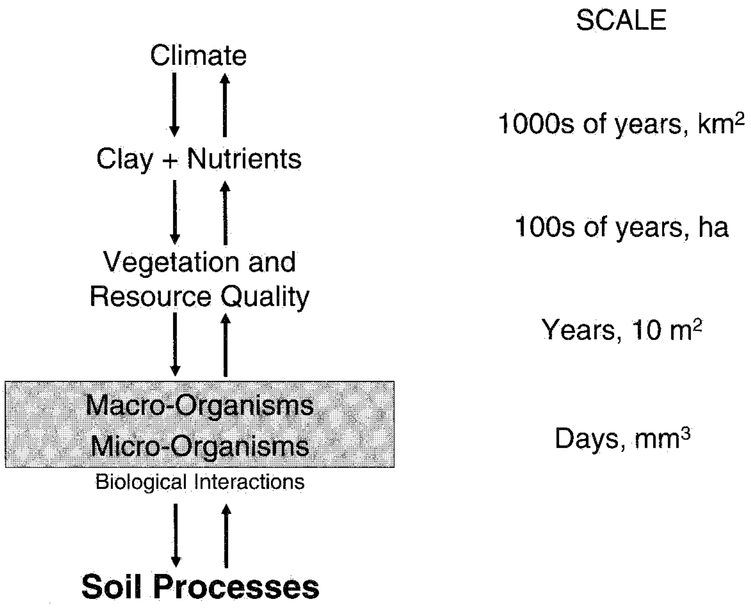

Figure 2.1. Hierarchy of the determinants of soil processes that provide ecosystem services (after Lavelle et al. 1993). Note that these determinants occur at different temporal and spatial scales.

Hierarchy of Environmental Controls of Soil Ecosystem Goods and Services

The contribution of soil organisms to ecosystem goods and services is determined by a suite of hierarchically organized abiotic factors, and by the nature of the plant community (Lavelle et al. 1993; Figure 2.1). At the highest level of the hierarchy, climate determines soil processes at regional and global scales (Gonzalez & Seastedt 2001). Climatic limitations, such as drought or low temperatures, directly determine the rates of the main physical, chemical, and microbiological reactions (Lavelle et al. 1997). At the second level in the hierarchy, the landscape and the original nature of parent material largely influence soil ecosystem goods and services. Nutrient heterogeneity of the substrate, along with the amount and quality of clay minerals, are the most important characteristics.

The third level in the hierarchy is the quality and quantity of the organic matter produced, and this depends on the nature and composition of plant communities. The release of energy and nutrients stored in dead organic matter depends strongly on the proportion of support tissues rich in lignin and lignocellulose; the proportion of secondary chemical compounds, such as tannins or polyphenols; and the ratio of nutrients to carbon (Grime 1979; Swift et al. 1979). Production of secondary products potentially affecting the decomposability of the organic matter may be enhanced by nutrient deficiencies and/or attack by herbivores (Waterman 1983; Baas 1989). The chemical composition of plants is, therefore, an important determinant of the composition and activity of the soil organism community. At the lowest hierarchical level, the soil organisms themselves operate within functional domains. A functional domain comprises a subset of the soil community that has similar functions or effects on, for example, soil structure (Lavelle 2002). The influence of each factor affecting soil ecosystems varies over temporal scales, from millimeters to kilometers.

Information on the sustainable delivery of goods and services originating from one region may not be directly applicable to another region; information on intensively managed soils, where functional domains differ considerably from those under extensive management, should not be generalized *a priori*. Therefore, our comparison of ecosystem management strategies for sustainable delivery of ecosystem goods and services as provided by soils should be regarded as a template, rather than as results that apply to the whole globe.

Biotic and Abiotic Drivers of the Underlying Processes in Soils

The complete destruction of the community of soil organisms—for example, due to erosion—results in obvious loss of soil ecosystem functions. Far less is known about the consequences of the loss of soil biodiversity for the sustainable delivery of ecosystem goods and services (Wall et al. 2001). Results from empirical studies on the relation between soil biodiversity and ecosystem functions range from positive to neutral or even negative (Mikola et al. 2002). However, it is obvious that soil biodiversity may act as a source of insurance, thereby making systems more stable. For example, when soil biodiversity is reduced by one stress factor or event, the soil community may be less able to recover from a repeated or second stress. Such accumulation of stresses may well result in the loss of stability of soil ecosystem processes (Griffiths et al. 2000).

Belowground processes that involve decomposition of organic matter, transformations of nutrients, and the supply of nutrients from the soil for plant growth are driven in the first instance by the activities of bacteria and fungi (Wardle 2002). Biotic drivers of microbially driven processes in soils include plants, their herbivores and pathogens, and other soil animals. Plant species differ in the quantity and quality of litter (dead organic matter that is sufficiently intact to be recognized) and rhizosphere materials that they return to the soil. This in turn governs the composition, growth, and activity of the microflora, and, hence, the rates of soil process (Hooper & Vitousek 1998). Aboveground herbivores can strongly influence soil organisms through a number of mechanisms by which they alter the quantity and quality of resources entering the soil (Bardgett & Wardle 2003). Soil animals have important effects on microbial activity at a range of scales (Lavelle 1997): by consuming microbes directly, by transforming litter and thus altering its physical structure, by creating biogenic structures, or by entering into mutualisms with microbes either in the "external rumen" or in the gut cavity (Lavelle 1997).

Some groups of soil organisms have a direct relationship with plant roots (Wardle et al. 2004). Soil pathogens and root herbivores are notorious for causing yield reductions of arable crops, re-sowing failures in grassland, disease in orchards that requires replanting, and die-back in production forest. Root pathogens and herbivores can also have strong impacts on the species composition of natural vegetation and the rate of changes therein (Brown & Gange 1989; van der Putten 2003). Root pathogens and herbivores contribute to primary and secondary plant succession (Brown & Gange 1992; van der Putten et al. 1993; De Deyn et al. 2003) and plant species diversity (Bever 1994; Packer & Clay 2000). Plant species that escape from soil pathogens may become invasive in new territories (Klironomos 2002; Reinhart et al. 2003). Root symbionts, such as mycorrhizal fungi and nitrogen fixing microorganisms (e.g., *Azobacter*, *Rhizobium*, and *Cyanobacter*), are important for plant nutrition in unmanaged systems and in non-tilled, low-input arable systems (Smith & Read 1997).

