Biodiversity and ecosystem services in agricultural landscapes: Are we asking the right questions?

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Abstract

The assumed relationship between biodiversity or local richness and the persistence of 'ecosystem services' (that can sustain productivity on-site as well as off-site, e.g. through regulation of water flow and storage) in agricultural landscapes has generated considerable interest and a range of experimental approaches. The abstraction level aimed for, however, may be too high to yield meaningful results. Many of the experiments on which evidence in favour or otherwise are based are artificial and do not support the bold generalizations to other spatial and temporal scales that are often made. Future investigations should utilise co-evolved communities, be structured to investigate the distinct roles of clearly defined functional groups, separate the effects of between- and within-group diversity and be conducted over a range of stress and disturbance situations. An integral part of agricultural intensification at the plot level is the deliberate reduction of diversity. This does not necessarily result in impairment of ecosystem services of direct relevance to the land user unless the hypothesised diversity-function threshold is breached by elimination of a key functional group or species. Key functions may also be substituted with petro-chemical energy in order to achieve perceived efficiencies in the production of specific goods. This can result in the maintenance of ecosystem services of importance to agricultural production at levels of biodiversity below the assumed 'functional threshold'. However it can also result in impairment of other services and under some conditions the de-linking of the diversity-function relationship. Avoidance of these effects or attempts to restore non-essential ecosystem services are only likely to be made by land-users at the plot scale if direct economic benefit can be thereby achieved. At the plot and farm scales biodiversity is unlikely to be maintained for purposes other than those of direct use or <u>'utilitarian'</u> benefits and often at levels lower than those necessary for maintenance of many ecosystem services. The exceptions may be traditional systems where intrinsic values (social customs) continue to provide reasons for diversity maintenance. High levels of biodiversity in managed landscapes are more likely to be maintained for reasons of intrinsic, serependic (‘option’ or ‘bequest ’) values or utilitarian (‘direct use’) than for functional or ecosystem service values. The major opportunity for both maintaining ecosystem services and biodiversity outside conservation areas lies in promoting diversity of land use at the landscape and farm rather than field scale. This requires however an economic and policy climate that favours diversification in land-uses and diversity among land users.

Keywords

agricultural landscapes, biodiversity, ecosystem services, functional groups, resilience

1. INTRODUCTION

The role of biological diversity in the provision of ecosystem goods and services and the way this role can be valued and managed during agricultural intensification is much debated but still poorly understood. A key problem in all debates on biological diversity is that the abstraction ‘diversity’ has often not been distinguished from the specific attributes of the community of organisms that is under study in any particular location or system. Likewise, evaluations of diversity have more often than not been assessments of the value of biological resources as such rather than assessments of the value of diversity per se (Nunes and van der Bergh, 2001). For instance if the interest lies in the functional roles of the community these may depend on the ‘structure’ of the vegetation and the relationships between different ‘functional groups’, rather than on diversity as such (Woodward, 1993). Experiments based on random species assemblages may be appropriate tests for hypotheses about ‘diversity’ per se, but tell us very little about the largely self-selected assemblages that make up natural ecosystems. In the case of agro-ecosystems, whilst the dominant crops or livestock are human choices, by far the majority of the species (as soon as one takes the belowground part of the system into consideration) are self-selected. So, are we asking the right question about the relations between biodiversity and ecosystem services? Does the loss of diversity at plot-to-global scales imply a threat to critical ecosystem functions? Can we identify thresholds in such a process?

Global diversity derives from the lack of overlap in species, genetic or agro-ecosystem composition between geographic or temporal domains. While ‘agricultural development’ directly affects local (ie. plot level) diversity, it probably has even stronger effects by homogenizing at higher scales, facilitating the movement of ‘invasive species’ and the introduction and spread of ‘superior’ germplasm of desirable species. Scale is thus of overriding importance in our analysis and we may well find that answers may appear contradictory between different ways of defining temporal and spatial boundaries to the system under consideration. In this review we will first consider the concepts of ‘biodiversity’ and ‘ecosystem functions’, and then the evidence that links relevant aspects of the two, before we embark on an exploration of how this relationship depends on scale and can be ‘managed’.

2. THE BIOLOGICAL BASIS OF ECOSYSTEM GOODS AND SERVICES

Humans have evolved as part of the world’s ecosystems, depending on them for food and other products and for a range of functions that support our existence. Natural ecosystems, as well as those modified by humans, provide many services and goods that are essential for humankind (Matson et al., 1997). Efforts and interventions to manipulate (agro)ecosystems in order to meet specific production functions, represent costs to the rest of the ecosystem in terms of energy, matter and biological diversity, and often negatively affects goods and services that so far were considered to be free and abundant. These are anthropocentrically regarded as services because they provide the biophysical necessities for human life or otherwise contribute to human welfare (UNEP, 1995; Costanza et al., 1997). Most if not all of these services are based on a ‘lateral flow’, or movement across the landscape of biomass (such as food, fibre and medicinal products derived from the sea, inland waters or lands outside of the domesticated ‘agricultural’ domain), living organisms and their genes, or earth (nutrients), water, fire or air elements. Examples of ecosystem services particularly important for agroecosystems and agricultural landscapes are: maintenance of the genetic diversity essential for successful crop and animal breeding; nutrient cycles; biological control of pests and diseases; erosion control and sediment retention; and water regulation. At a global scale other services become important such as the regulation of the gaseous composition of the atmosphere and thence of the climate. A list of such services is given in the first column of Table 1 of the Appendix, and their connection to lateral flows is discussed by Van Noordwijk et al (this volume, Table 1).

These ecosystem goods and services are biologically generated. The community of living organisms within any given ecosystem carries out a very diverse range of biochemical and biophysical processes that can also affect neighbouring systems. These can be described at scales ranging from the subcellular through the whole organism and species populations to the aggregative effect of these at the level of the ecosystem (Mooney and Schultze 1993). All ecosystems have permeable boundaries with respect to material exchanges but the within–system flows usually dominate those between systems, such as between land-use or land-cover types within a landscape. For purpose of this paper we define ecosystem functions as the minimum aggregated set of processes (including biochemical, biophysical and biological ones) that ensure the biological productivity, organisational integrity and perpetuation of the ecosystem. There are no agreed criteria for defining a minimum set of such functions but for the purposes of this paper the second column of Table 1 lists ecosystem functions alongside the ecosystem services they provide. Further explanation of these relationships is given below but it is useful to note that these functions can be pictured as having a hierarchical relationship. The energy captured in primary production is utilised in the herbivore and decomposer food chains. Interactions between these three subsystems occur through nutrient exchanges and a variety of biotic regulatory mechanisms as well as by energy flow. In particular the balance between the constituent processes of primary production and those of decomposition determines the amount of energy and carbon maintained within the system and is the major natural regulator of the gaseous composition of the atmosphere at a global scale (Swift 1999).

3. BIOLOGICAL DIVERSITY AND ITS VALUES

Most discussions and empirical studies on biodiversity have focused on issues of a relatively small range of organisms. In contrast, the Convention on Biological Diversity defines its area of concern as:

" …the variability among living organisms from all sources, including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems" (Heywood and Bates, 1995). Diversity within each one of these three fundamental and hierarchically related levels of biological organisation can be further elaborated as follows: genetic diversity is the variation within and between species populations; species diversity refers to species richness, that is, the number of species in a site, habitat, ecological zone or at global scale; ecosystem diversity means the diversity of assemblages (and their environments) over a defined landscape, ecological zone or at global scale.

Biodiversity in this paper refers to the totality of the species (including the genetic variation represented in the species populations) across the full range of terrestrial organisms i.e. invertebrate animals, protists, bacteria and fungi, above- and below-ground, as well as the vertebrates and plants which often constitute the main concerns of biodiversity conservation. With a definition as broad and inclusive as this, it is highly unlikely that any clear and precise statements about relationships between 'biodiversity' and functions can be formulated and tested that can be helpful in guiding human activity. Similar to the situation with 'watershed functions', which are considered in the next part of this volume, we may find that discussions on components of the overall biodiversity concept in relation to land use are more productive and open to progress than those that stay at the aggregate level. In the section immediately following we shall refer to the diversity within ecosystems (often termed alpha diversity) and in later sections to that at the broader scale of the landscape (which embraces concepts of both beta and gamma diversity).

