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Agricultural intensification, soil biodiversity and agroecosystem function

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Abstract

Soil is the habitat of plant roots and of a diverse array of organisms—bacteria, fungi, protozoa and invertebrate animals—which contribute to the maintenance and productivity of agroecosystems. As intensification occurs, the regulation of functions through soil biodiversity is progressively replaced by regulation through chemical and mechanical inputs. However, the causal relationships between (1) composition, diversity and abundance of soil organisms and (2) sustained soil fertility are unclear. Furthermore, in tropical agricultural systems undergoing intensification, large numbers of farmers have limited access to inputs, and therefore the maintenance and enhancement of soil biodiversity may be particularly relevant to such farmers. In this paper we propose a number of hypotheses which could be tested to explore the relationships between agricultural intensification, biodiversity in tropical soils and ecosystem functions. We also provide a conceptual framework within which such hypotheses can be tested. © 1997 Elsevier Science B.V.

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1. Introduction

Nature is comprised of biological diversity. Although not apparent to the naked eye, soil is one of the most diverse habitats on earth and contains one of the most diverse assemblages of living organisms. A single gram of soil has been estimated to contain several thousand species of bacteria (Torsvik et al., 1994), and of the 1 500 000 species of fungi esti-

mated to exist worldwide (Hawksworth, 1991) remarkably little is known of soil fungi, apart from common fungal pathogens and mycorrhizal species. Among the soil fauna, some 100 000 species of protozoa, 500 000 species of nematodes (Hawksworth and Mound, 1991) and 3000 species of earthworms (Lee, 1985) are estimated to exist, not to mention the other invertebrate groups of the mesofauna (e.g. Collembola, mites and enchytraeids) and macrofauna (e.g. ants, termites, beetles and spiders).

Although our knowledge of the biodiversity of organisms in all soils is shamefully poor, soils in the tropics deserve particular attention for a number of

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reasons. The majority of research has concentrated on soils of temperate regions, yet there is evidence that biodiversity of soil invertebrates is greater in the tropics than at greater distances from the equator (Swift et al., 1979). Although this is not borne out by recent studies on earthworms in the tropics (Fragoso et al., 1997), increases in diversity with decreasing latitude are found for many groups of organisms (Schluter and Ricklefs, 1993; Huston, 1994). In terms of potential future changes, the rate of intensification of agriculture in the tropics is greater than in other regions of the world, so that some ecosystems are under particular threat of major changes or loss of biodiversity. Given the reliance of cropping systems in many regions of the tropics on organic inputs for management of soil fertility, this implies that farmers in the tropics are more reliant on biological functioning of the soil, and the agricultural productivity of farmers may therefore be affected if losses of biodiversity lead to changes in ecosystem functioning.

A popular assumption is that anthropogenic interference in nature results in a loss of biological diversity. The most frequently cited example of agricultural intensification directly resulting in a reduction in biodiversity is that of the tropical rainforest clearance where the diversity of plant and animal species is reduced catastrophically. Yet examination of the literature suggests that there is little detailed evidence for agricultural intensification resulting in loss of biodiversity in soil. A rare example is that of the changes in earthworm populations on conversion from tropical rainforest to pasture where a single species survives (see Fragoso et al., 1997), which leads to soil compaction due to its massive surface casting activity. This is an important example where the reduction in diversity is coupled to, and presumably responsible for, a loss in function which has resulted in a substantial loss in agricultural productivity. In other cases, the extent to which soils can be mistreated and yet crops still continue to support abundant plant growth seems remarkable. Thus, not only is there no clear link between agricultural intensification and biodiversity, but the consequences of loss of biodiversity for functioning of ecosystems also await detailed investigation.

As global food production is already dependent on intensive agricultural production and demands for food are likely to increase substantially, the future

challenge is to match demands for production with forms of soil management that are sensitive to maintaining soil biodiversity. This paper aims to set the theoretical framework for the subsequent papers in this special volume, which each address the relationship between agricultural intensification, biodiversity and function of a particular group of organisms in the soil. We hope that this will serve to assist the current developments of a new challenge in soil biology research: the exploration and understanding of biodiversity in soil and how this influences the functioning of ecosystems.

2. Agricultural intensification, biodiversity and function

2.1. Agricultural intensification

Agricultural intensification is a set of patterns of land-use change with the common feature of increased use of the same resources for agricultural production, usually as a result of a switch from intermittent to continuous cultivation of the same area of land. Associated trends are specialization in crop or livestock species utilized, increased management intervention and greater reliance on markets. At one extreme of a gradient of agricultural intensification are extensive forms of shifting cultivation in which a given piece of land is often used for less than 1 year in 10. Fallow systems, where land is used for between one- and two-thirds of the time (Ruthenberg, 1980), can be viewed as systems of intermediate intensity. At the other extreme are forms of permanent agriculture. Along this gradient of increasing land-use intensification there is often a substitution of manual labour by mechanized power, and of organic manures and natural pest management by agrochemical use. The intensity of input use can vary enormously at any point along this gradient, and transitions from internally regulated to externally regulated systems, and from sustainable to degraded systems, may occur progressively or abruptly. A further factor that is important in determining the degree of intensification in seasonally arid or very wet climates, and in particular production systems, is the degree of management of the water by irrigation and/or drainage.