The various biotic and abiotic drivers in soil systems do not operate independently of one another, and interactions among them are important determinants of soil processes. For example, a recent litter exclusion study found that soil microarthropods play an important role in decomposition in a tropical forest but not in a temperate forest, where the abiotic drivers of microbial activity emerged as being of greater importance (Gonzalez & Seastedt 2001). Similarly, substrate fertility determines the role of microbially driven processes in supplying nutrients: in fertile conditions, plants produce litter of high quality from which ammonium (NH_4^+) is readily released by microbes and taken up by plants, while in infertile conditions plants produce poor-quality litter protected by polyphenols from which nitrogen is not readily mineralized. In these infertile systems, plants often bypass the mineralization process entirely by taking up organic nitrogen directly (e.g., Northup et al. 1995).

Context Dependence of Environmental Controls

Environmental controls of soil ecosystem processes and the delivery of soil ecosystem goods and services depend on climate, soil type, vegetation, and the local context (Figure 2.1). Stressed systems, whether they are stressed from extreme climatic seasonality (seasonal forests and savanna) or human interventions (managed grassland, managed forest, and tilled arable land), are usually characterized by lower diversity of soil fauna (there is little comparative information on microbes) and greater dominance of certain species (see Tables 2.2–2.4). Under these conditions the effects of key organisms, sometimes at species level, become more apparent (Anderson 1994). In arable soils, soil tillage consistently reduces the abundance of animals with large body sizes, whereas microbes and microfauna are not affected so much (Wardle et al. 1995). Here, we illustrate the consequences of the local context by discussing ecosystem processes, goods and services for three major types of land use: grassland, forest, and arable land and the role of soil organisms in controlling ecosystem goods and services (see Tables 2.2–2.4 for an overview of processes, goods, and services for grassland, forest, and arable land, respectively). Later, we discuss management trade-offs for each of these three systems and provide a conclusion on the importance of soil biodiversity.

Grasslands

Grasslands, including steppes, savannas, prairies, and tundra, are important terrestrial ecosystems covering about a quarter of the Earth's land surface. Grasslands build soil systems that differ from those of forests and other vegetation types. A key feature of grasslands, especially those that are more fertile, is their high turnover of shoot and root biomass, and the consequent large pool of labile organic matter at the soil surface. In contrast to many terrestrial ecosystems, heavy herbivore loads, both above- and belowground, are also a characteristic feature of fertile grasslands. This significantly influences plant growth and species composition, and the structure of grassland, since herbivores consume high proportions of annual aboveground (McNaughton 1983) and belowground (Stanton 1988) net primary production.

Aboveground herbivores also have a profound influence on nutrient pathways in grasslands through short circuiting both litter return and soil recycling processes (Bardgett & Wardle 2003). A large percentage of nutrients taken up by plants in grazing ecosystems is cycled directly through animal excreta, resulting in accelerated soil incorporation, particularly of nitrogen and phosphorus (Ruess & McNaughton 1987). Therefore, soils of grazed grasslands tend to have relatively small amounts of litter on the soil surface, but large amounts of organic nitrogen and carbon in the soil. These features combine to produce a soil environment that sustains, or is sustained by, an abundant and diverse faunal and microbial community.

In high latitude and high altitude grasslands, as well as in grasslands of semi-arid regions, soil processes and ecosystem goods and services are likely to be controlled more by abiotic factors than by biotic ones. This may be different in lowland temperate or tropical regions where soil processes are not so limited by climate. Carbon sequestration, for example, across the Great Plains of the United States, depends on interactions between annual precipitation and soil type (Burke et al. 1989). Nutrients can be lost due to a number of factors. For example, in tall-grass prairie, the major local pathways for nutrient loss are either abiotic (hydrologic fluxes and fire-induced losses) or biotic (gaseous fluxes via denitrification and ammonia volatilization) (Blair et al. 1998). In wet grassland systems, hydrology is indisputably the dominant controlling factor. However, in waterlogged soils, there can be considerable release of gaseous products from denitrification, while at the same time waterlogging limits nitrification and mineralization (Nijburg & Laanbroek 1997).

Forests

Of the total terrestrial net primary productivity of 62.6 Pg C yr^{-1}, forests are responsible for 52 percent (ca. 32.6 Pg C yr^{-1}) (IPCC 2001; Saugier et al. 2001; Gower 2002). When combined with the large land surface area covered by forests (boreal, temperate, and tropical), savannas, and shrubland systems (ca. 72×10^6 km^2), it is clear that nearly 50 percent of the organic input into soils are from forest litter and plant roots. The role of the forest soil biota is immediately highlighted when we realize that the majority of the world's forests rely heavily on internal nutrient cycling to maintain productivity (see, for example, Miller et al. 1979) and, in the total absence of soil biota, these systems would become extremely nutrient limited.

Not only is nutrient cycling controlled by the soil biota but several major sources of nutrient input to forests (e.g., mineral weathering and N fixation) are also mediated or strongly affected by soil biological activity. Thus, factors that impair soil biological activity (e.g., acidification, heavy metal pollution) have negative consequences for both nutrient inputs and subsequent cycling. There is also an increasing appreciation that our understanding of forest nutrient cycling and the high inorganic N concentrations currently found in many of the soils of the major developed regions of the world are atypical of unmanaged, pristine forests (Perakis & Hedin 2002), where more tightly coupled nutrient cycling, frequently involving intimate links between primary producers and soil biota, may dominate (Ohlund & Nasholm 2001). At the most basic level, forest soil biota are essential for the maintenance of the forest, but these organisms also have very direct effects on the ecosystem services provided within the forest.

Although examples exist that show where soil biodiversity is critical in maintaining an ecosystem service (e.g., specific edible fungal fruiting bodies, inoculation or manipulation of wood stump saprotrophs to control pathogens), in general we are ignorant of the extent to which soil diversity is important in maintaining services. The observation that increased inorganic N additions to forest soils can greatly impair methane oxidation rates (Wang & Ineson 2003) is an example of how soil organisms are clearly controlling an important ecosystem service, but direct information of the diversity of the species involved is proving extremely difficult to extract (Bull et al. 2000).