The analysis of biodiversity and its management is highly influenced by the perspective used. In particular different sectors of society attribute different values to biodiversity. Since biological diversity concerns different levels, from genes to species and ecosystems, the value of diversity can likewise be defined in a number of different ways. Broadly speaking four different types of value can be usefully recognised, although different terminology is often used by different authors (see Nunes and van den Bergh, 2001 for further details).

First is the intrinsic (sometimes called 'non-use') value of diversity to humans, or the value that biodiversity has on its own. This value comprises cultural, social, aesthetic, and ethical benefits. Some groups in society attribute high social and religious values to individual species or communities of organisms; others derive value from the simple fact of high diversity per se in such systems as tropical rainforests or coral reefs.

Second is the utilitarian (also called direct use, contributory, primary or infrastructure) value of components of biodiversity. These are the subsistence and commercial benefits of species or their genes derived by one or other sectors in society. The utilitarian value may be private and accrue to the land managers (farmers, local community, government). This is most obvious with respect to high value agricultural crops but also applies to the other types of good listed in Table 1. Utilitarian value may also accrue to other sectors in society, in addition to private land managers. For instance, the pharmaceutical industry values the tropical forest tree Prunus africana very highly because its bark contains chemicals used for manufacturing a drug. Another example is that in Africa, many farmers living near natural (and protected) forests withdraw substantial monetary benefits from their hunting and from collecting plants and tree products in these forests (Pottinger and Burley, 1992). Utilitarian value thus refers to the use of organisms that are part of the local diversity as inputs into consumption and production processes.

Thirdly, biodiversity can be said to have serependic (‘option’, or bequest) value. This is the belief in future but yet unknown value of biodiversity to future generations, for example the presence of a microorganism with an as-yet undiscovered genetic potential for industrial products. These three types of value of biodiversity are ethnocentric and depend very much upon the cultural values and preferences of different sectors of society. This is why some authors, interested in such values, stress that ‘the conservation of biological diversity depends as much on society’s ethical views as on facts’ (Barrett 1993).

Finally, biodiversity contributes to ecosystem life support functions and the preservation of ecological structure and integrity. We refer to these functions as the functional value of diversity. This category of value has only been relatively recently recognised in the economic literature as an important category per se which overlaps partially with concepts such as that of ‘indirect use’ value (see Kerry Turner, 1999). Part of this functional significance may result in direct utilitarian value for Homo sapiens in the production of goods and services that can be priced. Beyond this lie a range of ecosystem services that are of acknowledged benefit to humans but which generally lie outside the boundaries of recognised direct utilitarian benefit. The purpose of this paper is to analyse the functional values of biodiversity with particular reference to the diversity in agricultural landscapes.

4. WHAT IS THE RELATIONSHIP BETWEEN DIVERSITY AND FUNCTION?

4.1 Concepts

Biologists have for many decades speculated on the question of why there are so many species of living organism. As explored in the theory of island biogeography, the diversity within any ecosystem at any point in time is the result of a 'self selection' process, that involves co-evolution of the species comprising the biological community within a given ecosystem by interactions among them and with the abiotic environment through time. This is not an isolated process. New species may enter an ecosystem from neighbouring areas, some establishing themselves and others failing to do so. Partly as a result of successful newcomers or new adaptations emerging in existing ones (be they competitors, predators, pests or diseases), and partly as a result of fluctuations in abiotic environmental conditions, some of the existing species may become (locally) extinct over any period of time. The species richness of any given ecosystem or land unit is therefore a dynamic property.

Recently the conventional explanation of local diversity as well as its 'functionality' embodied in the niche concept has been challenged by theories that derive patterns close to the observed ones from 'random walks' in abundance of species without any a priori prediction of the direction of selection pressures and based on an equivalence of intra- and interspecific competition (Hubbell, 2001).

In agro-ecosystems farmers take a dominant role in this dynamic by the selection of which organisms are present, by modifying the abiotic environment and by interventions aimed at regulating the populations of specific organisms ('weeds', 'pests', 'diseases' and their vectors, alternate hosts and antagonists). The dynamic nature of the (local, patch level) diversity of any system, whether natural or agricultural, is often underrated, as is the importance of the selection pressure and process. The diversity of any system is not adequately represented simply by the number of species (or genotypes) present, but by the relationships between them in space and time. Attempts to assemble combinations of the same number of species under slightly different conditions and in particular without the history of interaction often fail (Ewel, 1986, 1999). But what makes any existing species combination into a 'system' is still largely elusive. Some insights obtained in analysing food webs may help. For example Neutel (2001) showed that the majority of belowground food webs constructed from random combinations of organisms did not meet dynamic stability criteria, even though all parameters such as abundance of groups and dynamic properties were chosen in a 'normal' range when considered one-by-one. Yet, systems with the actual parameter combinations that are attained in the field did meet stability criteria, suggesting that partly uncovered rules about the proportionalities and co-variance within the normal range are crucial.

Debate on the relationship between biological diversity and ecosystem function has a long history which has taken on new vigour (and sometimes even rancour) since the advent of the Convention on Biological Diversity (see Woodwell and Smith 1969 for the older literature and Schulze and Mooney 1993, Mooney et al 1995, 1996, and many of the citations below for more recent discussion). Vitousek and Hooper (1993) contributed a major focus to this debate through hypothesising three different possible relationships between plant diversity and broad-based ecosystem functions such as the rate of primary production (Figure 1). Their analysis of current evidence led them to propose that the asymptotic relationship shown as Curve 2 in Figure 1 was the correct one. This suggests that whilst the essential functions of an ecosystem, such as primary production, require a minimal level of diversity to maximise efficiency this effect is saturated at a relatively low number. Swift and Anderson (1993) proposed that this relationship could also apply to the decomposer system. Examples of essential functions in this case are the basic suite of catabolic enzymes (e.g. for cellulolysis, lignin degradation etc), the facilitation role that invertebrates play by reducing particle size by their feeding activity, and biophysical processes of pore formation and particle aggregation. It is interesting to note however that the communities of organisms contributing to the ecosystem function of decomposition are taxonomically much more diverse than those of primary production.

4.2 Experimental approaches

Over recent years a number of authors have reported on experiments investigating the links between diversity and specific functions (e.g. see Ewel et al 1991, Naeem et al 1994, Naeem and Li 1997; Tilman and Downing 1994; Tilman et al 1996,1997; Hooper and Vitousek 1997) that appear to broadly corroborate the predictions of the Vitousek-Hooper hypothesis for primary production. This has however generated an equal amount of discussion in refutation and the issue remains significantly a matter of interpretation and opinion (see Grime 1987; Hodgson et al 1998; Lawton et al 1998; Wardle 2000; Naeem 2000). There is no space here to review these studies in detail, but refer to Kinzig and Pacala (2001) and Tilman and Lehman (2001) for a synthesis that acknowledges the 'sampling effect' that probably dominates the initial phases of the experiments and the fact that 'niche assembly' will be a relatively slow process, especially where we are interested in stages beyond the pioneer phase. Each one of the experiments quoted can be criticised in one way or another. The strictest interpretation of many of the experiments would be that the conclusions apply only to the specific combinations of organisms used in the tests, and in most cases these are assemblages constructed for experimental purposes rather than naturally co-evolved communities. At a fundamental level such experiments suffer from a basic methodological paradox – in order to describe and understand diversity and complexity we need to simplify it, and take away the self-selection that governs real-world diversity. Dealing with the totality is impossible. For instance there is no single (or combination of) methods that would allow for the total inventory of the species richness of even a small volume of soil. It is thus difficult to draw general conclusions about ‘diversity’ as such and in particular with respect to naturally co-evolved communities. The results of such ‘un-natural’ experiments may however be more applicable to agricultural systems that in one sense can be said to have been assembled in a similar way.

4.3 The minimum diversity required within a functional group

One potentially valuable interpretation of the Vitousek-Hooper relationship has been that the minimal level of diversity required to maximise the production function consists of representatives of an essential set of ‘functional groups’ of plants (Schultze and Chapin, 1987). A functional group may be defined ‘ a set of species that have similar effects on a specific ecosystem-level biogeochemical process’. As Vitousek and Hooper put it the ‘essential’ plant species are those that contribute in different ways to the key ecosystem functions – in the case of primary production by exploiting different components of the available resources by differences in canopy structure to maximise light capture or symbionts and root architecture to optimise capture of water and nutrients. Drawing together the threads of this discussion we hypothesise that ‘the minimum diversity essential to maintain any given ecosystem function can be represented by one or a few functionally distinct species i.e. one or a few representatives of a small range of functional groups’ is a useful null-hypothesis to guide investigations of the functional significance of biological diversity in agricultural systems. It may need further operationalization for specific ecosystem contexts, however. The total diversity required then depends on the number of functions that are recognized and to the degree of overlap in ‘functional groups’ between these different functions.