Combining these points the degree of intensification may be estimated as:

$$I = L \times N \times P \times E \times W$$

where, all on a 0–1 scale, I is intensification, L is land-use intensity as defined by Ruthenberg (1980), N is nutrient use (0 for completely internal recycling, 1 for completely external manure/fertilizer inputs), P is pest management (0 for no intervention, 1 for full mechanical/chemical control), E is the energy input per hectare (whether based on labour or fossil fuels), and W is water management (0 for no intervention, 1 for completely controlled irrigation and/or drainage). As a certain value of I can be obtained by various combinations of L , N , P , E and W , this definition embraces the potential for management options with similar degrees of intensification which are more or less favourable for the maintenance of soil biodiversity.

Increasing specialization of crop or livestock species entails a deliberate reduction in the 'planned' above-ground biodiversity and thus in the spatial and temporal complexity of the system. It is unclear whether a decrease in the planned diversity reduces the total (i.e. planned plus associated) biodiversity, including that of the below-ground community.

Diversification is not necessarily a diametric opposite of intensification, as agricultural systems with the same intensity of land-use or inputs can differ in terms of the diversity of crops grown, both in space and time. It is, however, the simplest management tool to increase biodiversity in agriculture in terms of the crop and livestock species used, with possible implications for enhancing the biodiversity of other groups of organisms.

2.2. Biodiversity

Biodiversity is a shortened form of 'biological diversity', which has gained popular use in the last decade, especially since the declaration of Agenda 21 at the Earth Summit in Rio de Janeiro, Brazil, in 1992. The total biodiversity within a landscape (gamma diversity) is a function of local or 'within-habitat' diversity (alpha diversity) and differences in species composition, or 'turnover' of species, between habitats or localities (beta diversity) (Whittaker, 1972). Biodiversity cannot be directly added

across these scales: subhabitats of high internal (alpha) diversity can comprise a landscape of limited total (gamma) diversity if all the subhabitats are similar (low beta diversity), whereas if a landscape is made up of widely differing habitats (high beta diversity), all of fairly low alpha diversity, the gamma biodiversity may be fairly high.

Numerous difficulties obstruct the measurement of biodiversity in soil. Problems in the sampling and extraction of organisms from soil are common to many groups. For example, even dispersion of soil by gentle shaking can result in strong shearing forces as particles grind against one another. Furthermore, even at the level of alpha diversity, sample sizes must be determined both by knowledge of the ecology of the organisms in question and by knowledge of the spatial heterogeneity with the habitat under study, and thus cannot be generalized across groups. For example, larger soil animals such as termites can forage over distances of more than 50 m from their nests (Wood, 1988), and can disperse over much larger distances when they fly, whereas smaller animals are relatively sedentary. Even among microorganisms, basidiomycete fungi can forage over several metres (Dowson et al., 1988), and a single individual has been shown to cover an area of more than 15 ha (Smith et al., 1992), whereas the habitat for bacterial colonies is better estimated in terms of (micro)aggregates (Harris, 1994). Within a predefined and homogeneous sampling area, sample sizes can be optimized by determining the number of species detected in samples of increasing size (sometimes described as species/area curves). The optimum sample size is usually taken at the point above which there is little return (in terms of an increase in the number of species detected) for further increases in sample size. There is an obvious danger that changes in diversity might be overlooked if the resolution of sampling is insufficient, and sampling intensity must be decided based on knowledge or assessment of spatial heterogeneity. Whatever approach to sampling is adopted, it is hard to avoid undersampling rare individuals.

Once an acceptably representative sample has been obtained, there are problems in describing the diversity within the sample. It has been estimated that current methods for isolation of bacteria retrieve only 1% of those present in soil. Indeed, the selec-

tive culture methods commonly employed which use fairly readily degradable substrates result in the isolation of the faster-growing groups and underestimate the representation of slow-growing, more specialized types which can degrade more complex substrates. Direct extraction of DNA is one way that problems of selective media can be overcome and, although there are difficulties in isolating clean DNA from soil microorganisms *in situ*, there have been some recent exciting advances in this area (e.g. Smith and Stribley, 1994). Classifications of groups of organisms may be based on genetic and phenotypic characters, or may be purely functional, although most include a mixture of both approaches. The resolution of a taxonomic classification may allow easy distinction of species or individuals among some groups, but only genera can be distinguished in others. Whichever method of classification is used, there are different scales of biodiversity, and the choice of the scale of resolution for study is often determined largely by the degree of discrimination possible with the available methods. For example, the taxonomic classification of earthworms and other soil animals is largely based on morphology and is gradually evolving as more types are discovered. An ecological classification is also used for earthworms and other soil animals which is based on a variety of criteria (e.g. location in the soil profile, mode of feeding, diet, and morphological characteristics) and thus relates closely to their ecosystem function. For bacteria, until the last 20 years, classification was also largely determined by a combination of morphological and functional attributes. Currently, application of molecular biology methods are revolutionizing our understanding of the evolutionary relationships between bacteria. The phylogenetic classification has provided many surprises but has also confirmed many groupings determined largely by phenotypic characters (e.g. Kahindi et al., 1997). Such molecular tools for the development of phylogenies could potentially be applied to all phyla in soil, although bacteria lend themselves well to such analysis. Molecular biology methods also allow biodiversity of bacteria and fungi to be studied at the level of genetic diversity of individuals within populations of specific species, which is a much finer resolution than that currently employed for studies of soil fauna. Conversely, other molecular biology methods can be