In unmanaged humid tropical forests it is rare that any specific identifiable group of organisms have a role in soil processes. Litter breakdown is accomplished by many disparate groups of organisms such as crabs, millipedes, cockroaches, and so on. Within these groups there is always some marginal overlap in feeding-niche parameters. Similarly, soil-feeding termites (which exhibit particularly high species diversity in African forests) produce significant methane fluxes and play an important role in P cycling and soil organic matter turnover. However, all these processes are also mediated by other animals and microbes, and strongly buffered by the biophysical pools of soil organic matter and ion exchange sites (Anderson 1994). Rate determinants of key processes, such as hydrologic pathways and erosion, are affected by the combined activities of microbes, animals, and plant roots on aggregate stability and soil structure (Silver et al. 2000).

Arable Land

Intensive tilled arable farming systems occur worldwide, but are most prominent in industrialized countries in temperate regions. Intensive tilled agriculture bears little resemblance to highly complex unmanaged ecosystems. Arable soils are extremely disturbed by cultivation, fertilizers, and pesticides, all of which alter their biophysical composition (Anderson 2000). Plant communities of these conventionally managed, tilled agroecosystems are unnaturally simple. Intensive tillage farming negates the activity of many soil organisms, such as earthworms (Marinissen & de Ruiter 1993), ants (Decaens et al. 2002), and mycorrhizal fungi (Helgason et al. 1998), but some soil organisms continue to play an important role in the decomposition of crop residuals or organic manure, and are involved in the processes of nitrification and pesticide degradation (Anderson 2000).

In intensive tilled agriculture, short rotations and the use of high-yielding crops can trigger development of soil-borne pathogens and viruses, nematode infestations, and soil-dwelling insects, causing major yield losses. Overcoming these outbreaks requires the breeding of resistant crop varieties, the frequent use of soil pesticides (Epstein & Bassein 2001), or the development of novel biological control practices (Whipps 2001). In contrast, in traditional small-holder (predominantly tropical) farms, the role of organisms is apparent and the activities of a few species of earthworms, termites, and other fauna dominate soil communities. After hand tillage (mostly on tropical farms) or abandonment of the site in shifting agriculture, soil earthworm communities usually recover rapidly (Decaens & Jimenez 2002). This is in contrast with the microbial recovery of soil communities after intensive tilled farmed systems in temperate zones (Siepel 1996; Korthals et al. 2001).

Intensively tilled arable soils are primarily controlled by abiotic factors. For example, erosion is a constraint to soil fertility in 10 to 20 percent of the world's regions (Bot et al. 2000). In parts of the tropics, seasonal rains can cause severe soil erosion, degrading soils and making agriculture less sustainable. The adoption of minimum tillage or organic farming in some cropping systems to improve soil organic matter, or the adoption of erosion control for improved soil moisture, results in a significant recovery of soil biodiversity (Mader et al. 2002). However, this recovery, including the return of earthworms, has not been consistently linked to improvement in crop yields (Brown et al. 1999; Mader et al. 2002).

Arable soils may sequester carbon, but this ecosystem service depends on a combination of climatic factors (temperature/moisture conditions), topography and soil properties (texture, clay content, mineralogy, acidity) (Robert 2001), deposition history (VandenBygaart et al. 2002), and management strategy (Brye et al. 2002).

Management Trade-Offs and Functional Diversity in Grassland, Forest, and Arable Land

In evaluating the consequences of management options for ecosystem services, it is impossible to consider all possible combinations of potentially interacting factors, such as soil type, vegetation type, and climate. Therefore specific examples were chosen, which we believe may be adopted for any type of ecosystem at any place on earth. Tabulating our information (see Tables 2.2–2.4) gives us the opportunity to quickly assess where specific soil organisms contribute positively, neutrally, or negatively (relative to abiotic factors) to the sustainable delivery of specific ecosystem goods or services.

In the specific sections for grassland, forest and arable land, we discuss trade-offs for management versus no (or extensive) management. In the case of arable land, we compare tilled land with non-tilled land. There is little consistency across studies with regard to the role of species diversity within functional groups of soil organisms on ecosystem processes (Mikola et al. 2002). However, our method of representation enables us to draw some general conclusions about the importance of functional diversity of soil organisms for the sustainable delivery of ecosystem goods and services in the three major types of ecosystems considered.

Temperate systems were selected because they are the best characterized. We appreciate that the assessment is imperfect, as perceptions of the services provided by each system in a locale differ and we therefore cannot list and evaluate precisely the same services in each ecosystem. We have compared the extremes of unmanaged and managed systems to highlight the service trade-offs, which are implicitly brought about by management. In reality, there is usually a gradient of possible interventions.

The relative importance of ecosystem goods and services ranking from −3 (strongly negative) to +3 (strongly positive) under both unmanaged (pristine, semi-natural, or zero-input) and managed (with significant human inputs and/or anthropogenic disturbance) states are presented. We compare three specimen temperate ecosystems: grassland, forest, and arable land. Under each category we have distinguished between biotic (mediated by living organisms) and abiotic (mediated by chemical, physical, and geologically historical factors, over which living organisms have, essentially, no overwhelming control on the short- and medium-term) processes. This is done by allocating each an asterisk rating from * (weak) to *** (strong) relative importance in determining the impact of the biotic and abiotic process on the specific ecosystem good or service identified. Habitat support functions, such as decomposition, bioturbation, and so on, are included in the allocation of drivers to biotic and abiotic categories. This level of resolution indicates those systems in which the manipulation of soil biodiversity (within or between groups of soil organisms that perform specific functions) could be effective in reinforcing a particular service, and where the services appear most vulnerable to changes in the biological soil community (see Wardle et al., Chapter 5, where some processes have been valued slightly different owing to the comparison between non-perturbed and perturbed systems).

Grasslands

Unmanaged and lightly managed grasslands can be seen as having a low rank for ecosystem service for products directly consumed by human beings, but they often sustain populations of large herbivores that serve as food and other animal products used by humans (Table 2.2). Unmanaged grasslands are extensive in the tropics, and range along a broad gradient of precipitation that strongly influences both production and biological diversity, aboveground and belowground, merging into parkland and, ultimately, forest at the wet end. These grasslands are often the guardians of important watersheds. They have a disproportionately high aesthetic value, deriving from an inherently high biodiversity, the visibility of some wildlife, and a large recreational potential (McNaughton et al. 1983). Where grasslands are the product of low precipitation, management options are limited because animal production is ultimately a product of (inverse) stocking density (Ruess & McNaughton 1987). However, in mesic systems, where many managed grasslands are the product of historical forest clearance and/or intensive grazing, production can often be enhanced in proportion to fertilizer input and manipulation (through tillage and seeding) of plant species composition. Such management carries major implications for water quality (reduced by large rises in dissolved C and N compounds in runoff water) and for greenhouse gas emissions (Williams et al. 1998). There is also, arguably, a fall in aesthetic value and restrictions in the availability of land for recreational purposes.