5. WHICH FUNCTIONAL GROUPS OF ORGANISMS ARE ESSENTIAL?

The functional group concept is briefly discussed in the Appendix to this paper and Table 1 lists a minimal set that we propose are needed to provide the ecosystem goods and services we have been addressing.

The classification of plants into functional groups has drawn a great deal of recent attention because of the recognition of the pressure being exerted on terrestrial ecosystems by global climate change (Smith et al .,1997). The primary producers (together with the vertebrate herbivores) are our major source of food and are also the source of fibre and other useful materials such as latex. Molecules with antibiotic, therapeutic, pesticidal or similar biological activities utilised by humans are however synthesised by many groups of organisms (e.g. bacteria and fungi) and are often very specific in origin. Diversity is therefore an essential pre-requisite for maintenance of supply, particularly of new products, although the capacity to biologically generate or synthesise new compounds under laboratory conditions has been greatly increased by the advent of genetic engineering.

Decomposition and mineralisation of organic matter of plant and animal origin and synthesis and decomposition of soil organic matter are carried out by a very diverse community of invertebrates, protists, bacteria and fungi. Other elemental transformations often are carried out by a diverse set of functional groups with very specific biochemical capacities, for example certain of the bacteria of the nitrogen cycle. Diversity within these groups varies from very low to high, but it can be experimentally demonstrated that a single species per function may be sufficient under a given set of environmental conditions.

The dominant biological properties regulating water flow and storage in the soil are the plant cover, the soil organic matter content and soil biological activity. Macrofauna such as earthworms, termites and other invertebrates influence the pore structure. Bacteria and fungi modify the extent of aggregation of soil particles. All these organisms and an additional range of decomposer organisms influence synthesis and decomposition of soil organic matter.

Control of erosion and trapping of sediment is regulated by the architecture of the plants at and below the soil surface, the amount (and hence the rate of decomposition and movement) of surface litter, and the physical quality and organic matter content of the soil.

Under natural conditions the interactions between the populations of organisms at the various trophic levels i.e. plants, herbivores, symbionts, parasites, decomposers, predators and secondary predators result in a dynamic balance of population sizes. The total diversity is huge but any single population is only influenced by a relatively small number of interactions. Biological regulation of a specific pest, pathogen or disease vector of interest to humans is therefore dependent on a significant level of diversity among its parasites or predators. These in their turn may depend on other elements of diversity for their survival e.g. the presence of microhabitats, alternative hosts, nesting or egg laying sites, or refuges often provided by the vegetation.

Chemical transformation of toxic organic elements, chelation or absorption of basic elements and removal of toxic levels of nutrients or other chemicals from ground, running or soil water may be carried out by a diverse range of bacteria, fungi or protists often in association with invertebrates. In well-established waste disposal systems these organisms form 'guilds' which function in a very integrated way. As with decomposers distinct guilds may operate across different ranges of environmental gradients of temperature, pH, moisture, etc.

The earth's climate is regulated by the content of 'greenhouse' gases in the atmosphere – (CO_2, CH_4, NO_x, etc). Carbon dioxide is emitted or taken up under one circumstance or other by the majority of living organisms and is thus a phenomenon of such generality as to defy attempts to relate its dynamics to changes in diversity other than the totally catastrophic. Methane and the nitrous oxides are however the product and/or substrate for a relatively small number of bacterial species in the soil associated with soil, decomposing organic matter or the gut flora of animals. Diversity change may thus be more significant in these cases.

It is worth noting that even when the discussion of function-diversity relationships is reduced to considering only functional groups, the minimum extent of necessary diversity that is implicated is still very high.

5.1 What is the significance of diversity within functional groups?

If the above hypothesis is correct and ecosystem functions can be maintained by the minimal number of representatives of the essential functional groups then the questions remains as to what is the significance of the often high diversity within functional groups – which takes us back to the basic biodiversity question 'why are there so many species'? Answers to this question depend strongly on the scale of consideration. Different species often occupy similar ecological roles in geographically separated areas, and one of the major threats to local species is the lateral flow of organisms once such geographical barriers disappear. Replacement of local species by intrusive exotics does not necessarily change ecosystem processes, or local richness, although there are dramatic exceptions for specifically successful (from the perspective of the invader, at least) invasions. Such invasions are likely, however, to reduce global diversity and in fact have been identified as one of the major drivers of 'global change'.

Vandermeer et al (1998) summarized the main issues in the discussion on the role of diversity in agro-ecosystems in the following three hypotheses of links between diversity and function:

1. Biodiversity enhances ecosystem function because different species or genotypes perform slightly different functions (have different niches);
2. Biodiversity is neutral or negative in that there are many more species than there are functions and thus redundancy is built into the system;
3. Biodiversity enhances ecosystem function because those components that appear redundant at one point in time become important when some environmental change occurs.

It is valuable to note that these are not necessarily mutually exclusive hypotheses, as they may refer to different space and/or time aspects of the system and the function of specific concern. We need to clearly separate the question of how the current diversity came into being (the ‘self organization’ of the system, based on the success in the evolutionary history of all component species) from the human or teleological perspective of the relevance of this diversity. Just as we have to distinguish between ‘diversity per se’ and ‘diversity of actual systems’, we have also to recognize that not all components of a system have the same probability of being lost as a result of simplification of agro-ecosystems and some functions may therefore be more resilient than others. Differences in life histories of the key groups of organisms confer different temporal and spatial contexts to their role in the ecosystem and their responsiveness to its self-organising properties.

The third of Vandermeer et al’s (1998) hypotheses is extremely pertinent to the question of how much of this diversity is needed to maintain ecosystem goods and services in the face of agricultural intensification and other aspects of ongoing ‘global change’. There is certainly substantial experimental evidence that the many key functions can be maintained by only small numbers of species within a particular functional group. For example monotypic cover by perennial plants can be as effective as a diverse community in controlling erosion. Although the decomposer community of a particular soil may be very diverse only a minority of the hundreds of species of fungi, bacteria or invertebrates participate in the decomposition process at a given time and place. The extent of redundancy implied by this can be demonstrated under laboratory conditions where decomposition can be fully mediated by single species cultures of enzymatically-diverse organisms such as white-rot basidiomycete fungi whilst in nature the same process may be carried out by several species of fungi, bacteria and animals (Swift 1976, Giller et al 1997).

The third hypothesis raises questions whether key functions can be maintained by one (and the same) species under all circumstances. This addresses the issue of the capacity of ecosystems to adapt to changing circumstances that result from elements of stress and disturbance. The capacity of a system to respond to and recover from disturbance is termed its resilience. This property has been attributed to the degree of connectivity within an ecosystem, a feature that depends at least in part on the composition and diversity (Holling 1973, 1986; Allen and Starr 1982). Diversity within functional groups may provide an important means for increasing the probability that ecosystem performance can be maintained or regained in the face of changing conditions. For the below-ground community for instance there is evidence that the same enzymatic function is carried out by different species of bacteria or fungi from the same soil under different, and even fluctuating, conditions of moisture stress or pH (see Griffin 1972 for discussion of this). In the case of plants different species may play a similar functional role in different seasons, under varying conditions of climatic or edaphic stress and in different stages of patch-level succession.

6. RESILIENCE AND DIVERSITY THRESHOLDS

Functional diversity thresholds are thus likely to be higher in the real world than in the relatively controlled situations under which most of the experiments on diversity-function relationships have been conducted. Recognition of the importance of diversity to the property of resilience suggests furthermore that the implication of equilibrium in the way that Figure 1 is drawn (see also figures 2 and 3) may be misleading. The shifts between different states of functional efficiency with changes in diversity are more likely to be rather abrupt. Perhaps a case could be made recognising resilience as an ecosystem service rather than a property. An alternative view, however, is to see resilience as a property which varies among functions rather than a unitary ecosystem property. The decomposition function for example, may be substantially more resilient than that of the regulation of specific pest populations.