used to analyse diversity in DNA extracted directly from soil and which thus examine diversity across the whole microbial community (e.g. Griffiths et al., 1996).

In consideration of the roles of different groups within the soil biota, a pragmatic approach has been adopted in this volume which involves a hybrid of taxonomic and functional classification.

2.3. A diversity of biological functions

Having established methods for the study of the vast diversity of organisms inhabiting soils, the question remains: What do they do? As indicated above, both the sizes of soil organisms and the scales at which they operate differ vastly, and a consideration of their functions in the light of these differences in scales is warranted.

2.3.1. The hierarchy among diversities of different functional groups in soils

The activity, and potentially the diversity, of soil organisms are largely determined by a suite of abiotic and biotic factors that are hierarchically organized (Lavelle et al., 1993). Functional groups that operate at large scales of time and space tend to constrain groups that are smaller and/or live for shorter periods of time (Fig. 1). Climate, soil conditions and human and animal activities are essential determining factors that directly influence the productivity and structure of vegetation. The vegetation in turn influences soil invertebrate and microorganism communities through the abundance, quality and distribution of organic resources produced in both

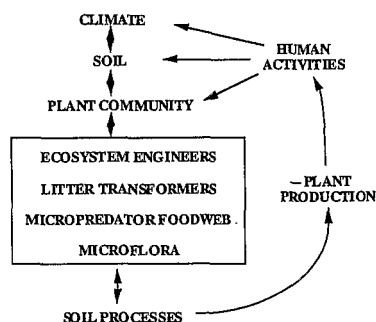


Fig. 1. A hierarchical model of factors that determine soil processes (modified from Lavelle et al., 1993).

space and time. Invertebrates may be classified into three broad functional groups depending on their size, the nature of structures that they create in soils and the major type of relationships they develop with microorganisms (Lavelle, 1994).

Ecosystem engineers build large and resistant organomineral structures that may persist for long periods of time (from months to years) and which profoundly affect the environment for smaller organisms. These invertebrates develop mutualistic relationships with microorganisms in their gut (internal rumen) and in the structures which they build (which can be considered as an external rumen). This group includes termites, earthworms and some ants.

At the next level down the hierarchy, litter-transformers produce purely organic structures that are much less persistent. Nonetheless, a degree of spatial organization of the environment is imposed by the accumulation of such structures, and regulation of microbial activity is observed inside them (e.g. Toutain et al., 1982). This group includes the vastly diverse fauna of micro- and macroarthropods which feed on and live in litter systems, plus some of the earthworms (epigeics) and termites (xylophagous), and the small Oligochaeta Enchytraeidae. These organisms are active comminutors that develop interactions of the 'external rumen' type with the microflora as well as grazing directly on the fungal biomass.

Finally, micropredators are small invertebrates, mainly protozoa and nematodes, that feed on microorganisms. These micropredators live in free soil water and do not develop mutualistic relationships with the microflora.

Predation of microorganisms, particularly by nematodes and protozoa, plays an important role in regulating the biomass of microorganisms and is likely to assist in maintaining diversity by preventing dominance of particular groups (Huston, 1994). This is arguably more important for bacteria, which tend to be strongly regulated by predation, than for fungi which are less susceptible to grazing (as they are more complex, both chemically and structurally) and are more strongly influenced by resource quality (Wardle and Lavelle, 1997).

2.3.2. Diversities of functions and their disruption by agriculture

The key biological functions in tropical agricultural soils, together with the principal groups of organisms responsible for them, can be related to agricultural management practices that have the most impact on them (Table 1). Whilst it can be argued that all of the principal management practices listed here will impact each of the key biological functions at some level, we have included only those that are likely to have the most significant effects.

