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Vulnerability to Global Change of Ecosystem Goods and Services Driven by Soil Biota

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Soil biota play an essential role in the delivery of a range of ecosystem goods and services. However, it is important to recognize that ecosystems are not static, and that human-induced global change phenomena have the potential to alter the capacity of soil organisms to provide this contribution. Given that global change phenomena directly or indirectly impact the soil biota in some way (Wolters et al. 2000; Wardle 2002), the question that emerges is how these phenomena may alter the goods and services, driven by soil organisms, upon which we all depend.

Predicting the effects of global change on ecosystem goods and services requires explicit acknowledgment of the vulnerability of ecosystems, and therefore of the organisms that drive those ecosystems, to global change. This chapter focuses on the vulnerability of goods and services to global change. In assessing this, we use the definition of *vulnerability* provided by the Resilience Alliance (www.resalliance.org), which is "the propensity of social and ecological systems to suffer harm from exposure to external stresses and shocks," a definition that involves three components: (1) exposure to events and stresses, (2) sensitivity to such exposures, and (3) resilience owing to adaptive measures to anticipate and reduce future harm. We first discuss conceptual issues regarding vulnerability of soil organisms and processes to global change in terms of effects of spatial scale, the extrinsic and intrinsic determinants of vulnerability, and the mechanistic bases of how the belowground subsystem responds to global change. We then demonstrate, through worked examples, the degree of vulnerability of those ecosystem goods and services driven by soil biota to selected agents of global change.

The Overarching Role of Spatial and Temporal Scale

The study of the vulnerability of ecosystems to global change requires explicit consideration of spatial and temporal scale. Agents of global change simultaneously operate over a range of scales; some operate mainly in the short term at local scales while others are more pervasive (Table 5.1). Further, ecosystem services are delivered at different scales of time and space from the immediate release of nutrients in the vicinity of a root tip to infiltration of water and storage in capillary porosity for periods of months to years.

Ecological processes that sustain provision of these services also operate at a variety of scales. The diversity of scales and the match between scaling of processes and their outputs may significantly influence their vulnerability.

Soil ecosystem services depend either on the direct and immediate outputs of organism activities (e.g., nutrient release from digestive processes) or their longer-term effects on soil physical properties (e.g., water retention in soil pores built by bioturbators). They may also depend on the direct effect of abiotic processes that operate at large scales (e.g., porosity created by alternations of drying and rewetting cycles). Biological processes that sustain ecosystem services may operate at four different scales of time and space depending on their nature and location (Lavelle 1997):

1. *Short-term digestion-associated processes.* Digestion occurs in the immediate vicinity of microorganisms where exoenzymes are active, in the guts of invertebrates or in the rhizosphere soil close to active root tips. Such microsites are a few cubic microns to millimeters in volume and processes develop during periods of hours to a few days.
2. *Intermediate phase in fresh biogenic structures.* Microbial activation triggered during gut transit or mechanical mixing of organic materials with soil culminates in fresh biogenic structures, such as fresh earthworm casts or termite fecal pellets. Activity then progressively decreases during the few days or weeks following deposition.
3. *Longer-term scale of stabilized biogenic structures.* Some structures created by invertebrates or roots are highly compact. These structures are the components of stable macroaggregate structures that determine soil hydraulic properties and resistance to erosion (Blanchart et al. 1999; Chauvel et al. 1999). Their life span may extend over periods of months to years depending on their composition and the dynamics of soil structural features (Decaëns 2000).
4. *Soil profiles.* Biogenic structures combine with other structures and elements of soil to form soil horizons. In some cases, creeping of soil along slopes may be triggered

Table 5.1. Vulnerability matrix, showing how different global change drivers have effects on the belowground subsystem that may be manifested at different spatial scales.

Note that some drivers operate mainly at local spatial scales while others are more pervasive.

	Global Change Driver					
Scale	*Land Use*	*Agricultural Intensification*	*Climate Change*	*Pollution*	*Invasive Organisms*	*Urbanization*
Global	X		X			
Regional	X	X	X		X	
Landscape	X	X	X		X	X
Field	X	X	X	X	X	X
Patch	X	X	X	X	X	X
Single Unit	X	X	X	X	X	X

by an accumulation of surface deposits by soil invertebrates (Nye 1955). As long-term plant successional processes and pedogenesis operate, changes occur in soil organism communities and their effects on soil structure over whole watersheds and timescales of years to centuries (Bernier & Ponge 1994).

Vulnerability of ecosystem services to perturbations may be dependent on the scales at which processes and the services operate, and their comparative sizes. In theory, four different situations may occur depending on the various combination of short or large scale of either component:

1. *Short scale for processes and short scale for services.* In this case, the output of the process directly affects the service. This is the case for mineralization of nutrients by microbial digestion. In such a situation, any direct damage to the decomposer community or impairment of its activity has immediate consequences for the service. Vulnerability is high, although rapid reversibility may be expected as soon as processes are reinitiated.
2. *Short scale for processes and large scale for services.* Here, a disturbance is temporary in nature and does not impair the provision of service. This is the case for water infiltration and retention in soils. Temporary interruption of activities of those invertebrates and roots that create or rejuvenate aggregates of different sizes does not have important consequences for soil hydraulic properties (Alegre et al. 1996). Soil aggregates of biological origin, once stabilized, can be very resistant structures that last for long periods in the absence of drastic direct physical impacts. In this situation, vulnerability is minimal (Blanchart et al. 1999).

3. *Large scale for processes and short scale for services.* Disturbance of a large-scale process will impair the services for a long period. This is the case of salinization, in which soil translocation processes result in the migration of salts toward the soil surface (Luna Guido et al. 2000). In saline soils, biological processes are severely limited. These long-term processes, when achieved, may impair the service for long periods and even be irreversible in the order of decades. Vulnerability is high, and restoration of the service will depend on changes in biological communities by such processes as colonization or local adaptation and genetic selection, which can be very slow.
4 *Large scale for processes and large scale for services.* Vulnerability can now be considerable and restoration of ecosystem services is very slow. This is the case for erosion processes that may affect large portions of soils that can be restored only after a long period of soil formation through pedogenetic processes (Lal 1984). All services linked to the presence of a thick soil with well-differentiated horizons will be severely affected by such an event.

Extrinsic and Intrinsic Determinants of Vulnerability

Soil organisms vary considerably in their susceptibility to global change, and even the same taxonomic and/or functional group may vary in its response according to the nature, extent, and frequency and intensity of perturbation (Wall et al. 2001). Thus, the vulnerability of individual components of the soil fauna is context dependent.

Determinants of vulnerability are wide ranging, encompassing both intrinsic and extrinsic factors. Many of these are intuitive, and empirical assessments of vulnerability to a particular driver of global change are surprisingly rare (but see Ruess et al. 1999). One conspicuous gap in knowledge lies in the significance of species interactions in determining the vulnerability of specific organisms or the assemblages they constitute.

Among the intrinsic determinants of vulnerability is a suite of life-history traits including body size, life-cycle longevity, and host plant and habitat specificity. Soil organisms are more vulnerable to perturbations if they are large bodied (Wardle 1995; Eggleton et al. 1998). Within this domain, surface-dwelling and relatively sedentary taxa are particularly prone to changes in soil moisture and texture (e.g., Brown et al. 2001). The life-history traits of high dispersal and migratory ability tend to counteract local extinctions, though the efficacy of these traits in stemming population decline is dependent on local source pools and inherent landscape diversity (Warren et al. 2001).