A large functional diversity of soil organisms in grassland soils contributes to the sustainability of ecosystem goods and services. In unmanaged grasslands, there is a strong positive role of soil organisms, whereas intensified grassland management results in reducing the role of soil organisms in the decomposition of soil organic matter and the mineralization of nutrients due to the addition of mineral fertilizers or liquid manure (Bardgett & Cook 1998). Reduced activity of burrowing soil organisms decreases the contribution of managed grasslands to water storage, which results in enhanced runoff of rainwater and, consequently, flooding in downstream areas (Bardgett et al. 2001). In managed grasslands, nitrifying microorganisms may contribute to the leaching of mineral nitrogen to surface water or groundwater because the amount of available mineral nitrogen exceeds the uptake by plants (Smith et al. 2002). The predominance of bacterial-based soil food webs reduces the capacity of managed grasslands to act as sinks for carbon (Burke et al. 1989; Brye et al. 2002; Mader et al. 2002).

The possible management interventions are mowing, stocking density, fertilization, pesticide application, seeding, tillage, and enclosure. In reality, there is a gradient of management from light to intensive, and also a major difference between dryland grassland systems and mesic ones. The total number of land uses imposed on managed grasslands is very large. Grasslands may also be created on a temporary basis when tropical forest is felled, or permanently by invasive species if the soil is subsequently exhausted

Table 2.2. Provision of goods and services in a temperate grassland ecosystem.

This ecosystem is considered in its unmanaged and managed states. A rank from −3 (strong disservice) through 0 (neutral) to +3 (strong service) is given for each good or service, indicating its value to human societies. Under each category we have distinguished between biotic (mediated by living soil organisms) and abiotic (mediated by chemical, physical and geological, climatological or historical factors, over which living organisms have, essentially, no overwhelming control on the short and medium term) processes. The relative contributions of biotic and abiotic processes (= ecosystem functions, including anthropogenic inputs and perturbations) to each good or service is given by asterisks * (small) to ***(large). Note that in Chapter 5, Tables 5.A1–5.A3 have been developed using the same principle, but there the relative contributions of abiotic and biotic processes have sometimes been slightly differently valued. This is due to the comparison between unmanaged and managed.

	Unmanaged Grassland #			*Managed Grassland* ##		
Goods or Services	*Rank*	*Biotic*	*Abiotic*	*Rank*	*Biotic*	*Abiotic*
Food production						
Plant products	0			0		
Animal products	2	*** decomposition, bioturbation, organic matter transformation + nutrient cycling, resistance to pests & diseases	** soil type, topography, fire, climate	3	* nutrient transformation, nitrification, etc.	*** chemical inputs, soil type, topography, climate
Water quality (Riparian context: quality to local streams and rivers)	2	*** retention of N in biomass, physical stabilization, interception of run-off, soil organisms	** soil type and cover, topography, fire, climate (esp. precipitation)	−3	*** nitrification, Phosphate liberation, DON, DOC, microbiological pollution of runoff, soil organisms	*** soil type and cover, topography, fire, climate (esp. precipitation), compaction
Water volume† (Flow to watersheds)	2	*** moisture retention by OM, evapotranspiration, soil organisms	** soil type and cover, topography, fire, climate (esp. precipitation), infiltration, runoff	−2	* moisture retention by organic matter, soil organisms	*** soil type and cover, topography, fire, climate (esp. precipitation), flood, run-off, infiltration, compaction

(continued)

Table 2.2. *(continued)*

	Unmanaged Grassland [#]			*Managed Grassland* [##]		
Goods or Services	*Rank*	*Biotic*	*Abiotic*	*Rank*	*Biotic*	*Abiotic*
Fiber (e.g., wool, leather)	2	*** decomposition, bioturbation, organic matter transformation + nutrient cycling, resistance to pests & diseases	*** soil type, topography fire, climate	1	* nutrient transformation, e.g., nitrification etc.	*** chemical inputs, soil type, topography, climate
Recreation	2	*** wildlife	** landscape	1	* wildlife, hiking, etc., according to habitat	*** amenity value reduction, e.g., topography amendment, fencing, denial of access
C sequestration (storage of carbon in biomass or soil organic matter, mitigating global warming)	2[‡]	*** organic matter formation/accumulation, $CaCO_3$ deposition	** complexing organic matter, texture, fire, $CaCO_3$ deposition	1	** net C accumulation (despite bacterial based foodwebs enhancing C loss)	** complexing organic matter, texture, fire, $CaCO_3$ deposition
Trace gases and atmospheric regulation (production of CH_4 and Noxides by microbes, also oxidation of CH_4)	2	*** maintenance of C and N balances	** texture, climate, pH	–3	*** nitrifiers, denitrifiers,loss of CH_4 oxidation	** texture, climate, pH

[#] includes lightly managed freerange grasslands with no fertilizer and pesticide inputs, excluding winter livestock feed.

[##] intensively managed animal and plant production systems with fertilizer and pesticide inputs and/or irrigation.

[†] not including charging of groundwater.

[‡] because of higher accumulation of surface and subsurface organic matter.

through subsistence agriculture. Unmanaged grasslands are mainly used for free-range animal production.

In conclusion, our example shows that in the type of grasslands considered, the largest impacts of management on ecosystem goods and services are on water quality and quantity and on trace gases. There may be a management trade-off between enhanced production and increased leaching and trace gas production, but in this trade-off the total area needed for food production as well as the price of land will undoubtedly play an important role.

Forests

Unmanaged forest ecosystems provide a diversity of ecosystem goods and services, and their ranks are moderate (food production) to strongly positive (e.g., fuel/energy, recreation, carbon sequestration, and regulating trace gases) (Table 2.3). Biotic and abiotic processes have almost equal contributions to the rate or efficiency of the delivery of these goods and services. Plant roots play an important role in the regulation of the quality and quantity of water volume and erosion control, whereas soil bacteria are particularly important for the regulation of the trace gases in the atmosphere (Wang & Ineson 2003). Mycorrhizal fungi play an important role in the formation of organic matter in coniferous forests (Smith & Read 1997), whereas earthworms have some impact in deciduous forests (Lavelle et al. 1997).