Burning is a central component of shifting cultiva-

Table 1

Key biological functions, the groups of soil biota principally responsible for these functions and management practices most likely to affect them

Biological function	Biological/functional group	Management practices
Residue comminution/ decomposition	Residue-borne microorganisms, meso/macrofauna	Burning, soil tillage, pesticide applications
Carbon sequestration	Microbial biomass (especially fungi), macrofauna building compact structures	Burning, shortening of fallow in slash-and-burn, soil tillage
Nitrogen fixation	Free and symbiotic nitrogen-fixers	Reduction in crop diversity, fertilization
Organic matter/nutrient redistribution	Roots, mycorrhizas, soil macrofauna	Reduction in crop diversity, soil tillage, fertilization
Nutrient cycling, mineralization/immobilization	Soil microorganisms, soil microfauna	Soil tillage, irrigation, fertilization, pesticide applications, burning
Bioturbation	Roots, soil macrofauna	Soil tillage, irrigation, pesticide applications
Soil aggregation	Roots, fungal hyphae, soil macrofauna, soil mesofauna	Soil tillage, burning, reduction in crop diversity, irrigation
Population control	Predators/grazers, parasites, pathogens	Fertilization, pesticide application, reduction in crop diversity, soil tillage

tion or slash-and-burn agriculture due to the mobilization of nutrients. Burning may influence the biological functions of organic matter decomposition, carbon sequestration and soil aggregation, both directly through a loss of organic matter inputs (Ladd et al., 1994) and indirectly through a change in the size and structure of biological communities (Rasmussen and Collins, 1991). Burning also results in microclimatic modifications in a bare soil with consequences on water regimes that affect soil faunal communities (Lavelle, 1994). Soil tillage has some of the most far-reaching effects on biological processes. Method of soil tillage, for example, strongly influences the placement and distribution of crop residues, resulting in differences in the composition and activity of microbial (Doran, 1980; Bowen and Harper, 1988; Beare et al., 1993) and faunal (Hendrix et al., 1986) communities, which can markedly impact rates of residue decomposition (Broder and Wagner, 1988; Beare et al., 1992) and carbon sequestration (Holland and Coleman, 1987) as well as the dynamics of nutrient mineralization/immobilization (Beare et al., 1992) and the availability of suitable refuges for plant pathogens (Sumner et al., 1981). The intensity of soil tillage may also indirectly impact physical processes in soils (e.g. bioturbation, soil aggregation) through changes in the diversity and composition of biological communities (Hendrix et al., 1992; Berry and Karlen, 1993; Beare, 1995), in addition to direct mechanical alterations in structure that result from cultivation. Additionally, soil tillage can directly disrupt earthworm populations and render them susceptible to predation by birds, and can destroy termite galleries.

The use of broad-spectrum pesticides in agriculture has both targeted and non-targeted effects on the composition and diversity of soil biological communities (e.g. Domsch, 1970; Eijsackers and van de Bund, 1980). While the targeted effects are often well characterized, the non-targeted effects, such as those reported for earthworms, microarthropods and certain beneficial (e.g. predatory) insects, are poorly known, particularly in tropical agricultural soils. Such pesticide-induced changes in the composition and structure of soil may have important implications for residue decomposition (Hendrix and Parmelee, 1985), soil bioturbation and nutrient cycling (Sharpley et al., 1979). As in temperate regions, the chemical

composition of crop residues in the tropics can have a marked effect on the structure of decomposer communities (Tian et al., 1995). The shift away from more diverse intercropping and rotational cropping systems to the more intensive monocultural cropping practices is known to promote the build-up of crop pest and pathogen populations (Sumner et al., 1981). However, this reduction in crop diversity and, hence, the diversity of resources and refuges that it provides may also impinge on the diversity of other soil organisms and the functions they perform (Swift and Anderson, 1993; Beare et al., 1995). Some of these relationships are discussed below.

The quantity, placement and timing of fertilizer application can influence the inputs from biological fixation and cycling of nutrients, both positively by phosphorus stimulating rates of nitrogen fixation by legumes and negatively by nitrogen fertilization suppressing nitrogen fixation rates (e.g. Giller and Cadisch, 1995; Kahindi et al., 1997). The incidence of pathogen damage and parasitic weeds is also strongly related to environmental factors such as soil fertility (Scott and Bainbridge, 1978). Furthermore, modifying soil-water relations through irrigation stimulates both the intensity of biological activity and types of biological transformations performed. These, in turn, may enhance the biological functions of soil aggregation and bioturbation as well as rates of nutrient turnover and mobilization (Anderson, 1988; Lee and Pankhurst, 1992).

2.4. The function of biodiversity in soil

The first and most obvious role of biodiversity is to ensure the multiplicity of functions that can be ascribed to soil organisms. But whether there are direct links between the rate and efficiency of these biological functions and the biodiversity of soil organisms remains largely a matter for conjecture. A second, interrelated role of biodiversity is further to ensure that these functions are maintained in the face of perturbations. A greater degree of biodiversity between, or within, species or functional groups will logically increase the inherent variability in tolerance or resistance to stress or disturbance. These two roles each address aspects of the long and continued debate over redundancy among soil organisms.

