

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

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7 **Abstract**

8 The assumed relationship between biodiversity or local richness and the persistence of ‘ecosystem  
9 services’ (that can sustain productivity on-site as well as off-site, e.g. through regulation of water flow  
10 and storage) in agricultural landscapes has generated considerable interest and a range of experimental  
11 approaches. The abstraction level aimed for, however, may be too high to yield meaningful results.  
12 Many of the experiments on which evidence in favour or otherwise are based are artificial and do not  
13 support the bold generalizations to other spatial and temporal scales that are often made. Future  
14 investigations should utilise co-evolved communities, be structured to investigate the distinct roles of  
15 clearly defined functional groups, separate the effects of between- and within-group diversity and be  
16 conducted over a range of stress and disturbance situations. An integral part of agricultural  
17 intensification at the plot level is the deliberate reduction of diversity. This does not necessarily  
18 result in impairment of ecosystem services of direct relevance to the land user unless the hypothesised  
19 diversity-function threshold is breached by elimination of a key functional group or species. Key  
20 functions may also be substituted with petro-chemical energy in order to achieve perceived  
21 efficiencies in the production of specific goods. This can result in the maintenance of ecosystem  
22 services of importance to agricultural production at levels of biodiversity below the assumed  
23 ‘functional threshold’. However it can also result in impairment of other services and under some  
24 conditions the de-linking of the diversity-function relationship. Avoidance of these effects or attempts  
25 to restore non-essential ecosystem services are only likely to be made by land-users at the plot scale if  
26 direct economic benefit can be thereby achieved. At the plot and farm scales biodiversity is unlikely  
27 to be maintained for purposes other than those of direct use or ‘utilitarian’ benefits and often at levels

28 lower than those necessary for maintenance of many ecosystem services. The exceptions may be  
29 traditional systems where intrinsic values (social customs) continue to provide reasons for diversity  
30 maintenance. High levels of biodiversity in managed landscapes are more likely to be maintained for  
31 reasons of intrinsic, serependic ('option' or 'bequest ') values or utilitarian ('direct use') than for  
32 functional or ecosystem service values. The major opportunity for both maintaining ecosystem  
33 services and biodiversity outside conservation areas lies in promoting diversity of land use at the  
34 landscape and farm rather than field scale. This requires however an economic and policy climate that  
35 favours diversification in land-uses and diversity among land users.

### 36 **Keywords**

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

### 38 **1. INTRODUCTION**

39 The role of biological diversity in the provision of ecosystem goods and services and the way  
40 this role can be valued and managed during agricultural intensification is much debated but  
41 still poorly understood. A key problem in all debates on biological diversity is that the  
42 abstraction 'diversity' has often not been distinguished from the specific attributes of the  
43 community of organisms that is under study in any particular location or system. Likewise,  
44 evaluations of diversity have more often than not been assessments of the value of biological  
45 resources as such rather than assessments of the value of diversity per se (Nunes and van der  
46 Bergh, 2001). For instance if the interest lies in the functional roles of the community these  
47 may depend on the 'structure' of the vegetation and the relationships between different  
48 'functional groups', rather than on diversity as such (Woodward, 1993). Experiments based  
49 on random species assemblages may be appropriate tests for hypotheses about 'diversity' per  
50 se, but tell us very little about the largely self-selected assemblages that make up natural  
51 ecosystems. In the case of agro-ecosystems, whilst the dominant crops or livestock are human  
52 choices, by far the majority of the species (as soon as one takes the belowground part of the  
53 system into consideration) are self-selected. So, are we asking the right question about the