Longer-lived taxa are particularly vulnerable to perturbation, since they have less chance to recover than multivoltine (producing several generations in one year) species. Within the invertebrates, soil-dwelling species are characterized by having longer generation times than their aboveground counterparts (Andersen 1987; Brown & Gange

1990), a trait that undoubtedly increases their susceptibility to change. The implications of the reduced mobility and dispersal and longer life spans of soil organisms are very apparent when trying to restore the lost diversity of a system. In the restoration of ex-arable land, it has been shown that the colonization and establishment of soil biodiversity lags behind that of aboveground organisms (Korthals et al. 2001). Organisms that are either food or habitat specialists are more susceptible to even minor changes in their resources. Strict host plant or vegetation structure specialist species may respond negatively to changes in the occurrence (Cherrill & Brown 1990) or quality of their resource (Masters et al. 1993), whereas generalist species may switch hosts or move to adjacent habitats with global change (Bale et al. 2002). Both spatial and temporal synchrony with their required resource is a pivotal requirement of specialist species, with even slight asynchrony potentially causing extinction. Specialism is therefore a key indicator of the extent and spatial scale of vulnerability to global change.

An organism's vulnerability is also related to its ability to withstand change, in terms of "flexibility" (resilience) or "rigidity" (resistance). These attributes will vary intrinsically, but also in response to local conditions. Species may be unchanged, susceptible and become locally extinct (depending on recruitment), opportunistic and increase their performance in the new environment, or elastic and change in the short term but then recover to their former level (Brown et al. 2001).

Extrinsic determinants of vulnerability reflect habitat characteristics, such as the diversity of habitat and landscape. It is a common assumption that mosaic landscapes (roughly defined as more than one land use or land cover per hectare) and the species they support are less vulnerable to perturbation and more likely to recover quickly from disturbance or depletion, but this is unproven. Small fragments of pristine ecosystems (for example patches of primary tropical forest as small as 0.25 ha) may retain high biodiversity, at least over the medium term, after isolation (de Souza & Brown 1994; Eggleton et al. 2002), but there are few measurements of associated processes and services, and long-term effects are largely unknown.

Mechanisms Underlying Vulnerability

Soil organisms and processes can be highly responsive to global change phenomena, and a variety of mechanisms are responsible. Below, we outline three main categories of global change drivers, which we consider briefly.

Belowground Responses to Different Global Change Drivers

There are those drivers that result from changes in atmospheric properties (e.g., CO_2 enrichment, N deposition, climate change), those that arise from direct manipulation of land (e.g., land use change, intensification), and those that involve shifts in organism presence or abundance (e.g., extinctions, invasions, outbreaks).

Of the human-induced changes in atmospheric composition, the enhancement of CO_2 concentration is arguably the most pervasive. Given the high levels of CO_2 in the soil, atmospheric CO_2 enrichment is unlikely to affect the soil biota directly, and effects of enrichment on the decomposer community are likely in the first instance to be plant driven. This can occur at the level of both the individual plant and the plant community. At the whole-plant level, CO_2 enrichment can promote soil organisms through increasing resource quantity, for example, by promoting NPP (Körner & Arnone 1992) and rhizodeposition (Paterson et al. 1996). Further, CO_2 enrichment can alter litter quality, frequently enhancing litter C:N ratios, although both positive and negative effects of CO_2 enrichment on decomposability of litters have been reported (Franck et al. 1997; Coûteaux et al. 1999). Elevation of CO_2 concentrations can also alter the role that soil fauna play in decomposition, since these organisms are more important in catalyzing breakdown of litter of poorer quality (Coûteaux et al. 1991). At larger spatial scales, CO_2 enrichment is also likely to alter plant community composition, frequently favoring plant species or functional types with faster growth and higher litter quality over slower growing plants (Collatz et al. 1998; Herbert et al. 1999). This is, in general, likely to favor decomposer activity.

Effects of CO_2 enrichment on the composition of the plant community directly alters the community of root pathogens and root herbivores, due to changed plant-soil feedback (Bever 1994). Trade-offs between plant growth rate and plant defense against herbivores and pathogens (van der Meijden et al. 1988) result in more specialist root herbivores and root pathogens following CO_2 enrichment. However, effects of root herbivores and pathogens are also influenced by factors other than resource availability and resource quality—such as the recognition of plant roots by pathogens, herbivores, and their natural antagonists—and by the ability of plants to culture and enumerate the antagonists of their enemies (van der Putten 2003). Litter with a high C:N ratio may not favor microbial decomposition, but it could still enhance specific microbial antagonists (Hoitink & Boehm 1999). Therefore, exposure of plant communities to CO_2 enrichment may lead to changed root pathogen and herbivore communities, reduced or more specialized activity of these root organisms, and to changed host recognition or altered exposure to the natural enemies of the herbivores and pathogens belowground.

Atmospheric N deposition also has positive effects on those soil biota that depend on plant derived resource quality through promoting NPP, and unlike CO_2 enrichment it often causes plants to produce litter with lower C:N ratios. Further, N deposition can have important belowground effects by altering the composition of the plant community, usually by favoring plant species that are adapted to fertile situations and that produce high-quality litter (Aerts & Berendse 1988). However, direct effects of N deposition on soil microbes can either promote or inhibit soil processes; chronic N deposition can either promote litter decay through enhancing microbial cellulolytic activity, or suppress it by inhibiting ligninolytic enzyme activity (Carreiro et al. 2000). Effects of N deposition on the root herbivore and pathogen community will be mediated primarily through the plant community, but changes in the physico-chemical soil properties may also exert direct effects on these soil organisms.

Global warming and associated climate change events resulting from atmospheric CO_2 enrichment can influence soil organisms directly, although the main effects of climate change on soil biota are again likely to be indirect and driven by plant responses. At the whole-plant level, increased temperature promotes the kinetics of nutrient mineralization, plant nutrient uptake, and NPP (Nadelhoffer 1992) that should in turn promote decomposer organisms. At the level of the plant community, elevated temperature has the capacity to promote plant functional types with either superior (Pastor & Post 1988; Starfield & Chapin 1996) or poorer litter quality (Hattersley 1983; Harte & Shaw 1995). In this light, the implications of climate-driven vegetation change for the decomposer subsystem are likely to be context specific. Global warming may also disrupt natural communities because of different dispersal and migration capacities of individual species (Warren et al. 2001). Migration of plant species without their natural root pathogens and herbivores may lead to enhanced abundance in the new territories, due to the escape from specific natural enemies and the presence of relatively aspecific mutualistic symbionts, for example, mycorrhizal fungi (Klironomos 2002).

Direct use of land by humans for production of food and fiber arguably has the greatest impact on terrestrial ecosystems of all global change phenomena. At the broad scale, forest, grassland, and arable systems differ tremendously in their functional composition of vegetation as well as disturbance regimes. This in turn has important implications for the composition, abundances, and activities of the soil organisms present; generally cropping systems contain lower levels of many components of soil fauna, microbial biomass, and organic matter than do comparable areas under forest or grassland (Lavelle 1994; Wardle 2002). Conversion of land to agriculture often has adverse effects on the performance of the decomposer subsystem, and artificial inputs are therefore required to substitute for services provided by soil biota. Agricultural intensification also influences the decomposer subsystem (De Ruiter et al. 1993; Giller et al. 1997). For example, agricultural tillage favored bacterial-based energy channels over fungal-based channels (Hendrix et al. 1986), promoted small-bodied soil animals relative to large-bodied ones (Wardle 1995), and altered the relative contribution of different subsets of the soil biota to litter decomposition (Beare et al. 1992). Comparable effects appear to result from intensification of forest management (Blair & Crossley 1988; Sohlenius 1996).