2.4.1. Resilience: a role for the unemployed?

Genetic variability within and between species confers the potential for resistance to perturbations, whether short- or long-term. If certain species, or individual strains or ecotypes within a species, have greater resistance to a particular stress, then they are likely to become predominant in the face of that stress. However, if the rate of genetic adaptation of the species to the stress is rapid, then new resistant individuals may emerge to mask such an effect. Assuming that rates of adaptation among most organisms are not sufficiently rapid to overcome new stresses, then the eventual effect of progressive local extinctions among a functional group will not necessarily result in a loss of function until a certain threshold is reached, below which there are insufficient individuals to sustain a particular process. It thus follows that functions that are particularly sensitive to disruption will be those that are performed by a limited number of species. Good evidence of this is the extreme case of *Rhizobium*, where loss of a single species can result in total loss of nitrogen fixation by a specific legume host. A further example would be the loss of dung beetles, which results in a drastic reduction in the rate of manure incorporation and consequently massive increases in gaseous nitrogen losses through the volatilization of ammonia. At the other extreme, it can be argued that as many as 99% of the organisms can be lost without a loss of function, as, for example, in the case of decomposition of both simple and complex substrates. In one of the few studies that have addressed this issue, Andr en et al. (1995) found little evidence that biomass or diversity among different groups of soil fauna regulated rates of barley straw, and concluded that this was due to a high degree of redundancy.

Implicit in these arguments is the assumption that a multiplicity of organisms can perform a particular function, and that the replication of the ability to perform particular functions means that a degree of functional redundancy exists. Whether organisms are ever truly redundant is a matter of debate which cries out for experimental investigation. Although redundancy in a single function may be common among many soil biota, the suite of functions attributable to any one species is unlikely to be redundant. Furthermore, functionally similar organisms have different environmental tolerances, physiological requirements

and microhabitat preferences. They are thus likely to play quite different roles in the soil system (Beare et al., 1995), particularly in fluctuating or unstable environments. To some extent the multiplicity of organisms may actually reflect their adaptation to microhabitats rather than their having differing functions. If this is true, then loss of species may lead to expansion of the niches occupied by the remaining species, thus compensating for the functional activities of the lost species.

Investigations of redundancy will certainly require the combined study of taxonomically distant groups of organisms which can perform the same specific function. An example of this would be where lignin decomposition is dominated by fungi, but in their absence the combined action of soil fauna comminuting the substrate and triggering a priming effect on bacteria through the provision of high-quality substrates in their gut (Lavelle and Gilot, 1994) might allow bacteria to substitute for the role of the fungi such that any impairment of function would not be apparent. Similarly, if earthworms are lost, their role in incorporating organic matter into the soil might be replaced by a concomitant increase in the activity of other soil invertebrates.

Consideration of whether or not particular species or groups are redundant also demands consideration of their positions within foodwebs in soil. The rules governing stability of foodwebs and the strength of trophic interactions between different groups are poorly understood but indicate that loss of some groups could have far-reaching and surprising effects on stability (De Ruiter et al., 1995; Wardle, 1995).

Given the estimates for the vast numbers of species present in soils and the rather limited number of functions that we can ascribe to the soil biota as a whole, then, even allowing for the fact that decomposition of plant material may require hundreds of enzymes, a degree of functional redundancy seems inevitable. Whilst it is logical that a greater degree of functional redundancy should lead to a greater ability of a particular function to withstand stresses or disturbances (i.e. the greater the resilience), this remains to be demonstrated for soil organisms.

2.4.2. Restoration of biodiversity and functions

If functions are lost as biodiversity is reduced and organisms become extinct, then restoration or en-

hancement of biodiversity should logically lead to the restoration of functions, and of resilience. At a simple level, this is perhaps easier to test in that introduction experiments can be performed and functions monitored to assess their effects. However, it is likely that restoration of biodiversity and associated biological functions may not follow the same pathway as their loss; that is, there may be a hysteresis effect (Swift et al., 1995).

Introduction experiments can give unexpected insights: Couteaux et al. (1991) demonstrated a strong effect of resource quality on decomposition rates of litter by animal communities of differing complexity. No effects on respiration from litter with adequate nitrogen content (1%) were observed, whilst adding nematodes, collembolans and isopods progressively increased respiration rates from nitrogen-poor (0.5%) litter. Such experiments are powerful ways of exploring interactions between different groups of organisms and will undoubtedly be useful in elucidating the importance of biodiversity.

2.5. Values and perceptions of soil biodiversity

Further layers of complexity are added to the analysis when human interventions and decision-making concerning soil biodiversity management and soil management policies are taken into consideration. In this section we argue that the inclusion of a policy component in soil biodiversity research would increase the relevance of this research for farmers. We show that individual farmers in tropical countries are unlikely to manage soil biodiversity in a fashion that is congruent with society's objectives in the absence of appropriate policy interventions.

A basic question which policy-makers and donors funding soil biodiversity research implicitly address in their decisions is: How important is soil biodiversity, and for whom? Or, in essence: What is the value of soil biodiversity, and does it differ for different groups in society? The answer to this question determines the way in which biodiversity is used by a given society and, thereby, the way in which it can be better managed.