In managed forests, the presence of soil pathogens, parasites, decomposers, and N_2 fixers is a more important factor, especially in monospecific stands for timber or fuelwood production (Waring et al. 1987). On the other hand, there are fewer natural sources of food, a less diverse range of macro- and microorganisms, and fewer soil habitats in managed forests. Conversely, the importance of abiotic factors in controlling the delivery of these ecosystem goods and services is little changed in managed forests, except for the potential role of external inputs, such as fertilizers and lime, in altering trace gas production, mineralization, and nitrate leaching.

Intensifying forest management decreases the potential for carbon sequestration into the soil, and it also reduces sources of biochemicals and medicines by providing fewer habitats for other organisms. There is considerable diversity of functions of soil organisms in unmanaged and managed forests. Soil fungi play a more substantial role in decomposition in forests than in grasslands, and the role of plant roots in the delivery of ecosystem goods and services, for example in erosion control, is also more prominent. Forest management has relatively little effect on functional diversity of soil organisms, but it may change the importance of symbiotic nitrogen-fixing microorganisms to nitrogen availability, especially when monocultures of nitrogen-fixing trees are established. Humans can affect the diversity of mycorrhizal fungi, as can atmospheric deposition (Smith & Read 1997).

In conclusion, trade-offs for forest management occur within narrower margins

Table 2.3 Provision of goods and services in temperate unmanaged and managed forest ecosystems.

For further explanations, see Table 2.2.

	Unmanaged Forest			*Managed Forest*		
Goods or Services	*Rank*	*Biotic*	*Abiotic*	*Rank*	*Biotic*	*Abiotic*
Food production	1	*** decomposition, fungal diversity	* soil type, pH	0		
Water quality and volume; flood and erosion control	3	*** evapotranspiration *** plant composition ** hydraulic lift *** rooting depth * soil organisms, bioturbation	*** shading/cover *** stabilization *** runoff, infiltration *** slope, topography soil physical properties, soil type	3	*** evapotranspiration *** plant composition ** hydraulic lift *** rooting depth * soil organisms, bioturbation	*** shading/cover *** stabilization *** runoff, infiltration *** slope, topography, soil physical properties, soil type
Fiber	2	** net primary production	*** soil type, climate	3	** net primary production	** soil type, climate *** chemical inputs
Fuel/Energy	3	** net primary production	*** soil type, climate	3	** net primary production	** soil type, climate *** chemical inputs
Biochemicals and medicines	3	decomposition ** microbial diversity		0		
Habitat provision	3	*** intrinsic biodiversity, NPP, ecosystem engineers	*** soil type, topography, climate	2	** intrinsic biodiversity, NPP, ecosystem engineers	*** soil type, topography, climate

Waste disposal	0			0		
Biological control	2	*** intrinsic biodiversity	** soil type and properties	1	** intrinsic biodiversity	* soil type and properties
Recreation	3	*** wildlife	** landscape	2	*** wildlife	** landscape
C sequestration						
Deciduous	3	organic matter formation/accumulation * litter quality * earthworms *** roots	* texture, climate, $CaCO_3$ deposition	2	organic matter formation/accumulation * litter quality * earthworms * roots	* texture, climate, $CaCO_3$ deposition
Coniferous (NB: no worms)	2	organic matter formation ** litter quality * roots **/*** mycorrhiza * pathogens	** texture, climate ** fire $CaCO_3$ deposition	1	** litter quality * roots ** pathogens **/*** mycorrhiza	** texture, climate */** fire, $CaCO_3$ deposition
Trace gases and atmospheric regulation	3	*** maintenance of C and N balances	** texture, climate, pH	3	*** nitrifiers, denitrifiers, CH_4 oxidation	** texture, climate, pH

than they do for grasslands, as most options differ by a unit of only one. However, forest management has large implications for biodiversity within forests, for example, the removal of wood, and/or soil erosion following large-scale tree felling (see Ineson et al., Chapter 9), can have important impacts on soil biodiversity and soil ecosystem services. Management for biodiversity and ecosystem functioning will have to balance the trade-offs of selective tree cutting against felling of entire forest stands (see Ineson et al., Chapter 9). Selective felling of trees leaves a large proportion of the forest system intact, while complete felling can result in complete loss of topsoil due to erosion. Moreover, selective forest management promotes more attractive forests for recreational use.

Arable Land

Agriculture ranges in management from non-tilled, or lightly managed, lightly cultivated fields and food-gathering systems to highly managed tilled fields that receive large inputs of pesticides, fertilizers, energy in tillage, and even irrigation water. Another type of distinction is conventional versus biological (or organic) agriculture. We choose soil tillage involving heavy soil disturbance as an example, which has a major impact on soil organisms (Marinissen & de Ruiter 1993; Helgason et al. 1998). It has been demonstrated that high yields can be obtained with monocropping and intensive tillage management, where natural biodiversity is overridden by high inputs of nutrients and pesticides (Tilman et al. 2002). This, however, often comes with high costs to the environment in water pollution by nitrates and toxic, partially decomposed, chemical inputs (Carpenter et al. 1998). It also can result in fluxes of CO_2 from fossil fuel combustion and N_2O (Hall et al. 1996), one of the most active greenhouse gases (Table 2.4).

Biodiversity, or the variety of life forms, does not necessarily increase the sustainable delivery of ecosystem goods and services in agriculture. Nitrifiers and denitrifiers are responsible for huge losses of nitrogen from the soil system while leading to pollution of the groundwater with NO_3 and the atmosphere with N_2O (van Breemen et al. 2002). Many closely coupled natural systems operate essentially without these organisms in that they have an NH_4-N nutritional system (Coleman & Crossley 1996). Nitrogen fixers are essential for food production, especially in farming systems where mineral fertilizers are costly and organic fertilizers are insufficiently available. Soybeans are considered a desirable crop because of their N-fixation potential that supplants the need for N fertilization. They, however, produce little crop residue that is easily degraded and thus are not desirable for carbon sequestration unless grown in a cropping sequence with a high residue producer such as maize, unless the maize shoots are used as fuel.

On average, most systems that have and produce soil biodiversity also favor carbon sequestration, good soil tilth, and high fertility (Sperow et al. 2003). This can occur in non-tillage systems and in systems with increased cropping complexity and perennial crops, as well as in systems where nutrient inputs are efficiently utilized. Site-specific

Table 2.4 Provision of goods and services in non-tilled and tilled temperate arable land ecosystems.