Resilience is a concept that requires consideration at different spatial scales. The resilience of any local system after shocks that lead to local loss of diversity depends strongly on the ability of organisms to recolonize from the neighbourhood, and thus on the distance to the nearest suitable habitat and the dispersal of the organisms in question.

7. MANAGING BIODIVERSITY AND ECOSYSTEM SERVICES IN AGRICULTURAL LANDSCAPES

7.1 What is the impact of agricultural intensification on biodiversity and ecosystem functions?

Our main concern in this paper is with biodiversity issues in agricultural landscapes i.e. landscapes containing agroecosystems. Agroecosystems can be defined as (natural) ecosystems that have been deliberately simplified by people for purpose of the production of specific goods of value to humans. The simplification down to one or a few productive plant or animal species is implemented for greater ease of management and specialisation of product to suit market demands, especially in highly mechanized forms of agriculture. In an ecological sense the system may be seen as one which is maintained by a high frequency of disturbance, in an early successional stage (Conway, 1993). In such systems a distinction has been made between 'planned' and 'associated' diversity (Swift et al 1996; GCTE 1997). The planned diversity is the suite of plants and livestock deliberately retained, imported and managed by the farmer. The composition and diversity of this component strongly influences the nature of the associated biota – plant, animal and microbial. The issue is more complex than the single issue of the extent of planned biodiversity that is maintained however. Agroecosystems are managed by substitution and supplementation of many of the natural ecosystem functions by human labour and/or by petro-chemical energy or its products. In addition to their direct effects on production these interventions provide the means to reduce the risk associated with reliance on ecosystem services, although it can be argued that this is serving to substitute one set of risks for another – that of dependence on the market. Furthermore whilst substitutions may buffer some of the functions they also run the risk of further damaging others. For instance the addition of pesticides may control diseases of immediate negative impact but also kill non-target organisms with other functions such as pollination or soil fertility enhancement.

During agricultural intensification the diversity of crops and livestock is reduced to one or a very few species of usually genetically homogenous species. The varieties are selected or bred for yield (e.g. high plant harvest index), taste and nutritional quality. Plant arrangement is commonly in rows, fallow periods are bare, sequences may be monospecific (varietal) or of two or rarely more species. This is in contrast to natural ecosystems where the genetic diversity of plants (both within and among functional groups) is high but varies in relation to environment. The effects of land use change and agricultural intensification on biodiversity and associated functions are still poorly understood but conversion to agriculture almost always results in fewer species of both planned and associated biota with lower genetic variation and representing less functional groups. Nonetheless the extent of diversity in even so-called monocultures may be underestimated by plot-level assessment of diversity at any point in time. A rapid interannual turnover of the germplasm is often employed to stay ahead of the evolutionary race with pests and diseases, adding a time dimension to diversity that may exceed evolution in natural systems, albeit with respect to a narrow genetic base. This varietal turnover depends however on ‘externalized’ functions of maintaining genetic diversity in gene banks, and on the mechanisms of rapid multiplication and transfer of such germplasm. This situation contrasts with that of extensive agricultural systems where diversity is deliberately maintained within the system with or without external exchange. Here a plot-level assessment may have more relevant boundaries of measurement, although lateral flows of organisms exist here as well. Production systems based on perennial crops and trees provide less opportunity for rapid turnover of varieties for obvious reasons, and there clearly is a much stronger need here for maintaining plot-level diversity as a risk management strategy (Van Noordwijk and Ong, 1999).

7.2 Primary production

Whilst many recent experiments have tended to confirm that community primary production may be maximised by a low-number diversity of functional types (see above) there is also abundant evidence that mono-typic stands can reach the same levels of production within relatively narrow environmental conditions. Biomass production is however not the only function or service performed by plants in ecosystems. The secondary functions related to ecosystem services may be more biodiversity-sensitive than that of food production. 'Intensive' production systems for specific high-value products (e.g. spices) can however be very diverse. Another exception may be in relation to pharmaceutical and agro-chemical goods. Most products of these types are initially gathered from natural or secondary vegetation or derived from microbial cultures obtained from soil. Once the markets for such products are established, however, the required control over the concentrations of biologically active substances tend to favour more technically advanced and intensive modes of production. Maintaining global diversity is thus essential for both present and future needs although the synthetic capacity brought by the molecular biological revolution is fast rendering this less so. Herbivore diversity is highest in heterogeneous systems with high plant and resource diversity but monotypic vertebrate herds can reach equivalent levels of production in simplified grazing systems. Pest epidemics tend to occur in circumstances of low genetic diversity of the host plants or livestock.

7.3 Nutrient cycling

Nutrient cycles become more open in agricultural systems with losses of nutrient through offtake in harvest, run-off from compact surfaces, increased volatilisation through a changed surface environment and increased leaching associated with decreased soil organic matter content. These losses can be substituted by inorganic inputs but the efficiency of return to the plant is often low and fertilisation is usually required at levels far in excess of direct crop demand, which further exacerbates the losses and can leads to pollution of groundwater etc. There is substantial evidence demonstrating gains in crop productivity from nutrient additions through mixtures of organic and inorganic sources of nutrients compared with either alone (e.g. Swift et al 1994). Maintenance of organic inputs to the soil is thus an important management strategy for efficient use of external inputs. Advantages in utilising a variety of such inputs have also been demonstrated because of the strong influence of input chemistry (‘’resource quality’) on patterns of mineralisation. The diversity of organisms involved in nutrient cycling may be substantially reduced under agricultural intensification but there is little evidence of significant effects on decomposition and mineralisation processes which has been attributed to a high level of functional redundancy among decomposer fungi, bacteria and microregulators such as nematodes or collembola (Beare et al 1994, 1997; Giller et al 1997). The significance of this loss of diversity should not however be assumed to be inconsequential. In particular it is unclear how the resilience of the system under conditions of change is influenced by such loss. Organisms with very specific functions, such as those exhibited by some bacteria of the nitrogen cycle, often show specialisation to particular soil conditions such as pH and specific genotypes may be lost as a result of soil degradation. Specific strains of dinitrogen-fixing bacteria may also be lost as a result of agricultural intensification resulting in the need for subsequent inoculation (Kahindi et al 1997).

7.4 Organic matter dynamics

Soil organic matter (SOM) is a keystone component of the ecosystem in the sense that its impact on overall system performance exceeds its relative share in the energy flow through the system. Soil organic matter (SOM) stores and buffers nutrient concentrations, influences water storage in the soil and is a major factor in determining soil structure and thence erosivity. Above all it is a store of energy in the soil that drives many of the soil-based processes. SOM synthesis and decomposition is brought about by much the same community of organisms as those involved in decomposition of plant litter. A well-charted phenomenon is the decline in SOM as a result of conversion of natural ecosystems to agriculture. Farmers utilize the nutrients mineralised as part of this decline of the SOM capital to support high initial levels of crop production after clearance. Soil tillage is also an effective additional way of stimulating the breakdown of SOM and plays a key role in promoting crop yields after land conversion to agriculture, until a new and lower equilibrium between breakdown and formation of SOM is reached. The level of the new SOM equilibrium, with its consequent impact on nutrient cycling, soil water regimes and erosivity, is related to the quantity of plant litter input, which is almost invariably lower than that of natural systems. Crops in intensive systems are usually selected for high harvest indices, and there may be uses for crop residues other than soil fertility maintenance (e.g. fodder or fuel). The SOM content is thus related to the quantity, diversity and mode of management of organic input to soil. A key feature of agroecosystem management is thus the trade-off between the gains in production from 'mining' the SOM versus the potential negative impact on its other ecosystem services and in particular on system resilience. This 'trade-off' between the different values of SOM has been rarely recognised but become a matter of greater interest as society has begun to realize the potential value of sequestering carbon in soil as a means to slow down the rate of global climate change. A research question of continuing interest is whether the functional properties of SOM are in any way influenced by the diversity of organic materials from which it is synthesised.