A few studies have recently attempted to assess the loss in biodiversity (above-ground) associated with tropical deforestation (e.g. Pearce and Moran, 1994), but no evidence is available concerning the

value of soil biodiversity and its perception by different groups in society as research on this topic is currently in an embryonic state. For example, recent work by Ortiz et al. (1994) is beginning to describe farmers' perceptions of the value of earthworms in smallscale farming systems in Mexico. In the absence of such evidence, concepts from natural resource economics and from ecology (hierarchy theory) can nevertheless be used to provide a conceptual framework for addressing this issue.

A basic notion in economics is that the value of an environmental asset is directly related to the various ecological and economic functions which it fulfils. More specifically, the total value of soil biodiversity can be defined as the sum of the values of each one of its ecological and economic functions, for the period of time over which they accrue (see, for example, Young, 1992, for details).

Thus:

$$V_t = \sum_{i=1}^m \frac{\sum_{j=1}^n V_j(f_i)}{(1+r)^t} \quad (1)$$

where V_t is total value of soil biodiversity, $V_j(f_i)$ is the value of i th function of soil biodiversity, $i = [1, n]$, t is the time period, $t = [1, m]$ and r is the social rate of time preference (this is the rate at which society is willing to trade off present consumption for future consumption, often taken to be equal to the rate of discount).

The principal ecological functions of soil biodiversity at the plot and farming system scales were just discussed. Soil biodiversity can also have economic functions and further ecological functions at other spatial scales, and these various functions are likely to be valued differently by different groups in society.

For example, at the farming system scale, soil biodiversity may have two principal functions: (1) it can contribute to the productive capacity of the system (e.g. crop yields, tree biomass, livestock production through grass biomass) by ensuring the mineralization of nutrients from organic resources, and (2) it may buffer the functions of the soil and their resilience to environmental risks (e.g. drought and fire). Farmers are the group in society most likely to assign a high value to these two functions because of their direct effects on production and risk reduction.

Second, at the regional and/or national scale, soil biodiversity may have three related functions: (i) it may contribute to regional/national food security (as a consequence of function (1) at the farming system scale); (ii) it may help to ensure sustained food security over the long-term (as a consequence of function (2) at the farming system level and, if a positive relation is hypothesized between soil and above-ground biodiversity, as a consequence of landscape patch dynamics which buffer regional agroecosystems from pest attacks); and (3) it may help to increase the aesthetic appeal of rural landscapes, assuming a positive relationship between below- and above-ground diversity. Regional/national governments and consumers are the groups in society which benefit most from these first two functions (food security is a stated policy objective of many governments) and which thus value them most. The third function at this scale is probably valued most by environmental groups in society.

Third, the function of soil biodiversity at the global or transnational level includes the serendipity of both below- and above-ground diversity (i.e. the value of future possible, but yet unknown, scientific discoveries associated with some aspect of soil biodiversity) and the broader option and bequest values of diversity (i.e. the value of diversity for future generations). Such functions are likely to be valued most by society at large, both in temperate and tropical countries, as demonstrated by the creation of the UNCED Convention on Biodiversity and the Global Environmental Facility (GEF).

The above examples have illustrated the fact that the ecological importance of soil biodiversity is not the only determinant of its social value; the issue of value is broader than that of ecological functions. Therefore, even though there appear to be easily demonstrated links between soil biodiversity and ecosystem functions across a broad-scale, it can be presumed that the direct use value of soil biodiversity for farmers is less than its value for the global society, since the latter results from the summation of all different values, including this use value (see Eq. (1)). Levels of soil biodiversity in agroecosystems will thus be congruent with the farmers' own valuations but will be suboptimal from society's viewpoint. That is to say, soil biodiversity is an environmental asset, the use of which generates a

number of externalities. These effects, which are external to the market mechanism, are not taken into consideration in the resource allocation and management decisions of farmers. What is an optimal level of diversity from the viewpoint of the farmers who manage soil biodiversity is thus a suboptimal level from society's perspective (for a demonstration of the suboptimality resulting from market failures such as externalities, see Herfindahl and Kneese, 1974, pp. 47–53). Policy interventions will therefore be required if socially optimal levels of soil biodiversity are desired. The data and information which soil researchers need to provide to policy- and decision-makers are discussed in the next section.

3. Research agenda

3.1. Relationships between agricultural intensification and biodiversity

Whilst we are unaware of any studies that have examined biodiversity across a wide range of agricultural intensification, there are abundant studies relating productivity and diversity. A general relationship emerges from a wide range of studies on animal and plant communities in which diversity first increases and then falls as productivity increases (Rosenzweig and Abramsky, 1993). A similar hump-backed, unimodal relationship is also commonly found between disturbance and species diversity (Connell, 1978; Grime, 1979) and between stress and diversity (Grime, 1979; Austin, 1987; Austin and Smith, 1989). The underlying reasons for such relationships are unclear, but such patterns seem to hold across a wide range of organisms and environments.