54 relations between biodiversity and ecosystem services? Does the loss of diversity at plot-to-  
55 global scales imply a threat to critical ecosystem functions? Can we identify thresholds in  
56 such a process?  
57 Global diversity derives from the lack of overlap in species, genetic or agro-ecosystem  
58 composition between geographic or temporal domains. While ‘agricultural development’  
59 directly affects local (ie. plot level) diversity, it probably has even stronger effects by  
60 homogenizing at higher scales, facilitating the movement of ‘invasive species’ and the  
61 introduction and spread of ‘superior’ germplasm of desirable species. Scale is thus of  
62 overriding importance in our analysis and we may well find that answers may appear  
63 contradictory between different ways of defining temporal and spatial boundaries to the  
64 system under consideration. In this review we will first consider the concepts of  
65 ‘biodiversity’ and ‘ecosystem functions’, and then the evidence that links relevant aspects of  
66 the two, before we embark on an exploration of how this relationship depends on scale and  
67 can be ‘managed’.

## 68 **2. THE BIOLOGICAL BASIS OF ECOSYSTEM GOODS AND SERVICES**

69 Humans have evolved as part of the world’s ecosystems, depending on them for food and  
70 other products and for a range of functions that support our existence. Natural ecosystems, as  
71 well as those modified by humans, provide many services and goods that are essential for  
72 humankind (Matson et al., 1997). Efforts and interventions to manipulate (agro)ecosystems in  
73 order to meet specific production functions, represent costs to the rest of the ecosystem in  
74 terms of energy, matter and biological diversity, and often negatively affects goods and  
75 services that so far were considered to be free and abundant. These are anthropocentrically  
76 regarded as services because they provide the biophysical necessities for human life or  
77 otherwise contribute to human welfare (UNEP, 1995; Costanza et al., 1997). Most if not all  
78 of these services are based on a ‘lateral flow’, or movement across the landscape of biomass

79 (such as food, fibre and medicinal products derived from the sea, inland waters or lands  
80 outside of the domesticated ‘agricultural’ domain), living organisms and their genes, or earth  
81 (nutrients), water, fire or air elements. Examples of ecosystem services particularly important  
82 for agroecosystems and agricultural landscapes are: maintenance of the genetic diversity  
83 essential for successful crop and animal breeding; nutrient cycles; biological control of pests  
84 and diseases; erosion control and sediment retention; and water regulation. At a global scale  
85 other services become important such as the regulation of the gaseous composition of the  
86 atmosphere and thence of the climate. A list of such services is given in the first column of  
87 Table 1 of the Appendix, and their connection to lateral flows is discussed by Van Noordwijk  
88 et al (this volume, Table 1).

89 These ecosystem goods and services are biologically generated. The community of living  
90 organisms within any given ecosystem carries out a very diverse range of biochemical and  
91 biophysical processes that can also affect neighbouring systems. These can be described at  
92 scales ranging from the subcellular through the whole organism and species populations to  
93 the aggregative effect of these at the level of the ecosystem (Mooney and Schultze 1993). All  
94 ecosystems have permeable boundaries with respect to material exchanges but the within-  
95 system flows usually dominate those between systems, such as between land-use or land-  
96 cover types within a landscape. For purpose of this paper we define ecosystem functions as  
97 the minimum aggregated set of processes (including biochemical, biophysical and biological  
98 ones) that ensure the biological productivity, organisational integrity and perpetuation of the  
99 ecosystem. There are no agreed criteria for defining a minimum set of such functions but for  
100 the purposes of this paper the second column of Table 1 lists ecosystem functions alongside  
101 the ecosystem services they provide. Further explanation of these relationships is given below  
102 but it is useful to note that these functions can be pictured as having a hierarchical  
103 relationship. The energy captured in primary production is utilised in the herbivore and

104 decomposer food chains. Interactions between these three subsystems occur through nutrient  
105 exchanges and a variety of biotic regulatory mechanisms as well as by energy flow. In  
106 particular the balance between the constituent processes of primary production and those of  
107 decomposition determines the amount of energy and carbon maintained within the system  
108 and is the major natural regulator of the gaseous composition of the atmosphere at a global  
109 scale (Swift 1999).