7.5 Watershed functions

The most important factors regulating water infiltration and retention are the extent of ground cover by plants and/or plant litter. The reduction in these, including interposing of periods when ground is bare, leads to greater run-off and diminished infiltration as well as increasing the risk of erosion. Substitution by mechanical tillage can ameliorate as well as aggravate these effects. Monospecific cover can be just as effective as a diverse one with respect to limiting run-off and erosion, trapping sediment and promoting infiltration, but to be effective it has to be present year round. Diversity of organic inputs is likely to have a positive effect by widening the probability of differences in timing of litterfall and rates of disappearance from the soil surface. As soil protection on slopes depends more on partially decomposed litter with good ground contact than on fresh leaves that can be easily washed away, the role of plant diversity on slopes is likely to be greater than on flat lands. The macrofauna moving between litter layer and soil strongly influence partitioning of water between surface runoff and infiltration as well as modifying water movement within soil. Interesting examples of the influence of these 'ecosystem engineers' show how circumstance-specific diversity effects may be. Soil engineers making macropores in the soil are not welcome in all circumstances. In bunded rice fields, farmers make an effort to destroy soil structure by puddling to reduce the porosity of the soil and building dykes to contain the water. These earthworks may be destroyed by the actions of earthworms and surveys by Joshi et al. (1999) in the Ifugao Rice Terraces (IRT), in the Philippines showed that 125 out of 150 farmers interviewed ranked earthworms as the most destructive pest of terraced rice fields. In a second example the conversion of Amazonian rainforest to pastures has been shown to lead to extinction of the natural earthworm community, which have been replaced in some circumstances by a single exotic species, Pontoscolex corethrurus. This has a negative effect on pasture productivity because the introduced worms compact the soil, whereas the native species improve soil structure (Chauvel et al 1999). Inoculation with species from the forest might reverse this effect, but remains to be tested.

7.6 Risks of pests and diseases

As already indicated the decreased genetic diversity of plant cover increases the risk of pest attack. Simplification of the ecosystem and in particular the use of broad-spectrum pesticides also decreases the diversity of natural enemies and increase risks of pest attack (Lawton and Brown 1993). Pesticides also have negative effects on non-target beneficial organisms including pollinators and beneficial soil biota.

7.7 Greenhouse gas emissions

Land-use change alters the balance of gas emissions and thence influences global climates. There are very large increases in the CO_2 output during clearing from natural vegetation and break down of soil organic matter reserves that are rarely if ever balanced by regrowth. The output of methane may be significantly increased in systems such as paddy rice and intensive cattle production and of nitrous oxides by N-fertilisation. These changes are linked to alterations in soil structure that dominate changes in the activity of a variety of soil organisms (e.g. methanogenic and methanotrophic bacteria) but we are not aware of any documented case where such effects are linked to the absence of functional groups or to biodiversity change per se.

7.8 A hierarchy of functions

There are a few general conclusions that may be drawn from this brief review of the impacts of agricultural intensification on the relationship between biodiversity and ecosystem services. First that whilst there are a number of clear examples where changes in diversity have threatened the provision of ecosystem services, especially relating to the regulation of pests and diseases, there are also others where the changes in biodiversity seem to be functionally neutral, at least within relatively stable environmental conditions. Second there may be some functional groups, particularly micro-organisms such as the decomposers, where the degree of functional redundancy is such that the resilience of the function is very high. These two observations may be generalised by stating that there are no rules to be derived for agricultural systems concerning the importance of biodiversity with respect to the maintenance of ecosystem services that apply across all functional groups and environmental circumstances. Both the concept of 'diversity' and that of 'ecosystem function' are too broad to make generalizations at this level testable. There is a need and potential however to investigate the issues of thresholds of diversity-function relationship within specific functional groups and under circumstances of change in stress and/or disturbance.

Finally we should re-emphasise the importance of the hierarchical control exerted by the plants over the other functional groups (Figure 4, Appendix).

This is a particularly important feature when determining management options, not only at the field and farm scale but also at that of the landscape. The plant, decomposer and herbivore subsystems of the biological community interact in a variety of ways but the productivity, mass, chemical diversity (resource quality) and physical complexity of the plant component exerts the strongest influence and is the single most important determinant of both the diversity and the functional efficiency of the other two subsystems. Wardle et al (1999a and b) and Yeates et al (1999) showed for example that arthropod and microbial communities were not adversely affected by agricultural intensification provided the type of management (eg. mulching) provided for increases in the quantity and quality of the organic inputs. The maintenance of total system diversity and of the major part of the ecosystem services is thus predominantly determined by the nature of the plant community. This is also of course the main point at which humans intervene in the agroecosystem – to decide the species richness, the genetic variability and the organisation in space and time of the planned biota in the vegetation subsystem.

8 IMPLICATIONS FOR THE DESIGN AND MANAGEMENT OF AGRICULTURAL LANDSCAPES

A substantial research investment has been made into agricultural systems that fall short of the full extent of genetic homogenisation and petro-chemical substitution. Examples are agroforestry and other inter-crops, rotations, mulch-based, minimum tillage and integrated livestock-arable systems. All these systems are characterised by maintenance of diversity of plant functional groups above the level of monocropping. The scientific justification for such approaches has generally been made on grounds of greater functional sustainability and the wider spread of risk associated with more diverse products as well as on the recognition that it is in line with the management choices of the majority of the rural poor in the tropics. For farmers labour saving and low investment and risk may be the preferred attributes of these systems. It is interesting to note however that, whereas scientists had introduced single-species fallow systems to farmers in Western Kenya, these farmers decided on their own to diversify tree species in these improved fallow systems (Bashir Jama, pers. com., 2001).

The simplicity of monocultures at field level is only possible as long as farms are part of a germplasm delivery system with rapid access to externalised gene banks and have access to risk buffering mechanisms such as insurance schemes or agricultural subsidies. Large parts of tropical agriculture still operate in a range where such 'externalized' risk management options do not exist and where thus a choice for monocultures carries unaffordable risks. At the farm level ecosystem resilience can be extended beyond resources maintained on farm or in the accessible neighbourhood by being part of a larger agricultural production and germplasm delivery system

Ewel (1986) and Moreno and Hart (1979) are among those who have advocated using plant functional groups as a basis for the (plot level) design of multi-plant agroecosystems. These designs also rely, explicitly or implicitly, on the impact that the effect of increasing the diversity of the vegetation system will have in enhancing the associated biodiversity both above- and below-ground and thence the probability of maintaining ecosystem services over a wider range of stress and disturbance. The evidence comparing such systems is almost entirely however based on assessments of yield, Vandermeer et al (1998) reviewed the literature on inter-cropping of all types and concluded that yield gains in comparison with mono-crops depends on the specific complementarities in resource use and seasonal development of the components. As risks for the farmer depend on farm level diversity of potentially productive resources rather than on plot-level diversity, the focus of much agroecological research may have been too narrow.

Another key aspect that needs to be changed is the continuing separation of different aspects of management interventions on the base of disciplinary experience, such as soil or nutrient management from pest management. Interventions to ameliorate the impacts on any one of the different ecosystem services (as well as on productivity) are likely to influence others. Practices targeted at productivity but well documented in terms of their supportive, ameliorative or regenerative effect on other ecosystem services should be a top priority.

9 . DOES THE RELATIONSHIP BETWEEN DIVERSITY AND ECOSYSTEM SERVICES CHANGE ACROSS SCALES?

Almost all the evidence that exists for the relationship between diversity and function in agroecosystems concerns the plot (and often the micro-plot or laboratory chamber) scale. But in order to provide policy makers with appropriate advice on the functional value of diversity it is necessary to consider the ways in which the three factors we have been considering – biodiversity, agricultural productivity and profitability, and ecosystem services – intersect at the landscape scale. Whilst the inter-relationships that we have described at the plot (patch) scale may help in understanding what happens at the landscape scale there is also the possibility that the rules change across spatial scales. The productivity of any land-use system can be expressed on an area basis and the aggregate productivity across a landscape on the basis of the fractions occupied by different land uses. Biodiversity however has more complex scaling relationships and cannot simply be aggregated in this way. Nor can many of the functions that have been discussed here.

Much of the diversity in a landscape may exist at scales beyond the farm (between farm variability being larger than within-farm diversity), and the dynamics of diversity thus depend on the degree to which different farms remain (or become more) different. As agricultural research and extension have been based on the economies of scale that are perceived as attainable by homogenisation of farms with similar demands for inputs and services and similar outputs for markets, the trend in agricultural intensification has often resulted in the reduction of inter-farm diversity. The green revolution provides a good illustration of this process which is generally supported by policy interventions that tend to promote homogeneity in farmer goals, practice and behaviour, at least over the short term. The agents of change in biodiversity beyond farm level are essentially different from those on farm.