Another major land use change is extensification, or even the complete abandonment of production on arable land and grassland to conserve, or restore, former biodiversity (van der Putten et al. 2000). However, there has been little work on the restoration of diversity belowground. Soil communities respond more slowly to changes imposed by land abandonment than communities above ground (Korthals et al. 2001), and responses are often idiosyncratic (Hedlund et al. 2003). Therefore, besides dispersal limitations of many organisms to restoration areas (Bakker & Berendse 1999), slow development rates of the belowground community may be an important controlling factor of ecosystem services and goods provided by these newly developing restored ecosystems.

Alien species are most likely to alter community and ecosystem properties when they show large functional differences to the native species of the community being invaded. The functional attributes of most alien species do not differ greatly from those of native biota (Thompson 1995), but differences, when they do exist, can cause profound implications for both the aboveground and belowground components of the ecosystem. For example, invasion of the N-fixing shrub *Myrica faya* into Hawaiian montane forests lacking nitrogen fixing plants has important effects on ecosystem N inputs (Vitousek & Walker 1989). Introduction of deer and goats into New Zealand rainforests, which lack native browsing mammals, has caused large shifts in the soil food web composition and diversity, and in ecosystem C sequestration (Wardle et al. 2001). Invasion of European earthworms into those North American forests that lack a native earthworm fauna has been shown to alter soil microbes, fauna, and supply of plant-available nutrients from the soil (Hendrix & Bohlen 2002). Human-induced extinctions of organisms may also be of functional importance, but only in instances in which the lost species plays an important functional role. Historical examples include probable large-scale alteration of soil processes following vegetation change caused by extinctions of dominant megaherbivore species, for example in Siberia (Zimov et al. 1995) and Australia (Flannery 1994).

Soil organisms and processes are capable of showing a variety of responses to drivers of global change, and the nature of these responses is likely to be context specific. Different global change drivers do not operate independently of one another; a given ecosystem is likely to be affected by several drivers operating simultaneously. Interactions between different global change drivers (e.g., between CO_2 enrichment and N deposition [Lloyd 1999]or between invasive plants and CO_2 enrichment [Smith et al. 2000]) may have important, though largely unrealized, implications for the decomposer subsystem and for the interactions between plants, root pathogens, and symbiotic mutualists (Richardson et al. 2000). This will in turn affect those ecosystem services driven by soil organisms. Importantly, soil biota do not function in isolation, and ecosystems are driven by feedbacks between the aboveground and belowground biota (van der Putten et al. 2001; Wardle 2002; Bardgett & Wardle 2003).

Relative Vulnerability of Different Biotic Components of Communities

Subsets of the soil biota may differ considerably in terms of how they are affected by global change phenomena. Of these phenomena, the best understood for the soil biota is land use change, including intensification of land management practices. The degree

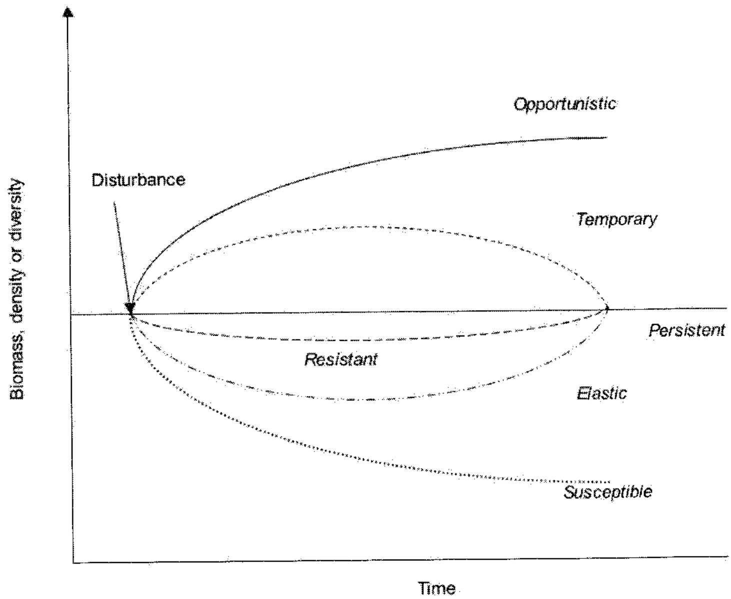

Figure 5.1. Different response dynamics of soil biota to disturbance (from Brown et al. 2001). The effect of a disturbance can result in changes to soil biomass, density, or diversity with very different results over time. This will affect the ecosystem services provided by the biota.

of impact of global change phenomena, such as land use change, is dependent on the organism's ability to withstand change, the organism's and ecosystem's resilience and resistance to the imposed changes, and the extent of the changes/disturbance imposed (difference from original environment). These can generally follow the different response strategies shown in Figure 5.1. Some organisms are susceptible to certain land management practices and become locally extinct, while others are opportunistic and take advantage of the modified conditions to increase their abundance, biomass, and activity. For example, the conversion of Amazonian rainforest to pastures north of Manaus led to the elimination of many (morpho-) species and groups of macrofauna, while one species of earthworm (*Pontoscolex corethrurus*) became the dominant soil macroorganism, reaching biomass values of up to 450 kg ha^{-1} (Barros 1999). This led to the progressive accumulation of macro-aggregates (worm castings) on the soil surface, dramatically decreasing soil macroporosity down to a level equivalent to that produced by heavy machinery, rendering it anaerobic and increasing methane emission and denitrification (Chauvel et al. 1999).

Some organisms may increase or decrease in numbers and biomass for only a short period (temporary or elastic) but then return to predisturbance proportions, while others remain unchanged or only slightly unchanged (persistent or resistant). For instance, if new land-use practices imposed maintain enough similarities to the previous ecosystem (e.g., conversion of native grass savanna to pastures), many soil organisms may resist the change, while some of those negatively affected in the land-preparation and conversion phase (tillage and seeding or transplanting) may eventually recover in the new system once proper soil cover and plant organic matter inputs are re-established (Jiménez & Thomas 2001).

Conversion from forest to agriculture usually results in an overall reduction in microarthropod populations (Crossley et al. 1992), but the response dynamics of component taxa varies. Continuous cultivation, rotations, monoculture, and application of pesticides soon eliminate species susceptible to damage, desiccation, and destruction of their microhabitats, especially those with a life cycle longer than one year, such as many oribatid mites. In contrast, practices such as drainage, irrigation, manuring, and fertilizer use encourage seasonal multiplication of species of prostigmatid mites and Collembola, and their predators, mesostigmatid mites (Crossley et al. 1992).

Several studies reveal that increases in the intensity of agriculture lead to reductions in the diversity of soil biota (Siepel 1996; Yeates et al. 1997). This diversity loss is not a random process. For instance, Siepel (1996) showed that declines in the diversity of soil microarthropods with increasing agricultural intervention were accompanied by dramatic shifts in the life-history characteristics and feeding guilds of the community. Loss of diversity in low-input agricultural systems was explained by the disappearance of drought-intolerant species because low-input grasslands are cut in summer, thereby increasing the chance of drought in the litter layer. However, the loss of species in high-input grassland was explained by the elimination of fungal-feeding grazers that were replaced by opportunistic bacterial-feeders. Moreover, abandoned high-input sites still lacked fungal-feeding mites, even after 20 years of management for nature conservation, due to the low population growth and dispersal rate of these species (Siepel 1996).