For further explanations, see Table 2.2.

	Non-Tilled Arable			*Tilled Arable*		
Goods or Services	*Rank*	*Biotic*	*Abiotic*	*Rank*	*Biotic*	*Abiotic*
Food production (plant + animal)	3	* plant breeding (roots and residues), bioturbation	*** climate, chemical inputs	3	*** plant breeding (roots and residues)	* climate, tillage, chemical inputs
Water quality	–1	* nitrification, pesticide degradation, leaching by biopores	** topography, climate, infiltration, runoff, soil type and cover	–2	* nitrification, pesticide degradation and mobilization	*** topography, climate, infiltration, runoff, soil type and cover, leaching, volatilization of NH_4
Water volume	–1	** moisture retention by OM, evapotranspiration, biopores by soil organisms	** topography, climate, run-off, soil type, cover		* moisture retention by OM, higher evapotranspiration and less biopores by soil organisms	*** topography, climate, run-off, soil type
fiber	3	* plant breeding (roots and residues), bioturbation	*** climate, chemical inputs	3	*** plant breeding (roots and residues)	* climate, tillage, chemical inputs
Waste disposal	1	** decomposition, co-metabolism, build-up of intermediate toxic products	* volatilization, water regime, soil properties, sequestration, incorporation by machinery	3	** decomposition, co-metabolism, build-up of intermediate toxic products	** volatilization, water regime, soil properties, sequestration, incorporation by machinery

(continued)

Table 2.4 *(continued)*

	Non-Tilled Arable			*Tilled Arable*		
Goods or Services	*Rank*	*Biotic*	*Abiotic*	*Rank*	*Biotic*	*Abiotic*
Biological control	−1	** crop rotation, predators, bacterial and fungal antagonists, mycorrhizal fungi, GMOs	* pesticides	0–1	** crop rotation, predators, bacterial and fungal antagonists, mycorrhizal fungi, GMOs	** pesticides, soil tillage
Recreation	1–2	** choice of crop species, composition of field margins	** landscape	1–2	** choice of crop species; composition of field margins	** landscape
C sequestration	0–1	* decomposition	* texture, nature of clay minerals, climate	−1–0	* decomposition	** topography, texture, nature of clay minerals, soil structure
Trace gases and atmospheric regulation	−1	** ammonification, nitrification, fungal decomposition	** moisture regime, soil structure	−3	** ammonification, nitrification, bacterial decomposition	** moisture regime, soil structure

exceptions require careful management. Non-tillage agriculture, when used with certain soils, increases the incidence of plant diseases. It can also lead to wet cold soils that delay planting. Increased cropping complexity and cover crops can have significant advantages in many agroecosystems, especially where the degree of mechanization is relatively low. On some soils, however, the moisture used by the cover crop results in lower crop yields and if not properly managed some cover crops can compete with the primary crop and act as weeds (Locke et al. 2002).

In conclusion, management trade-offs for arable land, for example non-tillage versus tillage, need to balance between the efficiency of fertilizer inputs and obtaining high crop yields. Indirectly, the price of land and labor will be weighed against that of fertilizer, pesticides, and the costs related to the resulting environmental pollution, such as groundwater contamination. Non-tillage favors soil C sequestration, but can enhance the need for disease control. When comparing conventional (highly intensive) agriculture with organic (or biological) agriculture, similar trade-offs may occur, possibly with a stronger emphasis on reduced outputs versus the price of land.

Discussion and Conclusions

Soil organisms play a major role in the delivery of ecosystem goods and services that are crucial for supporting human societies and for the sustainability of natural and managed ecosystems. Soil organisms act on very small scales, but their effects may range from local (diseased plants, nutrient mineralization) to very large scales (plant succession, carbon sequestration, production of trace gases that contribute to global warming). The diversity of soil organisms may matter more for a process that is accounted for by only a few species than for a process that is accounted for by many species. However, empirical evidence on effects of species diversity on ecosystem processes is still relatively rare and does not yet allow generalizations. It is probable that the diversity of functions is more important for the sustainability of ecosystem goods and services than species diversity *per se,* but this area is still wide open for further studies.

The role of soil organisms is more prominent in grasslands (especially natural ones), forests, and low-input (no-till) arable land than in intensively managed grasslands and arable land. However, the relative importance of soil organisms for the performance of ecosystem processes (as compared with the importance of abiotic influences) differs along climatic gradients or between soil types. There are also differences between the relative contributions of different taxa of soil organisms to ecosystem processes along climate gradients or between soil or vegetation types. In cold areas, for example, soil microorganisms play a lesser role in the decomposition of organic matter, whereas soil fauna have a more dominant role. Earthworms are key species in mesic grasslands, but enchytraeids are crucial in coniferous forests and some arable land.

Human interventions, such as plowing, fertilization, and using pesticides, often lead to shifts in the major decomposition channels or to a by-passing of the role of soil organisms. In intensively fertilized tilled arable land, the decomposition pathway is bacteria-based and the role of symbiotic mutualists (mycorrhizal fungi and nitrogen-fixing microorganisms) is largely redundant. Stability of nutrient pools in these systems may be achieved by high-input measures, but this results in, for example, the leakage of nutrients to ground- and surface water. In these cases, human activity to enhance the delivery of ecosystem goods, such as food production, result in the loss of ecosystem services, such as water purification occurring in soils.

Other human-induced changes, such as land use change, deforestation, soil drainage, erosion, enhanced temperature, and increased CO_2 concentrations may all affect soil ecosystem goods and services by affecting soil organisms either directly or indirectly. Erosion will affect soil communities through the direct loss of habitat, whereas rising temperature and CO_2 concentration may lead to more incipient changes in soil communities and, therefore, of the functioning of soil systems and the sustainability of the delivery of ecosystem goods and services.

There are clearly management trade-offs for the role of soil organisms in the delivery of ecosystem goods and services. We do not have much evidence that these trade-offs act through the loss of species diversity, but this is mainly due to our limited knowledge on the diversity of, for example, soil microbial communities and consequences for ecosystem processes. Management trade-offs clearly act through effects on the diversity of functions. Intensive tillage farming practice reduces the abundance of earthworms, which negatively affects both the water-holding capacity of soils as well as the population of mycorrhizal fungi. This, as well as changes in the soil due to deforestation, may enhance flooding incidence in lowlands due to increased peaks in run-off water.