### 110 **3. BIOLOGICAL DIVERSITY AND ITS VALUES**

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

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

123 Biodiversity in this paper refers to the totality of the species (including the genetic variation  
124 represented in the species populations) across the full range of terrestrial organisms i.e.  
125 invertebrate animals, protists, bacteria and fungi, above- and below-ground, as well as the  
126 vertebrates and plants which often constitute the main concerns of biodiversity conservation.  
127 With a definition as broad and inclusive as this, it is highly unlikely that any clear and precise  
128 statements about relationships between ‘biodiversity’ and functions can be formulated and

129 tested that can be helpful in guiding human activity. Similar to the situation with ‘watershed  
130 functions’, which are considered in the next part of this volume, we may find that discussions  
131 on components of the overall biodiversity concept in relation to land use are more productive  
132 and open to progress than those that stay at the aggregate level. In the section immediately  
133 following we shall refer to the diversity within ecosystems (often termed alpha diversity) and  
134 in later sections to that at the broader scale of the landscape (which embraces concepts of  
135 both beta and gamma diversity).

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

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

147 Second is the utilitarian (also called direct use, contributory, primary or infrastructure) value  
148 of components of biodiversity. These are the subsistence and commercial benefits of species  
149 or their genes derived by one or other sectors in society. The utilitarian value may be private  
150 and accrue to the land managers (farmers, local community, government). This is most  
151 obvious with respect to high value agricultural crops but also applies to the other types of  
152 good listed in Table 1. Utilitarian value may also accrue to other sectors in society, in  
153 addition to private land managers. For instance, the pharmaceutical industry values the

154 tropical forest tree Prunus africana very highly because its bark contains chemicals used for  
155 manufacturing a drug. Another example is that in Africa, many farmers living near natural  
156 (and protected) forests withdraw substantial monetary benefits from their hunting and from  
157 collecting plants and tree products in these forests (Pottinger and Burley, 1992). Utilitarian  
158 value thus refers to the use of organisms that are part of the local diversity as inputs into  
159 consumption and production processes.

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

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

## 177 **4. WHAT IS THE RELATIONSHIP BETWEEN DIVERSITY AND FUNCTION?**

### 178 **4.1 Concepts**

179 Biologists have for many decades speculated on the question of why there are so many  
180 species of living organism. As explored in the theory of island biogeography, the diversity  
181 within any ecosystem at any point in time is the result of a ‘self selection’ process, that  
182 involves co-evolution of the species comprising the biological community within a given  
183 ecosystem by interactions among them and with the abiotic environment through time. This  
184 is not an isolated process. New species may enter an ecosystem from neighbouring areas,  
185 some establishing themselves and others failing to do so. Partly as a result of successful  
186 newcomers or new adaptations emerging in existing ones (be they competitors, predators,  
187 pests or diseases), and partly as a result of fluctuations in abiotic environmental conditions,  
188 some of the existing species may become (locally) extinct over any period of time. The  
189 species richness of any given ecosystem or land unit is therefore a dynamic property.  
190 Recently the conventional explanation of local diversity as well as its ‘functionality’  
191 embodied in the niche concept has been challenged by theories that derive patterns close to  
192 the observed ones from ‘random walks’ in abundance of species without any a priori  
193 prediction of the direction of selection pressures and based on an equivalence of intra- and  
194 interspecific competition (Hubbell, 2001).