Effects of land-use practices on soil biota in turn exert profound effects on key ecosystem processes that they perform, and ultimately on the delivery of ecosystem services. Enhanced disturbance regimes tend to favor the bacterial-based energy channel of the soil food web over the fungal-based channel, and management practices which are known to favor the bacterial channel include conventional (vs. non) tillage (Hendrix et al. 1986), nitrogen fertilization (Ettema et al. 1999) and forest clear-cutting (Sohlenius 1996). Domination of soil food webs by bacterial energy channels leads to greater short-term mineralization rates of carbon and nutrients, leading to greater net losses of soil organic matter and reduced retention of nutrients in the soil in the longer term. The tendency of agricultural intensification practices to favor soil animals of smaller body sizes probably also has similar effects on ecosystem nutrient losses (Wardle 1995).

Therefore, effects of land-use practices on the composition of soil biota may have important flow-through effects on key ecosystem services provided by soil organisms, in particular those relating to the maintenance of soil fertility and plant-available nutrient supply.

Unfortunately, given the overwhelming diversity of soil organisms and their functions and interactions in soils, information on the response dynamics of various groups/taxa and species of soil organisms to land-use change and its possible effects on soil function is not available for many sites/land uses. Furthermore, there can also be important differences in the effects on the same organism/function to forces of change, depending on local climate or soil conditions. Processes occurring locally or influenced by organisms at a small scale are less likely to be influenced by change at a large scale, unless it undermines their populations or ability to maintain activity. However, cascading effects of loss of a particular organism or function within the ecosystem could have consequences far beyond the small scales at which they were initially operating.

Assessment of Vulnerability

Arable, grassland, and forest ecosystems are managed primarily for the purpose of providing material goods such as forage, food, and fiber. However, terrestrial ecosystems also provide a range of other goods and services, notably through the improvement of environmental quality (e.g., water purification, flood and erosion control, atmospheric regulation), recreational and amenity values, provision of habitats for species and conservation of biodiversity, and mitigation of anthropogenic CO_2 enrichment through sequestering carbon. The soil biota play an important role in the delivery of all of these services. This is in part because the above- and belowground components of terrestrial ecosystems are inextricably linked. Therefore, any global change agent that affects the soil community will affect not only the ability of the soil to provide services that are directly driven by the soil biota (e.g., soil carbon sequestration, prevention of leaching of nutrients), but also those that are driven by the plant community.

To illustrate the nature and mechanistic basis of vulnerability of ecosystem goods and services driven by soil biota to global change, we now present some examples. In Chapter 2, an assessment was made of the importance of contributions of soil biotic and abiotic factors to the delivery of ecosystem services in representative temperate arable tilled, grassland, and forest ecosystems. These were quantified on a scale of * (unimportant) to *** (highly important). In the present assessment, we considered, for each of these ecosystems, the vulnerability of each of those ecosystem services identified in Chapter 2 to three scenarios of global change: global change agents that (1) operate over large scales via the atmosphere (drought, resulting from climate change), (2) operate at the landscape scale (change of the ecosystem to a new land use), and (3) operate directly through individual species effects (invasions by alien species with radically different functional attributes to that of the resident species). For each of these scenarios, we considered how each ecosystem service is modified by the global change agents, how abiotic and biotic drivers of that service are modified, and how the role of soil biota in providing that service is altered. We used our understanding of current knowledge in the published literature, and assigned semi-quantitative scores. Specifically, we assessed the extent to which the ability of the soil biota to provide each good or service was vulnerable to each global change agent for each ecosystem type, assigning a score to each ability by using a scale of 0 to 3 (with increasing values indicating greater vulnerability). We also assessed the net impact of the global change factor (positive, neutral, or negative) on the delivery of the good or service.

The Quantification Exercise

Arable tilled ecosystems represent the most biologically simple of the three ecosystem types that we evaluated. The three perturbations that we considered were (1) invasive species: root parasites; (2) climate change: drought; and (3) land-use change: to forest. The quantification exercise (Table 5.A1 in the appendix on page 121) revealed high vulnerability of the primary ecosystem services provided by arable systems (food and fiber production) to both the invasive species and climate change scenarios, and also high vulnerability of fiber production to land-use change. However, there were also several instances in which secondary services (e.g., water quality, flood and erosion control, habitat provision, recreational values, carbon sequestration) were vulnerable to specific global change phenomena. For the majority of cases, negative impacts of both the invasive root pathogen and drought on the ecosystem good or service under consideration was predicted. This is because most of these goods and services are maximized by plant productivity, and both scenarios operate to reduce productivity, as well as reduce the ability of the soil biota to maximize productivity. In contrast, the land-use change scenario—that is, afforestation—had positive effects on many ecosystem services (Table 5.A1 in the appendix on page 121). This relates to forests representing a more complex, integrated ecosystem than arable tilled systems, and one in which the soil biota, rather than artificial inputs, plays a much greater role in the delivery of ecosystem services. Afforestation is therefore likely to enhance the role that soil biota plays in the delivery of such varied services as ecosystem carbon sequestration, nutrient retention, atmospheric regulation, habitat provision, and flood and erosion control.

Temperate grasslands are usually dominated by perennial plant species, and therefore typically represent a more complex, lower input ecosystem type than do arable ecosystems. The three perturbations that we considered were (1) invasive species: a generic invasive plant (weed) species; (2) climate change: drought; and (3) land-use change: to arable land. The quantification exercise (Table 5.A2 in the appendix on page 126) again predicted strong effects of global change phenomena on material goods provided by the ecosystem, such as food and fiber, and these effects were frequently negative. Global change effects on these goods arise through their influences on plant community composition and productivity, the ability of soil food web organisms to maximize this productivity, and linkages between the plant and soil community. This can involve important shifts from dominance by fungal based food webs and soil animals with large body sizes to bacterial based food webs and small bodied soil animals, especially in the case of the land-use change scenario. Global change phenomena also have wide ranging (and in the majority of cases, negative) effects on environmental services provided by the soil biota, including maintenance of water quality, habitat provision, bioremediation, recreation, carbon sequestration, and atmospheric regulation of gases (Table 5.A2 in the appendix on page 126). The effects of invasive plant and climate change on these types of services may arise through their adverse effects on plant productivity and soil biotic activity. Meanwhile, land-use change may affect these services through the grassland changing to a more biologically simplistic system in which the importance of the soil biota relative to that of artificial inputs in providing services diminishes.

Forest ecosystems represent the most complex and biologically organized of the three ecosystem types that we considered. The three perturbations evaluated in this case were (1) invasive species: exotic earthworms; (2) climate change: drought; and (3) land-use change: deforestation. The quantification exercise (Table 5.A3 in the appendix on page 132) revealed likely effects of all three agents on material goods provided by the forest, notably timber and wood-based products. Although deforestation directly and obviously impairs the ability of the forest to produce wood, there are also mechanisms through which drought and earthworm invasion may influence performance of both the aboveground and belowground subsystems that ultimately affect timber production (Table 5.A3 in the appendix on page 132). Forests, through virtue of being less disturbed by humans than grassland or arable systems, frequently have far greater recreation and biodiversity conservation values; the ability of the plant-soil system to provide these values are potentially indirectly responsive to both deforestation and drought (Table 5.A3 in the appendix on page 132). Environmental services provided by forests to which the soil biota contributes (e.g., water retention, erosion control, carbon sequestration, and regulation of atmospheric gases) are all maximized by forest stands with high biomass, which are in turn maintained by both decomposer food web activity and mycorrhizal associations. Ultimately, the type of global change agent operating will determine the direction of responses of ecosystem services; of the examples presented here, invasion of earthworms may increase plant productivity and the role of soil biota in providing these services, while drought and forest clearance may be expected to have generally detrimental effects.