The template that we have developed for the analysis of the contribution of soil organisms and abiotic soil factors to the organization of soil processes, and to the delivery of ecosystem goods and services, is applicable to a wide range of environmental contexts. The examples that we have presented, however, apply to temperate systems. The approach adopted here may well prove valuable for comparison with tropical systems, where the potential for soil biotic diversity may be higher.

The obvious weakness of the present approach is that the relative importance of the services and the relative contributions of biotic (essentially manageable) and abiotic (only partially manageable) processes are expressed only in comparative terms. To make absolute (monetary) valuations possible, some of the services (e.g., food and fuel production) could be costed for a given local economy, while other services could be assigned financial status from these by reference to the relative importance we have suggested. The difference between these biological valuations and other schemes of costing, which are the stock-in-trade of economists, is that in each defined ecosystem some processes are amenable to management, and others are not. The prices of services, which essentially reflect their availability for manipulation by humans, should be adjusted accordingly.

Research Needs and Recommendations

Soil biota provide many services in a wide range of terrestrial ecosystems. Our knowledge of how to manage and protect species in the soil and the processes that they drive is, however, limited (Wall et al. 2001). Areas that need further studies in order to enhance the effectiveness of management are:

1. *Incorporate the role of soil organisms and soil biodiversity in crop protection.* Soil organisms influencing plant defense against aboveground insects and pathogens and soil management may, therefore, influence plant protection in arable ecosystems.
2. *Acknowledge the role of soil biota in restoration and conservation of aboveground biodiversity.* Soil organisms are strongly involved in primary and secondary succession and in the regulation of plant species diversity in unmanaged ecosystems. More studies are needed to determine how these processes operate and how they can be used and influenced in order to reach management goals, such the conversion from arable land to more natural systems in order to conserve and protect biodiversity.
3. *Use soil organisms in bioremediation.* Many soil organisms can play a role in cleaning polluted soils and the sheer diversity of microbes provides ample opportunities for reducing pollution loads in contaminated soils.
4. *Use food web modeling to improve the conservation and use of soil nutrients.* Soil ecology has been strong in developing functional group approaches and in modeling the interactions between functional groups in order to assess the stability of ecosystem processes. These food web models may be further developed for use in testing land management options—for example, in relation to land use history, current status of the soil abiotic and biotic conditions, and management goals.
5. *Communicate the role of soil biota and soil biodiversity to land managers and policy makers.* Soil organisms for too long have been "out of sight, out of mind." However, increasingly, land managers and policy makers express interest in the sheer diversity underneath their feet. Communication of the relation between soil biota, soil biodiversity, ecosystem processes, and ecosystem services and practical recommendations are, therefore, of top priority. We hope that this chapter will inspire end users and stakeholders to start collaborative actions leading to enhancing both knowledge about soil biodiversity and ecosystem functioning and the application of these results in order to improve the sustainability of ecosystem goods and services as provided by the soil biota.

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Appendix 2.1

Narratives to Tables 2.2, 2.3, and 2.4

NARRATIVE TO TABLE 2.2 ABOUT GRASSLANDS

- *Food production:* In both unmanaged and managed grasslands, plant products are considered insignificant because plant materials are harvested by herbivores, but they would be affected by biotic and abiotic factors in the same way as animal products. Management shifts decomposition and organic matter transformations toward bacterial dominance, with a reduction of faunal diversity, especially macroarthropods.
- *Water quality:* Water quality refers to runoff to streams. The context is essentially riparian; as in dryland systems, potential evapotranspiration exceeds precipitation. Different dynamics exist in mesic systems. Simplification of soil organisms reduces the retention of nutrients (C, N, and P) in living biomass. Nutrients released or transformed may be directed more into runoff than may percolate to the water table. Higher stocking densities introduce undesirable bacteria into runoff and reduce infiltration by compacting the soil.
- *Water volume:* Factors reducing evapotranspiration will be paramount in dryland systems. These include plant diversity (root depth, root architecture, and hydraulic lift), organic matter stratification and particle size distribution, and biopore formation by macrofauna.
- *Other products:* Fiber production (e.g., hides, carcass contents) is not an objective in managed grasslands, but a by-product. Animal production is roughly inversely proportional to population density in unmanaged grasslands (i.e., it is a function of plant production, which in turn depends on nutrient recycling and transformations by microorganisms).
- *Recreation:* The service rank of unmanaged grasslands for recreation is derived from both wildlife and the aesthetic value of biological diversity and landscape heterogeneity. Managed (and fenced) grasslands are harboring some wildlife, and in some areas access is given to hiking. Access to fenced land may be the subject of legal disputes, and landscape simplification or dissection reduces overall aesthetic value, but this has enormous potential for recreation in many industrialized countries.
- *C sequestration:* A managed grassland means it has been tilled. The C dynamics of untilled pastures are uncertain. Again, a large difference would be expected between the responses of dryland and mesic grassland systems. Accumulation of organic matter at the surface of the soil profile is greater in unmanaged systems with stratification downward and more C directed into complex long-term stable pools by fungal-dominated organisms.
- *Trace gases and atmospheric regulation:* The C and N fluxes of unmanaged grasslands are probably not very significant in terms of the global cycles of these elements, as out-

puts of greenhouse gases to the atmosphere by components of the soil organisms (fungal decomposers, nitrifiers, and denitrifiers) are restricted by corresponding sequestrators (primary producers and nitrogen fixers). Fertilizer input (chemical or animal dung) causes a large increase in both nitrification and denitrification (according to context), from which process greenhouse-forcing NO_x gases are by-products. Disturbance of any kind (including compaction) strongly reduces CH_4 oxidation by archaea in soils.