In Figure 2 we hypothesise that the relationship between species richness and specific ecosystem services at the landscape scale may follow a relationship analogous with that of the Vitousek-Hooper model – together of course with all the attendant qualifications. That is to say that ecosystem services at the landscape scale are optimised by a diversity of land-uses, but the number that are required for optimisation is relatively small. If the hypothesis is correct then it would suggest that the presence of a relatively small number of different land-use types should be sufficient to satisfy the functional needs of the majority of ecosystem services. This generality needs however to be detailed for any given landscape into specifics with respect to not only the types but also their sizes, shapes, their patterns and location on the landscape and practices of management.

It can be further hypothesised that at the higher scales of landscape and region the frequency and intensity of disturbance and stress (both natural and anthropogenic) is greater than those at the plot or farm scale and increasingly beyond the control of the land users. Prevention of decreases in the stability of agroecosystems and management of restoration become more difficult and costly and eventually become impossible from both biological and economic perspectives because connectivity is too high and disturbances too large. The ecosystem services that enhance the resilience and adaptation of systems, such as biodiversity, thus become more and more important a feature of sustainable management as the scale of operation widens.

Figure 3 hypothesises a number of relationships implied in the above discussion. We have argued that at the plot and farm scales individual land managers and farmers manage biodiversity largely through simplification (i.e., by decreasing connectivity and maintaining agroecosystems at a stage of early succession) and substitution. Decreases in connectivity may, under specific conditions reach a threshold level of irreversibility, in which case the agroecosystem loses its resilience. However, the individual land user can in most cases manage and control agroecosystem disturbances and stresses, such as pest outbreaks or sudden changes in relative prices, by making adjustments in the management of resources (land, water, germplasm, knowledge, labour, capital) at the farm scale.

Curves 1 and 2 of Figure 3 deal with this case of diversity management at the plot to farm (ie. land-use) scale and are therefore concerned with alpha diversity – that is within these boundaries. (Curves 3 and 4 refer to higher landscape scales and are discussed in the next section). The arrow linking Curve 1 to Curve 2 represents the capacity of farmers to maintain the ecosystem services necessary for their production goals whilst sacrificing diversity., This shift thus hypothesises that at the plot and farm scale management interventions can compensate for losses of diversity, although of course both the economic and oof-site ecological consequences of this remain unstated and will be very circumstantial. We know, as shown for small-scale farms in Kenya by Osgood (1998), that many farmers do value genetic and species diversity on their farms, as they are aware that it minimises economic risk by enhancing on-farm diversification of plant and animal production. The history of agriculture provides many examples of how even extreme reductions in biodiversity can be managed, through periods of disturbance, by individual land users by substitution (e.g. chemicals, labour). Therefore, even though biodiversity has important ecological functions at the farm scale, it is nevertheless possible to decrease biodiversity levels very substantially at that scale while maintaining the productivity and resilience of agroecosystems. We hypothesize below however that at higher scales the control and management of disturbances and stresses becomes more and more problematic and costly and the resilience function of biodiversity thus becomes an increasingly important issue in management.

9.1 Keep it simple: maintain ground cover

We have already emphasised the over-arching influence of the plant cover and diversity on the associated functional diversity and thence on the properties of resilience. The simplest rule for managing landscapes is thus to say that if the vegetation is diverse then the associated diversity and functions will be taken care of. The immediate implication of this is that monotypic landscapes – vast areas of the same crop or livestock system – are likely to be the most vulnerable to the same dangers to ecosystem services pictured earlier for the farm or plot scale. Examples of these effects are the pollution of ground water by nitrates and pesticides in large-scale chemical-based agriculture and the difficulty of controlling epidemics in genetically homogeneous stands of vast area. These however seem simply to be the same issues as those at the plot scale only writ larger. The mechanism for correction generally proposed is that of diversification of the type of land-use system in space and time. What are the consequences that may flow from this?

9.2 Landscape mosaics

The majority of agricultural landscapes in the tropics, in contrast with most of the northern temperate zones, are mosaics of different land uses. How does this influence the biodiversity-ecosystem service relationship? At the plot scale the ecosystem services which is probably the most sensitive to biodiversity loss is the biological pest control system. The management opportunities for this increase with widening scale as greater opportunity for diversity in both genetic signals and physical structure of the vegetation permit a wider diversity and larger reservoir of control organisms. Similarly many of the endangered invertebrates and microorganisms of the soil community are mobile, or may be carried by vectors, and can thus recolonise degraded areas from within mosaics that provide suitable reservoirs. Others (e.g. earthworms) are less so however and re-inoculations may be necessary. In each of these cases the size, pattern of arrangement and rotation in time of land-uses on the landscape will have significant effect on the efficiency of ecosystem service provision. Management at the landscape scale offers greater opportunity than at the plot and farm for varying land-use over time. Izac and Swift (1994) argued that sustainable land management could most easily be achieved at this scale by means of balance between aggrading and degrading areas i.e. between patches of high exploitation and those of fallow or rest, in contrast to advocacy of high protection and diversity over the entire landscape. Soil organic matter change is a specific and far-reaching example. In areas of intensive production and harvest the soil carbon content may decrease but under fallow or tree-based production it can be re-built. The balance between these two options affect nutrient cycling, soil structure, water regimes and the emission of greenhouse gases. The policy requirements for such integrated management of landscape mosaics are however very different to the production-related approaches that currently prevail in favour of landscape homogenisation.

The third hypothesis of Vandermeer et al (1998) predicts that a higher diversity of species will be required to provide a buffer against stress and disturbance at the landscape scale than will be the case for any single patch within it (i.e. gamma diversity will be higher than the sum of alpha diversity). This is pictured in Figure 3 by the difference between curves 1 and 3. Humans can intervene relatively easily (although not necessarily cost-effectively) at the plot scale to substitute for diversity loss – as represented by the difference between curves 1 and 2. At the landscape scale however intervention by humans, including these substitutive actions, will tend to widen the range of stress and increase the frequency of disturbance. We therefore hypothesise that this will result in yet greater need for diversity to ensure the maintenance of ecosystem services and resilience. This is shown by the arrow linking Curves 3 and 4 in figure 3.

Substitutive management for purposes of restoring ecosystem services (ie to achieve a shift back from Curve 4 to Curve 3, analogous to the Curve 1 to 2 shift in Figure 3) is likely to be both technically difficult and prohibitively expensive at this scale and may suffer from a 'free rider' problem where it is difficult to get all beneficiaries to share the costs. We contend therefore that the implication of this hypothesis is of the very high risk associated with ignoring landscape scale management and focussing only on policies that promote plot scale interventions. Plot scale activities are more likely to exacerbate landscape scale problems than repair them. On the other hand landscape scale interventions offer great opportunity for improvements at the plot scale by increasing overall integration and resilience. There is thus more functional justification for arguing in favour of maintaining or enhancing biological diversity at the landscape scale than there is at the scale of the plot.

This model is of course simplistic and does not provide any guide to other features such as the size, shape and position (pattern) of patches on the landscape or on the temporal relationships between them. The hierarchical relationship between ecosystem services should assist in developing rules for these aspects. The regulation of erosion and water flows operates at a higher level in the hierarchy of controls than do aspects of nutrient cycling, soil structure and gas emissions or pest controls. The next part of this volume takes up these higher-level aspects of landscape management under the title of 'watershed services'. The lower level services such as nutrient cycles and biological control activities may then be built in through focus on aspects such as the degree of connection between the patches and the location, direction and intensity of the flows between them. It may be useful to classify land-use types into 'functional groups' in a manner analogous with that for species in order to develop more meaningful relationships between diversity and function at the landscape scale.

10. POLICY IMPLICATIONS

The changes associated with agricultural intensification, including the attendant processes of diversity reduction and substitution of function, are made in response to food need, market opportunity, and perceptions of increased management efficiency associated with specialization. These factors remain a dominant reality within market-orientated agriculture where a small number of specific products have high value and specialisation thus becomes a desirable target. Van Noordwijk and Ong (1999) discussed the paradox that urban consumers have access to an increasingly diverse array of food resources that are produced on specialized farms of greatly reduced internal diversity. Observed changes in diversity at one scale may thus not represent changes at other levels. The risks to agroecosystem services of simplifying ecosystems and substituting biodiversity by labour and chemicals (e.g., in pest control) are those of losing some keystone functions including the ability of an agroecosystem to adapt to change without yet further substitutive interventions. The evidence, as briefly described above, that ecosystem services might be significantly impaired in agroecosystems as intensification increases is substantial although the role of biodiversity is far from clearly understood. The farmer may not perceive these effects to be serious if the economic environment enables continuing profit based on subsidies related to the substitution process, within markets that do not price environmental services or externalities. This has been the basis of agricultural development in Europe and North America for many decades. It thus appears that in the absence of specific policy interventions, to attain profitability, even without petro-chemical substitution, agroecosystem diversity is likely to be kept low.