Conclusions

There are many determinants of vulnerability of soil biota and the services that they provide to global change. The overarching determinant is spatial and temporal scale; global change phenomena are simultaneously manifested at a range of scales, and can affect soil biota at each of these scales. Soil organisms and the processes that they regulate also function at several scales, and this in turn results in the effects of global change on services provided by the soil biota being inherently scale dependent. Further, a range of extrinsic and intrinsic factors influences the vulnerability of services delivered by the soil biota to global change. Among these are life-history traits that determine the resilience and resistance of organism populations to perturbations, including those created through global change, and therefore the processes driven by these organisms. There are numerous mechanisms through which global change phenomena can affect soil biota, and these have varied and complex effects on both the organisms themselves and the services that they regulate. The direction of these effects depends upon the global change phenomenon considered, spatial and temporal scale, and the community composition of both the aboveground and belowground biota (Wardle et al. 2004). A recurrent theme is the overarching role of linkages between the aboveground and belowground subsystems: these subsystems do not operate in isolation but are instead mutually dependent upon one another. Global change factors that directly affect organisms on one side of the aboveground-belowground interface will therefore promote feedbacks through their indirect effects on organisms on the other side of the interface.

The quantification exercise (Tables 5.A1–5.A3) serves to reinforce the important role that soil organisms have in driving ecosystem services, as well as the extent to which they are affected by global change. Although specific entries and scores can be debated, and it is recognized that this exercise has the usual limitations of any survey based on expert opinion, the tables nevertheless provide clear evidence that the soil biota play an important role in the delivery of a range of ecosystem services in very different ecosystem types, and that this role can be affected (either positively or negatively) by a spectrum of global change phenomena. Due to the many linkages of aboveground and belowground subsystems, soil biota probably play at least some role (however indirectly) in every terrestrial ecosystem service that has a biological component. Ultimately, if we are to understand better how ecosystems deliver goods and services upon which we depend and how these can be managed under scenarios of global change, then it is imperative that we recognize the considerable contribution that soil biota make to these services and their response to global change phenomena.

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Appendix Table 5.A1. Vulnerability of ecosystem goods and services in arable tilled ecosystems provided by the soil biota to three agents of global change: invasive species, climate change, and land-use change.

The "service rank" (range −3 to +3) indicates the importance of the ecosystem under consideration (arable, tilled) in providing each ecosystem good and service; positive and negative values indicate positive and negative effects, respectively, of the ecosystem in providing that good or service. The importance of "biotic" and "abiotic" factors in providing each good or service ranges from unimportant (designated by *) to highly important (***). "Vulnerability" scores (range 0 to 3) relate to the vulnerability of each good or service provided by the ecosystem to each perturbation, greater values indicate greater vulnerability; text in brackets explains vulnerability score. "Net impact" refers to the direction of change in the ability of the ecosystem to provide each good or service after perturbation, and is scored as − (reduction), 0 (no change), or + (increase).

				Perturbations					
	Unmanaged (Arable Tilled)[1]			*Invasive Species: Root Parasites*[2]		*Climate Change: Drought*[3]		*Land-Use Change: To Forest*	
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*
Food production	3	** plant breeding, roots and residues	*** climate, tillage, soil type, fertilizer	3 [can lead to destruction of crop]	−	3 [abiotic controls, especially soil properties and fallow practices, most important; reduced NPP; drought-resistant plant breeds important[5]]	−[4]	0 [litter system developed; annual roots replaced by perennial; increased role for soil food web; change from bacterial to fungal-based food web[6]]	0
Water quality	−2	* nitrification; pesticide degradation	*** topography; leaching; NH_4 volatilization	2 [increased application of pesticides negatively impacts water quality.]	−	0 [service is effectively cancelled.]	−	0 [improvement in quality through restoration of ecosystem engineering communities and creation of biogenic structures]	+

(continued)

Appendix Table 5.A1. *(continued)*

				Perturbations					
	Unmanaged (Arable Tilled)[1]			*Invasive Species: Root Parasites*[2]		*Climate Change: Drought*[3]		*Land-Use Change: To Forest*	
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*
Flood and erosion control[8]	−3	*** plant cover, crop type (roots)	*** topography, soil properties	0	0	3 [abiotic controls, especially fallow practices, most important[9]; drought-resistant plant breeds important[10]]	+[7]	0 [restoration of strong biotic control through change in root architecture, mycorrhizal associations and creation of biogenic structures]	+
Fiber	1	** plant breeding, roots and residues	*** climate, tillage, soil type, fertilizer	3 [can lead to destruction of crop]	–	3 [abiotic controls, especially soil properties and fallow practices, most important; reduced NPP]	–	3 [litter system developed; annual roots replaced by perennial; increased role for soil food web; change from bacterial to fungal-based food web[6]]	+
Waste disposal/ bio-remediation	3	** decomposition, co-metabolism, build up of intermediate toxic products	** volatilization, water regime, soil properties, sequestration, incorporation by machinery	1 [dependent on rates of decomposition]	– / +	3 [dependent on soil type and pre-drought conditions]	–	0 [no fundamental change in service, but change in rate and performed by different food web communities[6]]	+
Biological control[11]	−1	** rotation, GMOs[12], micro-food webs	** pesticides, tillage	1	–	1 [can cause shift from specific to generalist pests[13]]	0	0 [restoration of strong biotic control]	+

Recreation and other uses	−1	** odor, monoculture/ low landscape heterogeneity	*** erosion, topography seasonally bare land; noise, air pollution, pesticides	1 [increased pesticide use]	–	2 [potential loss of landscape features through erosion, increase in bare land and salinization]	–	0 [dependent on forest type and management[14]]	+
Carbon sequestration	−1	* decomposition	** topography texture; nature of clay minerals; climate; soil structure	0–1 [dependent on changes in rate of decomposition]	–	0–1 [dependent on abiotic factors, irrigation, vulnerability to fire]	– / +[15]	0 [dependent on forest type[16], litter quality and quantity, humification and sequestration in biogenic structures]	+
Trace gases and atmospheric regulation	−3	** ammonification, nitrification	** moisture regime, soil structure	0 [dependent on whether other biotic factors affected]	– / +	0 [biotic activity slowed, thus decrease in production of trace gases]	– / +	0 [dependent on litter quality and quantity and nitrifiers, denitrifyers, methane oxidizers]	+
Fuel	0	NA	NA	NA	NA	NA	NA	NA	NA
Habitat provision[17]	−2	*** crops at landscape level; management of field margins and riparian areas	*** topography, soil properties	0	0	1 [negative impact on field margins and riparian areas]	–	1–2 [increased habitat heterogeneity; extent of change dependent on forest type and forest management[18]]	+
Soil formation and structure	1	* organic matter, bacteria, fungi, roots	** climate, parent material, erosion	0–3 [dependent on soil type and pre-parasite conditions]	– / +	0–3 [dependent on soil type and pre-drought conditions]	– / +[19]	0 [dependent on litter quality[20] and quantity, humification and sequestration in biogenic structures]	+

(continued)

Appendix Table 5.A1. *(continued)*

	Unmanaged (Arable Tilled)[1]			*Perturbations*					
				Invasive Species: Root Parasites[2]		*Climate Change: Drought*[3]		*Land-Use Change: To Forest*	
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*
Nutrient cycling	3	** microbial activities including mycorrhizae micro-food web control	* climate, soil properties P-cycling	0–1 [dependent on whether biotic factors, e.g., microbial activities, micro-food web slowed]	– / +	2 [biological activity decreased[21]; possible further reduction in NPP through salinization]	–	0 [change to nutrient conserving mechanisms]	0
Biodiversity	–3	* roots, biogenic structures	** climate, soil resource quality microhabitats	0–1 [dependent on impact on rhizosphere biota]	– / +	0 [dependent on abiotic drivers, resource quality, microhabitats, roots]	–[22]	0 [dependent on forest type, litter quality and quantity. increased biotic processes and invertebrate engineers]	+

[1] Other arable systems—for example, no-till, ridge-till—are not considered, but subject to similar vulnerability; magnitude may vary.