As indicated earlier, the planned, above-ground diversity of plants and animals is often reduced (crop/animal specialization) and soil disturbance (tillage) is increased as agriculture becomes more intensive, and it is tempting to predict that both of these factors would result in reductions in the biodiversity of soil organisms. In fact, herbicides, which result in reductions in plant diversity, and cultivation both have unpredictable effects on the species diversity of various groups of soil fauna, which are in fact consistent with a hump-backed model for the species

Table 2

Some hypotheses which explore the relationships between agricultural intensification, biodiversity and ecosystem function

Global hypothesis I: 'Agricultural intensification results in a reduction in soil biodiversity leading to a loss of function detrimental to resilience and sustained productivity'

Hypotheses

1. The diversity and abundance of structures created by soil organisms is essential to the conservation and dynamics of soil organic matter turnover, nutrient release and soil physical properties essential for sustained productivity.
 - Does reduced biodiversity result in loss of function?
 - Are key functional processes independent of structural diversity?
2. Redundancy protects key functional groups of organisms from reduction to crucial thresholds below which agroecosystem function is impaired.
 - What are key functional groups the loss of which is detrimental to system resilience and productivity?
 - Can changes in soil biodiversity be detected before loss in function? (early warning signals)
 - Can the appearance or extinction of key functional groups or individuals within a group be an indicator of degradation?
3. Intensification triggers a spatial and temporal decoupling of organisms which alters the regulation of soil structure development and nutrient cycling.
 - Does loss of biodiversity disrupt the cascade of organic transformations necessary for effective and timely decomposition and nutrient release?
 - Can an external input reduce the role of one key functional group whilst boosting another and thereby enhance net productivity?
 - Can relationships between key functional groups be used to increase soil biodiversity?

Global hypothesis II: 'Agricultural diversification enhances ecosystem resilience and sustained productivity by increasing soil biodiversity'

Hypotheses

1. Above- and below-ground biodiversity are interdependent across scales of resolution from the pedon to the landscape.
 - Are above- and below-ground diversities interdependent?
 - Are roots, through differences in the amount and quality of inputs and in architecture, a primary mediator of diversity and function in soils?
2. Increases in the spatial and temporal diversity in biological resources, refuges and habitats (and hence biodiversity) buffers against impairment of agroecosystem function.
 - Does bioturbation result in improved dispersal of favourable organisms and a reduction in pests?
 - Can synergistic interactions, both above- and below-ground, be used to enhance function in degraded soils?

Table 2 (continued)

3. Soil organisms are more readily conserved through management than key specific functions are re-established through introduction.
 - Does enhanced soil biodiversity confer greater functional resilience?
 - Is re-introduction a feasible management tool?
4. Resource-limited farmers have the most to gain in the short-term from enhancement of soil biodiversity, although all will benefit in the long-term.
 - Is biodiversity a prerequisite for ecosystem resilience and long-term productivity but not for short-term production?
 - Does soil biodiversity buffer farmers against risk?
 - Are the most resource-limited farmers the most reliant on soil biodiversity?

response (Wardle, 1995). Together with the alleviation of nutrient stresses, which also occurs as agricultural systems intensify, these relationships with productivity, disturbance and stress lead us to postulate that the greatest diversities among soil organisms may well be found at intermediate stages of agricultural intensification.

3.2. Hypotheses relating agricultural intensification, biodiversity and ecosystem function

The conclusions of a discussion workshop on this subject identified two 'global' hypotheses which need to be tested (Table 2). The first main hypothesis explores several of the assumptions frequently made. These are: that biodiversity declines as a result of agricultural intensification; that reductions in soil biodiversity, and eventual extinction of species, may cause a catastrophic loss in function; and that reductions in biodiversity may reduce the ability of agricultural systems to withstand further disturbances or unexpected periods of stress. A direct causal link in this chain has yet to be proven.

The second main hypothesis (Table 2) concentrates on the potential for diversification of agriculture to increase the resilience of agroecosystems and the sustainability of agriculture through enhancing soil biodiversity. It thus aims to test the possibility for management of soil biodiversity to restore functions, to enhance the ability to withstand further stress and disturbance and the potential that this may improve agricultural productivity.

Diversity in cropping systems and management practices is widely accepted to buffer farmers against short-term risk. Agricultural diversification at both the scales of field and landscape may also have long-term benefits through the enhancement of functional and taxonomic diversity among the soil biota. This may be particularly true in degraded lands. If there is a direct link between above-ground biodiversity in the vegetation and below-ground biodiversity, then enhanced biodiversity above-ground will contribute to the re-establishment and multiplicity of soil organisms able to carry out essential biological functions. This will restore the resilience of the soil and thus buffer agroecosystems against risk, and help to sustain productivity. A rare example which supports the hypothesis that above-ground diversity and below-ground diversity might be related is the link between increased heterogeneity of substrate input and greater genetic diversity in the soil bacterium *Burkholderia cepacia* (McArthur et al., 1988).