Associated with this low diversity there is a risk of crossing threshold levels for the maintenance of ecosystem services the restoration of which is likely to be extremely costly, let alone feasible. Decisions about the management of agroecosystems in market economies do not normally take into consideration the costs of interfering with ecosystem services, including those in which biodiversity plays a strong influence. But when agroecosystems are driven across thresholds from a desired to an undesirable state, the costs to society of being in this new undesirable state, or of restoration of a more desirable one if it is feasible, can be extremely high. Therein lies the risk of simplifying ecosystems. Holling (1986) provided a seminal analysis of the consequences of a number of such irreversibilities.

Policies for sustainable agriculture, i.e. to promote integrative practices that focus on the conservation of resources (including genetic diversity) as well as productivity, have proved elusive. If the policy needs are extended to include the management of biodiversity at the landscape scale in order to protect and enhance a wide range of ecosystem services, the problem becomes more acute. There are two particular reasons why the problem is exacerbated at higher scales. First, population pressure and globalisation of trade and the concomitant land use changes (expansion of cities into agricultural lands and of agriculture into marginal areas) result in increased frequency and intensity of disturbances and stresses by comparison with those at the farm scale. The capacity to correct these effects also diminishes because the sensitivity of the systems increases in concert with their connectivity as one moves up the hierarchy of scales (Holling, 1986).

Second, the higher the scale under consideration, the more difficult it is for the increased numbers of individual land users to develop an effective management strategy for agroecosystem disturbances, that takes ecological interactions and connectivity into consideration. Even at the scale of small watersheds, it is not often the case that land users have been successful in developing collective and effective means of control and management of disturbances. Furthermore, even if these land users have full knowledge of the relevant level of connectivity necessary to ensure resilience at the watershed scale, different sectors of society place differing levels of importance on ecosystem services and diversity. Farmers in tropical countries are unlikely to place as high a value on these functions of landscape diversity as does the community at large or the national society. They are furthermore highly unlikely to value the serependic (i.e. future) value of diversity, which is much more likely to be valued by national and global communities.

In economic terms, farmers value some of the on-farm benefits of diversity and very few of the off-farm benefits, for the usual reasons that costs and benefits outside of the managers' domain (i.e. externalities) are generally not taken into account by individual decision-makers. The argument is however not simply about off-farm effects of biodiversity being ignored. Farmer knowledge varies greatly. There may be many on-farm ecosystem services of which farmers are unaware (e.g., the role of micro-organisms), and thus cannot value, as well as services they may be aware of but will not consider important (e.g., reduction of greenhouse gas emissions). The same services may be valued by other groups in society, with a different perspective and set of interests. What is a beneficial service for one group may also be a cost for another (e.g. the perception of earthworms as 'pests' for paddy rice farmers, the trade-off between carbon sequestration and SOM mining). For these reasons, management of ecosystem services, and of biodiversity at the landscape scale, as well as management of disturbances in agroecosystems in land use mosaics, is unlikely to be optimal, from either an ecological or an economic perspective, in the absence of specific policy or institutional interventions. Lack of knowledge of threshold levels in connectivity at different scales, different perspectives on the value of biodiversity, externalities and difficulties in large groups of land users coming together in developing effective means of controlling disturbances at the landscape scale thus result in biodiversity being managed by individual farmers in a sub-optimal manner.

We therefore conclude, on the basis of the relationships we have hypothesised earlier, that it will prove very costly to manage ecosystem services at the watershed, landscape and higher scales unless the functional value of biodiversity for productivity at the plot and farm scale and its interaction with 'externalities' beyond are perceived and valued. Furthermore, unless in particular the role of biodiversity in enhancing resilience is understood and factored into effective policy or institutional interventions, ecosystem diversity is unlikely to be maintained at the landscape scale without deliberate policy interventions at national and sub-national levels which take into account the real value of maintaining ecosystem services, given the externalities they generate and given their contribution to resilience. The biggest challenge is in the realization that most of diversity as well as much of its positive role in resilience probably exists beyond the farm scale, and that thus diversity of management decisions by farmers rather than any specific management system is key to its maintenance in the landscape. Assessments of biodiversity values of different management scenarios will have to form the basis of discussions of the effectiveness of different policy interventions. These policy implications and the need for diversity enhancing communal action remain largely unexplored territory.

Finally, the absence of clear evidence should not be taken as evidence for the absence of effects and thus as a reason for doing nothing. Some economists have proposed that, in view of our relatively poor understanding of the exact roles of biodiversity in ecosystems on the one hand and of the potentially devastating effects of biodiversity loss on the other hand, a precautionary principle should be used in managing diversity. This principle acknowledges that while we may not be able to justify what some see as redundant species, there may be an extinction threshold that would result in an unacceptable level of ecosystem failure.

Consequently, extreme care and precaution must be taken, and it is preferable to err on the conservative side (Perrings, 1991). The precautionary principle introduces an important concept, namely that of the risk of managing agroecosystems in such a way that threshold levels of biodiversity loss in relation to ecosystem services are ignored. The 'risk premium' that the precautionary principle suggests is hard to quantify as yet.

11. CONCLUDING REMARKS

In the above discussion we have quoted or proposed a range of hypotheses concerning the relationships between biological diversity and ecosystem functions, and their implications for the management of agricultural landscapes. The general relationships that have been proposed may have to be replaced by more specific hypotheses of the relation between components of overall biodiversity and specific environmental functions, bounded in space and time. Sweeping generalizations from experiments that are necessarily restricted in space and time, and for example do not include major parts of the diversity-generating processes (including 'lateral flows' of dispersal and migration for re-establishment), are unlikely to be helpful in guiding the development of agro-ecosystems that have to provide for short, medium and long term service functions. Future investigations should utilise co-evolved communities, be structured to investigate the distinct roles of clearly defined functional groups, separate the effects of between- and within-group diversity and be conducted over a range of stress and disturbance to identify threshold levels of irreversibility of functional losses. This might include: testing the basic functional-biodiversity rule by experimentally determining the minimal level of diversity between and within functional groups that is necessary to maintain productivity, integrity and perpetuation of ecosystems; characterising the functional groups of organisms necessary to maintain specific ecosystem services; determining the ecosystem function and service effects that ensue from elimination or substitution of key functional groups, including particular investigation of controls over below-ground diversity and function exerted by particular plant functional groups and other keystone organisms; and determining (and developing indicators for) the biodiversity thresholds for different ecosystem services. An interesting extension of the latter study might be to investigate whether similar thresholds exist for the intrinsic, utilitarian and serependic values of biodiversity.

Society as a whole has an interest in ecosystem services that are manifested substantially at scales above that of the field, plot or farm. At the scale of the watershed or landscapes there is, in comparison with any single patch, a greater range of environmental stress and higher frequency of disturbance, including of extreme events. The maintenance of ecosystem services at these scales thus requires either a higher diversity of species within functional groups or a greater investment in substitutive management to maintain ecosystem services. These increments in diversity and/or investment are unlikely to be simply additive in view of the significant shifts in complexity that occur with shifts across scale. Optimal maintenance of ecosystem services at the landscape scale may be most readily achieved by a mosaic of a relatively few land-use types. This model is however likely to be overly simple because of: (a) differences in functional impact of different land-use types; and (b) the importance of organisation at the landscape scale in terms of the size, shape and location pattern of the constituent land-uses.

In developing appropriate land-use scenarios landscapes should be compared with respect to the aggregate values of their component land-uses for intrinsic, utilitarian and functional (ecosystem service) values of biodiversity. This would be assisted by establishing a typology of land-uses in terms of their efficiency in maintaining ecosystem service and in the trade-offs between this and profitability. The results of the ASB project provide a model for this approach with respect to the interactions between carbon sequestration potential and profitability. The relative costs and benefits of segregating the intrinsic, utilitarian and functional uses of biodiversity between different land-use or landscape units compared with integrating them within such units is another parameter that should be of significant value for policy development.