[2] Considers general case of root parasite invasion, for example, root knot nematode (*Meloidogyne* spp.).

[3] *Drought* is defined as 20 percent decrease in summer precipitation, based on an average for a 10-year period. This is in contrast to episodic drought, for example, in semi-dry African savanna.

[4] Drought can have a significant economic impact on agriculture. For example, the cumulative damage from the four drought years (1996, 1998, 1999, and 2000) to the agricultural industry in Texas is US$5.515 billion since 1996. (Myers 2002; see also http://www.txwin.net/dpc/dpc%20biennial%20report.pdf)

[5] Plant varieties are bred for resistance to drought, but success is variable. See (http://www.hort.purdue.edu/newcrop/proceedings1999/v4-060.html).

[6] Hunt et al. 1989.

[7] Bingham 2001.

[8] Refers to runoff to streams.

[9] There are many levels of drought and types of managed arable soils, thus vulnerability and net impact is highly context dependent. For example, in the prairies under drought conditions, farmers allow fields to go fallow to store water. However, soil is left bare, and if drought continues, soil erosion by wind and the loose stability of the soil surface are negative consequences.

[10] Response by farmers to drought can include switching the crop planted.

[11] Refers to biological control of diseases and pests of crop plants.

[12] Refers to genetically modified crops.

[13] Can have change in types of pests under extensive drought. For example, grasshopper and locust populations can be extensive, some nematodes can thrive, but generally caterpillar populations are reduced. Furthermore, there may be a possible exacerbation of plant-pest interaction with drought: for example, plants previously weakened by drought may be more susceptible to pests.

[14] Service of recreational land use is very culturally dependent and dependent on type of forest planted: for example, landscape with a monoculture of tree species may not be an improvement on a landscape of crop monocultures.

[15] There is a gradient in microbial activity, decomposition, and organic matter buildup along a drought gradient. Whether a drought starts in a moist situation or in a dry situation will influence services such as carbon sequestration (www.ornl.gov/carbon_sequestration/).

[16] Service of carbon sequestration is very dependent on forest type; for example, although pine forests have the same aboveground productivity as deciduous forests, they have lower carbon sequestration.

[17] Habitat provision for high visibility and/or threatened species.

[18] Habitat provisioning may not increase significantly if land-use change is from annual monoculture to perennial monoculture.

[19] Effects of drought on soil formation and structure are very soil texture dependent. For example, drought has a major effect in sandy soils, but effects are less dramatic in clay soils.

[20] Service of soil formation is very dependent on forest type: for example, soil formation under pine can lead to development of podsol.

[21] Buljovic & Engels 2001.

[22] With severe drought, earthworms will be lost from soil, but numbers of termites and ants may increase. In general, biodiversity in cultivated soil is only marginally affected by drought, as most species under arable conditions are resistant and resilient.

Appendix Table 5.A2. Vulnerability of ecosystem goods and services in unmanaged grassland ecosystems provided by the soil biota to three agents of global change: invasive species, climate change, and land-use change. Scoring system used is as for Table 5.A1.

	Unmanaged (Grassland)[1]			Perturbations					
				Invasive Species: Plant Species[2]		*Climate Change: Drought*[3]		*Land-Use Change: To Arable Land*	
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*
Food production[4]	2	*** decomposition, nutrient cycling, bioturbation, resistance to pests and diseases	** soil type, topography, fire, precipitation	1–3 [unpalatable species, indirect and subtle effects on soil food web]	–[5]	2–3 [reduced NPP[6]]	–	3 [change from fungal to bacterial-based food web[6], reduced earthworm abundance and mycorrhizal infection, build up of pests and diseases]	– / 0 / +
Water quality and quantity Flood, erosion control[7]	2	*** retention of N in biomass, physical stabilization, soil aggregate formation increasing infiltration rates, interception of runoff, moisture retention by organic matter	** soil type, topography, fire, precipitation	1 [transpirational losses from deep-rooted shrubs and trees[13]]	–[5]	3 [increased particulate matter and nutrient load in surface runoff and erosion[8], flush of biological activity following re-wetting events, increased plant uptake and decreased retention]	–	3 [nitrification, DON, phosphate, DOP, increased surface runoff and erosion[8] resulting from decreased plant cover and destabilized soil surface]	–

Animal fiber Wool, leather	2	*** decomposition, nutrient cycling, bioturbation, resistance to pests and diseases	*** soil type, topography, fire, precipitation	1–3 [unpalatable species, indirect and subtle effects on soil food web]	–	2–3[9] [Reduced NPP]	–	2–3[10] [decline in grazing animals]	– / 0 / +[11]
Plant fiber	1	** plant breeding, roots and residues	*** climate, tillage, soil type, fertilizer	3 [can lead to destruction of crop]	–	3 [abiotic controls, especially soil properties and fallow practices, most important; reduced NPP]	–	3 [litter system developed; annual roots replaced by perennial; increased role for soil food web; change from fungal- to bacterial-based food web[6]]	+ / 0 / –
Recreation and other uses	2	*** decomposition, nutrient cycling[12]	** soil type, topography, fire, precipitation	1 [altering system structure, decreased native animal grazing]	–	1 [potential loss of landscape features and loss of some fauna as a result of changes in vegetation]	–	1 [altering system structure, decreased native animal grazing[14]]	– / +[13]
Carbon sequestration	2	*** organic matter accumulation, $CaCO_3$ deposition	** complexing organic matter, texture, fire, $CaCO_3$ deposition	1 [accumulation of woody material and recalcitrant litter, decreased animal grazing]	+	2–3[9] [reduced NPP]	–[15]	3 [enhanced decomposition and microbial access to C within soil aggregates]	–[15]
Trace gases and atmospheric regulation	2	*** maintenance of C and N balances	** texture, precipitation, pH	0	NA	1 [modified changes in vegetation]	–	3 [increase in NO due to increased nitrification and denitrification rates]	–

(continued)

Appendix Table 5.A2. *(continued)*

				Perturbations					
	Unmanaged (Grassland)[1]			*Invasive Species: Plant Species*[2]		*Climate Change: Drought*[3]		*Land-Use Change: To Arable Land*	
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*
Habitat provision[16]	3	*** decomposition, nutrient cycling, bioturbation, resistance to pests and diseases, biota providing food resources and habitat	* soil type, topography, fire, precipitation	1–3 [unpalatable species, indirect and subtle effects on soil food web, altering habitat structure]	– / 0 / +[17]	1[18] [change in vegetation structure, shift in taxa due to drought leading to increased small mammals and predatory bird populations]	+ / –[19]	3 [shift to a relatively homogeneous habitat, change from fungal to bacterial-based food web, removal of native plants]	–
Waste disposal/ bioremediation	1	*** decomposition of brewery waste and sewage sludge	* compounds binding to humic material and clays	1 [unpalatable species, indirect and subtle effects on soil food web altering ability of microflora to degrade organic compounds]	– / 0 / +	2 [increased heavy metal concentration, decreased decomposition rates]	–	3 [increased accumulation of heavy metals from sewage sludge applications]	–