Under each of these two main hypotheses, a number of other related hypotheses are listed, together with a number of questions which relate to those hypotheses. These lists are in no sense exhaustive, but serve to illustrate the types of questions which, if answered, would provide evidence to falsify these hypotheses. The greatest challenge is perhaps to test the hypothesis of resilience in soil.

As already mentioned, field research on the different values of soil biodiversity has yet to be undertaken. Likewise, no research on the appropriate policy instruments needed to bring about socially optimal degrees of soil biodiversity has been initiated. To start generating some of the evidence needed for policy-makers and donors, the following hypothesis could be tested in soil biodiversity studies: 'Resource-limited farmers have the most to gain in the short-term from soil biodiversity enhancement, although all members of society will benefit in the long-term' (Table 2). This hypothesis could be tested with a sample of farmers stratified into categories of resource endowments. The principal parameters which would have to be measured for each category of farmers are: (1) biodiversity in farmers' fields and in off-farm 'biodiversity reservoirs' (e.g. communal lands); (2) contribution of off-take from these different sources of biodiversity to household income, wealth accumulation and household nutritional sta-

tus; (3) changes in climatic and environmental risks during the period of the study. This provides a point of departure for studies focusing on the assessment of the different values of soil biodiversity for other groups in society and on the development of appropriate policy instruments for enhancing and maintaining soil biodiversity in farmers' fields in tropical countries.

3.3. Establishing causal links: words of warning

There are a number of approaches that can be used to test the above hypotheses. Almost all will inevitably rely on the correlation of the degree of agricultural intensification, the biodiversity of organisms in a given soil with the presence or efficiency of a particular function. There is often difficulty in finding representative examples for comparison in which a different degree of agricultural intensification is the only parameter which differs between given fields. Even when adjacent fields differ in the intensity with which they are used for agriculture, this will often relate to differences in the inherent fertility of the soils. Field boundaries often occur close to the junction of soil types for this reason. The danger in interpretation of such data is that a correlation is not proof of causal relationship.

More powerful approaches to unravelling the relationships between intensification, biodiversity and function are: (1) to study soil biodiversity and ecosystem function along gradients of intensification where trends can be explored (although as indicated above intensification may be influenced by environmental factors), or (2) to study soil biodiversity and functional relationships in field experiments which compare agricultural practices of differing intensity.

A further, simpler approach to exploring these relationships is to study the manipulation and restoration of functions by progressive (re)introductions of organisms into agricultural systems which have been degraded, or to diversify the agricultural system and monitor whether this leads to changes in biodiversity and function with time. From the stance of management interventions this approach is important in terms of designing strategies for the corrective management of degraded systems.

Except in the case of deliberate reintroductions of species lost from a soil, the re-establishment of

functions is dependent on the recolonization of the soil by particular organisms. This will depend on the dispersal and migration rate of the organisms and the distance by which the organism is separated from the soil—encapsulated in the theory of island biogeography (MacArthur, 1975; Stanton and Tepedino, 1977). Further, if the niche of a given (group of) organism(s) has been occupied in its absence by another (group), then it may not be possible for the original organism(s) to re-establish.

Selection of the scale for study will critically influence conclusions drawn in relation to the importance of biodiversity in various roles. Further dangers which complicate interpretation of pattern in biodiversity arise from periodic variations in biodiversity in the short-term due to seasonality or in the long-term due to progressive successional change. Whilst problems and pitfalls in the study of biodiversity in soils can readily be identified, this is a fascinating and important field ripe for exploration.

Environments that are uniform, highly stable and with adequate resources are likely to allow the domination by a particular species or group, resulting from competitive exclusion (see Grime, 1979). Factors that are often important in maintaining biodiversity and preventing competitive exclusion by a particular (group) of organisms are, for example, a degree of spatial heterogeneity, instability and predation (Huston, 1994). All of these factors may lead to reductions in biodiversity if intense. Thus a simple relationship between increasing intensification and reductions in biodiversity is unlikely to be encountered in all cases.

4. Conclusions

There is an enormous amount that we do not know about diversity in soil, and we are certainly unable at present to assess the values of soil biodiversity fully. Given the currently intangible dimensions of biodiversity in soil, the furthering of our understanding is best placed within study of functions which biodiversity confers on the soil.

There is evidence that ecosystem function may be significantly impaired by loss of soil biodiversity, if not inevitably, at least within a range of defined conditions, and that it might not be possible to fully

substitute this in all circumstances. There is a need to clearly define the conditions in which such impairment is critically important to agricultural production and sustainability and to determine what management interventions may be made to alleviate or ameliorate problems resulting from loss of diversity.

In our concern for protection of our planet for future generations, it would be a travesty should we not act urgently both to improve our understanding and to protect the vast biodiversity inherent in soils.

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Agricultural intensification, soil biodiversity and agroecosystem function

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