NARRATIVE TO TABLE 2.3 ABOUT FORESTS

- *Food production:* A side benefit especially of unmanaged forests. Fungal fruiting bodies are a forest food product. Fungal diversity in unmanaged systems may be higher due to the higher diversity of trees and other plants than occurs in managed systems. Many species of soil invertebrates (e.g., ants) are an important food source for birds/wildlife, which in turn are important for recreation. Soil pH is a moderately important determinant of fungal diversity. Managed beech systems also produce truffles.
- *Water quality and volume:* Flood and erosion control. Different plant species have widely different attributes, which can affect soil water quality and quantity (evapotranspiration, different rooting depths/architecture, hydraulic lift). Soil organisms can affect water quality through production of NO_3. Bioturbators affect soil physical properties, which, in conjunction with topography, affect runoff and infiltration.
- *Fuel:* When in the form of wood, fuel is a potentially important service of both unmanaged and managed systems. However, wood fuel may be more commonly extracted from unmanaged systems since managed systems are typically intended for fiber production.
- *Biochemicals and medicines:* Unmanaged forests are used extensively for bio-prospecting, particularly for microbial diversity, genes, and potentially useful products (antibiotics, yeasts, etc.) for industrial or medicinal properties. The diversity of genes, and of useful products, is likely to be related to the diversity of the forest.
- *Habitat provision:* Soil organisms encourage nutrient cycling for plant growth. Ecosystem engineers (e.g., earthworms) create new habitat and provide food for other animals.
- *Waste disposal:* Soil fungi and bacteria affect the accumulation of heavy metals in plants and indirectly into animals. Soil texture and drainage affects a system's ability to hold pollutants, pathogens, and heavy metals. However, we have ranked them with 0, as forests are not intended to be used for waste disposal.
- *Biological control:* Ants predate Lepidoptera pests; mycorrhizae and fungi discourage root pathogens. Water logging of soils encourages fungal pathogens such as root rot.
- *Trace gases and atmospheric regulation:* Soil organisms (nitrifiers, denitrifiers, methane oxidizers) are important to trace gas production and to scrubbing the atmosphere of NO_x, N_2O, SO_2, CH_4, and NH_x. Soil pH, texture, and structure provide anaerobic

microsites for trace gas production. Forest ecosystems are particularly important for methane oxidation. When fertilized or limed, the dynamics of emissions are changed: up to 10 percent of N fertilizers may be denitrified. There exists some doubt as to the organisms responsible for CH_4 in forest ecosystems, but the organisms responsible have been identified as type II methanotrophs. Forest ecosystems are well known to act as sinks for a variety of air pollutants, such as SO_2, NO_x, and NH_x. Diversity has been used as an indicator of aerial ecosystem pollution.

NARRATIVE TO TABLE 2.4 ABOUT ARABLE LAND

- *Food production:* Crop variety, rooting type, and the nature and composition of residues are critical to the quality and quantity of food service provided. Animal production is indirectly affected by the use of arable products for fodder.
- *Water quality:* No-till agriculture is considered to leach fewer nutrients to ground and surface water than occurs when the soil is tilled regularly. Topography is an important factor influencing water runoff, more in tilled than in non-tilled systems: soil tillage leads to exposed soil, which is sensitive to erosion.
- *Water volume:* Non-tillage systems have more biopores formed by earthworms than tilled systems, which benefits water storage volume. Moreover, non-tilled systems are less sensitive to topography than tilled systems because of constant surface cover. On slopes, for example, the direction of soil tillage (along or across altitude lines) is also crucial for runoff of surface water.
- *Other products:* A number of crop plants are used for fiber production (cotton, flax), and effects of biotic and abiotic processes are similar to those for food production.
- *Waste disposal:* Detoxification of waste products is lower under no-till systems because wastes cannot be incorporated, leading to volatilization from the soil surface. The role of soil biota, however, is higher than in tilled systems, where the waste may be directly introduced into the soil. In addition, under no-till systems, concentrations of intermediate toxic products and pesticides can build up in surface soil layers, along with organic matter and nutrients.
- *Biological control:* We define biological control as control of pathogens/weeds by another organism. Rotations in tilled conditions—through maintaining microbial activity and diversity, and through disrupting disease and arthropod cycles and also mycorrhizal networks—improve biological control more in till than in no-till monoculture. However, multi-year rotations may not be economical. Earthworms can have a negative effect on plant parasitic nematodes: for example, in India, joint management of earthworm communities and organic resources doubled tea production while regenerating degraded soils. The effect of earthworms is hypothesized to be obtained through different processes, including suppression of nematode parasites and release of plant growth promoters through enhancement of mycorrhizae. There is little known on the effects of biological agriculture and landscape management (small-scale

or fragmented landscape versus large-scale landscape) on soil-borne disease management. However, whereas no-till conventional agriculture uses herbicides to control weeds, in organic agriculture (e.g., Brazil), cover-crops are used to kill weeds. Effects of GMOs are currently strongly disputed, and the potential solution of GMOs for one problem (weeds) may enhance others (more disease incidence). Therefore, we have weighed the GMO effect neutral.

- *Recreation:* Our concept is habitat for soil biodiversity. The key biotic aspect here is how field margins and riparian areas are managed. Field margins managed for habitat not only harbor diversity, they can also act as refuges for biological control agents, especially predatory arthropods such as beetles. Landscape aspects are important for aesthetic value and crop species matter, since some crops (e.g., corn) do not allow landscape-wide views. Riparian areas managed for habitat enhance surface and groundwater quality. On average, we assessed the recreational value of tilled and non-tilled systems to be equal, especially due to landscape effects.
- *Carbon sequestration:* Carbon sequestration ranks slightly higher in non-tilled than in tilled systems, because the rate of decomposition of crop residues and roots can be slightly less. When the organic matter pool is in balance, effects of C sequestration will be neutral in most cases.
- *Trace gases and atmospheric regulation:* Soil structure is considered under abiotic factors only, though it is clearly a product of both abiotic and biotic factors, especially macro- and microengineers that form aggregates. Specific aspects of macrofauna can alter trace gas emission, for example, denitrification can intensify in earthworm casts.
- *Nutrient cycling:* The microbial community and their activity are essential for nutrient cycling and are moderated by the micro–food web. Synchrony of mobilization and immobilization depends on the dynamics of the micro–food web. The shift from a bacteria-based soil food web under till to a fungal-based food web in no till triggers an associated shift in the nematode and microarthropod assemblage, and alters the micro–food web.

  P-cycling is dependent on soil properties; for example, the amount and nature of clay, the nutrient content of the parent material, and soil enzymes. Cultivation (till) can decrease the enzymes (arylsulfatase and acid phosphatase) involved in S and P transformations. P uptake by mycorrhizae is variable, and is more important in no till systems.
- *Other goods and services:* We have not mentioned habitat provision, biochemicals and medicines, and fuel/energy in the table. These goods and services may indeed be provided by arable land, but these aspects are so context dependent that they are preferably explored in individual case studies.