Biological control[20]	1	*** native soil pathogens and predators may inhibit the rapid spread of exotic and ruderal plant species	* soil type	1 [individual plant species may influence soil communities, activity, and/or function[21]]	–	1 [changes in climate may positively or negatively impact native soil community]	– / +	1 [possible decrease in soil pathogen richness]	–
Soil structure	3	** organic matter, bacteria, fungi, roots, invertebrate fecal pellets, invertebrate[22] engineering[23]	** climate, parent material, topography, erosion	0–1 [may exert strong impacts on soil biota]	–/+[24]	0–1[25]	–	3 [altered soil structure due to plowing, compaction, increased salinity, decreased fungal biomass, simplified soil food web]	–
Nutrient cycling	3	organic matter, microbial activity, microbial root symbionts, invertebrate microbial grazers	*** climate, soil texture, topography, pH, dry and wet deposition of nitrogen and sulfur	0–2 [may influence soil biota or be a novel nitrogen fixer]	–/+[26]	2 [decreased plant and soil biota activity]	–	3 [shift from a fungal to bacterial-based food web, simplified soil food web, additions of inorganic fertilizers]	–/+[27]
Biodiversity	3	** the presence of plants can influence the community composition of soil biota[28]; plant species can influence soil microbial physiological attributes[29]	** climate, physical and chemical soil heterogeneity	0–2 [altering soil physical and/or chemical properties, facilitate persistence of exotic invertebrates[30]]	–	1[31] [decreased plant inputs into soil, low soil moisture]	–	3 [simplified food web, decreased soil structure, increased soil salinity, limited plant input into soil due to harvesting, relatively homogeneous plant community, biocides and GMOs influencing non-target soil taxa[32]]	–

(continued)

Appendix Table 5.A2. *(continued)*

	Unmanaged (Grassland)[1]			*Perturbations*					
				Invasive Species: Plant Species[2]		*Climate Change: Drought*[3]		*Land-Use Change: To Arable Land*	
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*
Fuel	0	NA	NA	NA	NA	NA	NA	NA	NA
Biochemicals/ medicines	1	** plant compounds and microbial enzymes	** NA	1 [possible loss of native plant species]	– / +[33]	1 [changes in microbial community]	– / +[34]	3 [change from fungal- to bacterial-based food web, removal of native plants]	–

[1] Lightly managed free-range grasslands (i.e., including supplemental winter livestock feed, but excluding fertilizer or pesticide inputs).

[2] Considers general case of a plant species invasion.

[3] Drought is defined here as a 20 percent decrease in annual precipitation, based on an average for a 10-year period.

[4] Animal products are considered here.

[5] Hirsch & Leisch 1998; Jacobs & Sheley 1998.

[6] Hunt et al. 1989.

[7] Refers to runoff to streams. In dryland systems, potential evapotranspiration generally exceeds precipitation, so these services may be less significant.

[8] Branson et al. 1981.

[9] Range depends upon organic matter and moisture retention. Therefore this good and/or service will be more susceptible in more xeric, low–organic matter grasslands.

[10] Range depends upon whether the arable land supports winter grazing by cattle (e.g., on winter wheat fields) and if fiber crops are planted (e.g., cotton).

[11] Direction of net impact will probably be negative, but could be positive if fiber production in arable land is higher (e.g., from the production of cotton) than wool or leather production of the original grassland.

[12] Hikers, bicyclists, birders, hunters, etc. are often attracted to a site because they find it visually pleasing and/or because the site serves as habitat for charismatic and/or edible animal taxa (e.g., birds and deer). In part, it is the feedbacks between the soil and plant systems that result in the visually appealing structure (from a human perspective) and produces habitat and food for animals of interest to the public.

[13] Some charismatic animals may increase in arable lands (e.g., some game bird species).

[14] Creating a more structurally homogeneous landscape will limit the number of charismatic animals found at the site and thus will decrease public interest in using the site for recreational purposes.

[15] Burke et al. 1989.

[16] Habitat provision for high visibility and endangered/threatened species.

[17] Direction of net impact will depend upon whether or not native taxa can utilize the invasive plant species for food or habitat.

[18] Assumes that the taxa important in habitat provision are adapted to the ecosystem and the ecosystem is normally subject to drought.

[19] Impact could be positive or negative depending upon the response of important taxa to drought. Some taxa may be favored in drought conditions.

[20] Refers to biological control of parasites and diseases of native species.

[21] Wardle et al. 1999; Kourtev et al. 2002.

[22] Rusek 1985.

[23] Refers to termites and earthworms Lavelle et al. 1997.

[24] Impact could be negative or positive depending on if the invasive plant species inhibits or stimulates soil biota via root exudates, above- and/or belowground litter inputs, or altering soil microclimate.

[25] Assumes biota are adapted to periodic drought conditions.

[26] A negative impact suggests that the rate of cycling of a given nutrient is slowed with the addition of an invasive plant species while a positive impact suggests an increase in the rate of cycling. Whether or not humans desire an increase or decrease in nutrient cycling rates is probably context dependent.

[27] The net positive impact suggests an increase in the rate of nutrient cycling that may benefit crop plants. However, this increase can also lead to increased nitrogen and carbon losses that may contribute to greenhouse gas emissions.

[28] Wardle et al. 1999.

[29] Westover et al. 1997. Changes in microbial physiological traits may be suggestive of a change in microbial community structure.

[30] Kourtev et al. 1999. Facilitating the persistence of nonnative invertebrates may decrease the biodiversity of native invertebrates.

[31] Assumes biota are adapted to periodic drought conditions and will probably reach pre-drought biodiversity relatively quickly following the end of the drought.

[32] GMOs are genetically modified organisms. There is evidence that the insecticidal toxin from the bacterium *Bacillus thuringiensis,* encoded into some crop plants, is released from the engineered plants into the soil environment (Saxena & Stotzky 2000).

[33] Direction of net impact will be affected by any biochemical/medicinal products that could be obtained from the invasive plant species.

[34] Direction of net impact will depend upon what components of the microbial community are inhibited or favored during drought conditions and whether those microbes can yield any biochemical/medicinal products.

Appendix Table 5.A3. Vulnerability of ecosystem goods and services in unmanaged forest ecosystems provided by the soil biota to three agents of global change: invasive species, climate change, and land-use change. Scoring system used is as for Table 5.A1.