This review confirms two unsurprising but crucial elements for policy development: first that whilst a number of important analogies can be drawn across scales with respect to the management of the relationships between biodiversity and ecosystem services, there are also emergent properties that necessitate different approaches; second that the value placed on the relationship between biodiversity and function (ecosystem services) by individual land-users is markedly different than those perceived by the community at different levels of society.

We have indicated a number of biological and socio-economic issues that need to be clarified in order to provide more explicit advice to policy makers. No single optimal value can be placed on the biodiversity within a landscape. Land-use decisions are likely to be optimised if decision makers can be provided with scenarios showing how various land-use combinations result in different levels of diversity and the efficiency of different ecosystem services, and the associated values of biodiversity. In so-doing it will be important to include aspects of temporal change as well as pattern on the landscape as both these factors influence the resilience of the landscapes which should be regarded as a factor of over-riding importance. These scenarios can then be used to identify policy interventions and institutional arrangements necessary to achieve the desired objective, whether it is one dominated by agricultural productivity targets or the maintenance of ecosystem services or the conservation of biodiversity, or a combination of all three.

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Table 1: Relationship between key functional groups of organisms, the ecosystem level functions they perform and the ecosystem goods and services they provide

ECOSYSTEM GOODS AND SERVICES	**ECOSYSTEM FUNCTIONS**	**KEY FUNCTIONAL GROUPS**
Ecosystem goods including:		
Food	Primary and secondary (herbivore) production	Plants, Vertebrate herbivores
Fibre and Latex	Primary production and secondary metabolism	Plants
Pharmaceuticals and Agro-chemicals	Secondary metabolism	Plants, Bacteria and Fungi (Decomposers etc)
Ecosystem services including:		
Nutrient cycling	Decomposition Mineralisation and other elemental transformations	Decomposers Elemental transformers
Regulation of water flow and storage	Soil organic matter synthesis Soil structure regulation – aggregate and pore formation	Decomposers Ecosystem Engineers
Regulation of soil and sediment movement	Soil protection Soil organic matter synthesis Soil structure maintenance	Plants Decomposers Ecosystem engineers
Regulation of biological populations including diseases and pests	Plant secondary metabolism Pollination Herbivory Parasitism Micro-Symbiosis Predation	Plants Pollinators[1] Herbivores[1] Parasites[1] Micro-symbionts[1] Hyper-parasites[2] Predators[2]
De-toxification of chemical or biological hazards including water purification	Decomposition Elemental transformation	Decomposers Elemental transformers
Regulation of atmospheric composition and climate	Greenhouse gas emission	Decomposers Elemental Transformers Plants Herbivores

Notes to Table 1.

Primary Production

In some ecosystems photosynthetic micro-organisms may constitute as significant group eg. rice ecosystems). Here we deal only with plants.

Note 1.

Plants. There is a long history of classification of plants into functional groups. The groupings have been based on a variety of reproductive, architectural and physiological criteria. For the purposes of this paper the efficiency of resource capture is suggested as the main criterion. This will be determined by features of both architecture (eg. position and shape of the canopy and depth and pattern of the rooting system) and physiological efficiency. A very simple classification could for instance distinguish the roles of trees, shrubs, vines and cover plants etc. and then subdivisions within each of these groups. Much more detailed consideration of these aspects is given by Smith et al (1997).

Primary Regulation (Note 1).

These are a set of functional groups which have a significant regulatory effect on primary production and therefore influence the goods and services provided by the plants.

Pollinators. This is a taxonomically very disparate group of organisms including many insect groups and vertebrates such as birds and bats. However there does not appear to be any generally accepted categorisation based on feeding behaviour or similar criteria (Barbara Gemmill, personal communication).

Herbivores*:* A great variety of organisms feed directly on primary producers. Vertebrate grazers and browsers are readily distinguished from invertebrate pests although their impacts on the plants may have similar functional significance at the ecosystem level. Each of these major groups are sub-divisible in terms of, for instance, feeding habits. The balance between different types of browser for instance can influence the structure of the canopy.

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

Micro-symbionts: There is a wide range of microbial infections that are beneficial rather than destructive of which the most familiar are di-nitrogen fixing bacteria and mycorrhizal fungi.

Service Provision.

The functional groups within this category also strongly influence primary production but not in the directly destructive or stimulatory way of the primary regulators. They also provide a set of ecosystem services distinct to those deriving mainly from the primary producers.

Decomposers: This is a group of great diversity which can be sub-divided taxonomically (bacteria, fungi, invertebrates etc) and in relation to size both of which correlate somewhat with functional roles in the breakdown (eg. detritivorous invertebrates) and mineralisation (fungi and bacteria) of organic materials of plant or animal origin (Swift et al 1979, Lavelle and Spain 2001).

Ecosystem Engineers: These are organisms that change the structure of soil by burrowing, transport of soil particles and formation of aggregate structures. The term is often confined to the macrofauna such as earthworms and termites but fungi and bacteria also play a key role in the binding of soil aggregates. Many of these organisms also contribute to the processes of decomposition.

Elemental Transformers: This may be the most diverse group of all and deserving of substantial subdivision. It includes a range of autotrophic bacteria that utilise sources of energy other than organic matter (and therefore not classifiable as decomposers) that play key roles in nutrient cycles as transformers of C, N, S etc. In addition there are heterotophs that thus have a decomposer function but also carry out elemental transformations beyond mineralisation (eg. free-living di-nitrogen fixers).

Secondary Regulators (Note 2)

Hyper-Parasites and Predators: This is diverse group of microbial parasites and vertebrate and invertebrate predators that feed on decomposers, herbivore, pollinators etc. They have particular significance in agriculture because of the service of biological control of pests and diseases that they play.

FIGURE LEGENDS

Figure 1: Possible relationships between biological diversity and ecosystem functions for the plant subsystem (from Vitousek and Hooper 1993). The authors hypothesised that curve 2 was the most probable of the three propositions.

Figure 2: Hypothesised relationship between the diversity of ecosystem or land-use types and the efficiency of function of (the totality of) ecosystem services at the landscape scale.

Figure 3: Hypothesised relationships between diversity (as measured by species richness) and the efficiency of function of ecosystem services at the patch-ecosystem (i.e. plot) scale (Curves 1 and 2) and the scale of the landscape (Curves 3 and 4). Curve 1 repeats hypothesis 2 of Figure 1: Curve 2 shows how in an intensively managed agricultural plot ecosystem services may be maintained by substitution of diversity by inputs derived from human and petro-chemical energy. Curve 3 shows, by comparison with curve 1, that the threshold of ‘essential’ diversity is greater as the land area increases. Curve 4 represents circumstances of high disturbance of the landscape by human intervention.

Figure 4: Hierarchical relationships between different categories of Functional Group – see Table 1 and Notes

Appendix

KEY FUNCTIONAL GROUPS: A PRELIMINARY CLASSIFICATION

We have defined a Functional Group in the text as ‘ a set of species that have similar effects on a specific ecosystem-level biogeochemical process’. There are many examples of classification of species in this way within specific taxonomic or trophic groups (e.g. for plants or pests). . There is no single classification to suit all purposes. In each case it is clear that the number of functional groups that is recognised, the criteria that are used to classify them and the degree of sub-division that is applied is a function of the question that is being addressed. We propose here a classification into the ten major groups that are briefly described below, together with such sub-division as may be necessary, for the purposes addressed in this paper, i.e. the relationships between biodiversity and function with particular respect to agriculture and ecosystem services. These Key Functional Groups are listed in Table 1 in relation to the ecosystem services they provide. The relationships between them are pictured in Figure 4. We suggest that this could provide a useful framework for investigating and testing key questions on this topic. A hierarchical structure is suggested (Figure 4). At the highest level are four major categories related to major trophic functions at the ecosystem scale i.e. Primary Production, Primary Regulation, Service Provision and Secondary Regulation. At the next level are the ten groups listed in Table 1 that perform distinct ecosystem functions; and at the third level are sub-divisions which it may be functionally and/or taxonomically useful to distinguish (e.g. vertebrate grazers versus invertebrate pests among the herbivores). Further levels of subdivision may also be useful or necessary in some cases.