				Perturbations					
	Unmanaged (Forest)[1]			*Invasive Species: Exotic Earthworms*		*Climate Change: Drought*[2]		*Land-Use Change: Deforestation*	
Goods and Services	*Service Rank*	*Biotic*	*Abiotic*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*	*Vulnerability*	*Net Impact*
Food production	1	*** fungi, fruits for animals	* pH	1 [altered fungal diversity, increased fungal dominance[4]]	–	1 [reduced fruiting body abundance[5], changes in phenology/ synchrony]	–	1 [loss of mushrooms, fruits, hunting, etc.[6]]	–
Water quality and quantity Flood, erosion control	3	** plant species composition, soil organisms, bioturbators	*** topography, soil texture, porosity	1 [increased soil erosion, nitrate leaching[7]]	–	3 [reduced water yield, solute concentrations increased]	–	3 [increased decomposition, increased nitrification, acidification, increased water yield[8]]	–
Fiber (wood) production	3	* pathogens, parasites, decomposers, N_2 fixers	*** soil factors affecting NPP	0 [increased NPP[9]]	+	3 [reduced NPP[10]]	–	3 [absence of trees]	–
Fuel[11]	3	* pathogens, parasites, decomposers, N_2 fixers	*** soil factors affecting NPP	0 [increased NPP]	+	3 [reduced NPP]	–	3 [absence of trees]	–
Biochemicals/ medicines[12]	1	** microbial diversity	*	0	+	0	–	0	–

Habitat provision[13]	3	*** decomposers, ecosystem engineers	*** humus type, pH, soil fertility, parent material, topography	0	0	1 [changes in understory vegetation[14]]	–	2 [changes in habitat types[15]]	–
Waste disposal/ bioremediation	1[16]	* decomposers, ecosystem engineers	* forest type, pH, soil fertility, parent material, topography	0[17]	0	2 [reduced decomposition rates, increased solute concentrations[18]]	+	1 [higher throughput of water[19]]	–
Biological control[20]	1	* insect taxa, mycorryhizal and fungal pathogens	** waterlogging, pH, soil texture and structure	0 [modification of plant growth]	+	1 [unpredictable disease interactions[21]]	+	1 [stumps may be important disease sites[21]]	–
Recreation and other uses	3	** ants and insects for wildfowl, game	*** structure of the vegetation[22]	0 [increased resources for birds and other animals, fishing]	–	3 [increased fire risk, drier soils may ease access]	–	2 [tree loss, reduced hiking, negative visual impact]	–
Carbon Sequestration deciduous forest	3	* litter quality, worms, roots	*** soil texture	1 [rapid litter loss]	–	2 [reduced NPP]	–	3 [increased decomposition, major C loss]	–
Trace gases and atmospheric regulation	3	*** nitrifiers, methane oxidizers, denitrifiers	*** tree species, pH, soil texture, aeration[23]	1 [increased N_2O production[24]]	–	1 [decreased N_2O production, increased CH_4 oxidation[25]]	+	2 [increased N_2O production, decreased CH_4 oxidation[25]]	–
Soil Structure	3	*** earthworms, roots, arthropods, bacteria, fungi	** climate, parent material, erosion	0–3 [dependent on aspects of soil structure considered[26]]	+/–	1 [some reduced activity and leaching]	–	3 [compaction, erosion, soil community shifts]	–

(continued)

Appendix Table 5.A3. *(continued)*

	Unmanaged (Forest)[1]			Perturbations					
				Invasive Species: Exotic Earthworms		Climate Change: Drought[2]		Land-Use Change: Deforestation	
Goods and Services	Service Rank	Biotic	Abiotic	Vulnerability	Net Impact	Vulnerability	Net Impact	Vulnerability	Net Impact
Nutrient cycling	3	*** microbe-faunal interactions	* climate, soil properties, topography, P cycling	3 [accelerated cycling of nutrients]	+/–	2 [biological activity decreased]	–	3 [higher rates of decomposition and leaching from system]	–
Biodiversity	2	*** roots, substrate for soil organisms	* climate, soil resource quality, microhabitats	3 [displacement/ extirpation of native soil organisms]	+/–	0 [dependent on abiotic drivers, resource quality, microhabitats, roots]	–	3 [community shifts to opportunistic species, increased dominance]	–

[1] Entries are for a typical temperate deciduous forest, principally managed for timber yield.

[2] Drought is defined as 20 percent reduction in summer precipitation, based on an average for 10-year period. The important impacts of fire have not been considered, but risk of fire would increase dramatically under drought conditions.

[3] Deforestation is assumed to be conventional felling, involving timber removal but non-removal of felling debris.

[4] Introduction of earthworms into forest soils has been shown to increase the diversity of fungi in burrow walls (Tiunov & Dobrovolskaya 2002), but can also have an effect on mycorrhizal colonization and, hence, potentially fruiting bodies (Lawrence et al. 2003).

[5] Dry years are typically associated with strongly negative effects on fungal fruiting bodies (e.g., see Wiklund et al. 1995). This importance of forests as sources of edible fungi differs greatly between regions.

[6] Forests act as habitats for a number of food species, including deer and boar. The overall impact of deforestation on these foods depends on the subsequent use of the land after deforestation, but a felled forest will generally act as a poorer service provider in this respect.

[7] Experimental evidence suggests increased N mineralization and nitrification after earthworm introduction (Robinson et al. 1992). This may have local impacts on soil solution chemistry but is unlikely to have a major impact on stream chemistry.

[8] Classic studies (e.g., Hubbard Brook) have clearly demonstrated the impacts of deforestation on forest streamwater chemistry. The effects are largely due to changes in deposition and hydrology, due in turn to canopy removal and to the dramatic switches in physical status of soil that impacts decomposition rates.

[9] In the laboratory, increased growth of tree seedlings has been demonstrated as a result of earthworm addition (Haimi & Einbork 1992).

[10] Decreased NPP with drought, with slower growth. Timber quality may actually improve, however. Mycorrhizal fungi may play a significant role in forest drought resistance (Garbaye 2000).

[11] Only the provision of wood is considered.

[12] Current role of temperate forests as sources of biochemicals and medicines is limited in temperate regions. However, future potential and nontemperate forest use cannot be totally ignored and the loss of even one plant species may be of importance.

[13] Habitat provision for high-visibility/threatened species.

[14] Changes in understory vegetation may occur as a consequence of drought. Reductions in understory density may reduce value as a habitat.

[15] Deforestation may have a range of impacts on small and large mammal, bird, and invertebrate populations.

[16] Production forest has been evaluated as disposal sites for sewage sludge (Ferrier et al. 1996); the disposal process depends heavily on the activities of soil biota. Production forest is also a suitable land use for revegetated mine wastes.

[17] Interaction not investigated, but evidence suggests that earthworms may help break down waste. Reclamation engineers use the viability of earthworms as an index of soil condition.

[18] Shortage of water would have the direct physical effect of decreased dilution of wastes, while limitation to microbial activity could lead to decreased degradation.

[19] Increased channel bypass flow and decreased interaction time between water and soil would reduce ability to deal with certain pollutants (Bardgett et al. 2002).

[20] Refers to biological control of parasites and diseases of natural species.

[21] Strong interactions between site management and root pathogens with drought have potentially beneficial effects, whereas untreated stumps after felling may act as sources of root pathogen inoculum (Thies 2001).

[22] Tree species and planting density have a major affect on recreational use of forests, for both hikers and hunters.

[23] Trace gas consumption by forests depends on water status, species, management and, in particular, extent of fertilizer addition (Ineson et al. 1991).

[24] Associated with increased N mineralization and earthworm casts (Elliott et al. 1991).

[25] Soil water content has a major effect on methane transfers in soils, with optimum contents for methane oxidation and nitrous oxide production (Del Grosso et al. 2000). Both drought and deforestation have marked effects on these fluxes.

[26] Earthworms contribute to soil structure through bioturbation and redistribute organic materials over a large vertical range in the soil profile; however, as invasives they displace enchytraeids and microarthropods that are also critical for soil structure and development.