195 In agro-ecosystems farmers take a dominant role in this dynamic by the selection of which  
196 organisms are present, by modifying the abiotic environment and by interventions aimed at  
197 regulating the populations of specific organisms (‘weeds’, ‘pests’, ‘diseases’ and their  
198 vectors, alternate hosts and antagonists). The dynamic nature of the (local, patch level)  
199 diversity of any system, whether natural or agricultural, is often underrated, as is the  
200 importance of the selection pressure and process. The diversity of any system is not  
201 adequately represented simply by the number of species (or genotypes) present, but by the

202 relationships between them in space and time. Attempts to assemble combinations of the  
203 same number of species under slightly different conditions and in particular without the  
204 history of interaction often fail (Ewel, 1986, 1999). But what makes any existing species  
205 combination into a 'system' is still largely elusive. Some insights obtained in analysing food  
206 webs may help. For example Neutel (2001) showed that the majority of belowground food  
207 webs constructed from random combinations of organisms did not meet dynamic stability  
208 criteria, even though all parameters such as abundance of groups and dynamic properties  
209 were chosen in a 'normal' range when considered one-by-one. Yet, systems with the actual  
210 parameter combinations that are attained in the field did meet stability criteria, suggesting  
211 that partly uncovered rules about the proportionalities and co-variance within the normal  
212 range are crucial.

213 Debate on the relationship between biological diversity and ecosystem function has a long  
214 history which has taken on new vigour (and sometimes even rancour) since the advent of the  
215 Convention on Biological Diversity (see Woodwell and Smith 1969 for the older literature  
216 and Schulze and Mooney 1993, Mooney et al 1995, 1996, and many of the citations below  
217 for more recent discussion). Vitousek and Hooper (1993) contributed a major focus to this  
218 debate through hypothesising three different possible relationships between plant diversity  
219 and broad-based ecosystem functions such as the rate of primary production (Figure 1).  
220 Their analysis of current evidence led them to propose that the asymptotic relationship shown  
221 as Curve 2 in Figure 1 was the correct one. This suggests that whilst the essential functions of  
222 an ecosystem, such as primary production, require a minimal level of diversity to maximise  
223 efficiency this effect is saturated at a relatively low number. Swift and Anderson (1993)  
224 proposed that this relationship could also apply to the decomposer system. Examples of  
225 essential functions in this case are the basic suite of catabolic enzymes (e.g. for cellulolysis,  
226 lignin degradation etc), the facilitation role that invertebrates play by reducing particle size by

227 their feeding activity, and biophysical processes of pore formation and particle aggregation.  
228 It is interesting to note however that the communities of organisms contributing to the  
229 ecosystem function of decomposition are taxonomically much more diverse than those of  
230 primary production.

#### 231 **4.2 Experimental approaches**

232 Over recent years a number of authors have reported on experiments investigating the links  
233 between diversity and specific functions (e.g. see Ewel et al 1991, Naeem et al 1994, Naeem  
234 and Li 1997; Tilman and Downing 1994; Tilman et al 1996,1997; Hooper and Vitousek  
235 1997) that appear to broadly corroborate the predictions of the Vitousek-Hooper hypothesis  
236 for primary production. This has however generated an equal amount of discussion in  
237 refutation and the issue remains significantly a matter of interpretation and opinion (see  
238 Grime 1987; Hodgson et al 1998; Lawton et al 1998; Wardle 2000; Naeem 2000). There is no  
239 space here to review these studies in detail, but refer to Kinzig and Pacala (2001) and Tilman  
240 and Lehman (2001) for a synthesis that acknowledges the ‘sampling  
241 effect’ that probably dominates the initial phases of the experiments and the fact that ‘niche  
242 assembly’ will be a relatively slow process, especially where we are interested in stages  
243 beyond the pioneer phase. Each one of the experiments quoted can be criticised in one way  
244 or another. The strictest interpretation of many of the experiments would be that the  
245 conclusions apply only to the specific combinations of organisms used in the tests, and in  
246 most cases these are assemblages constructed for experimental purposes rather than naturally  
247 co-evolved communities. At a fundamental level such experiments suffer from a basic  
248 methodological paradox – in order to describe and understand diversity and complexity we  
249 need to simplify it, and take away the self-selection that governs real-world diversity.  
250 Dealing with the totality is impossible. For instance there is no single (or combination of)  
251 methods that would allow for the total inventory of the species richness of even a small

252 volume of soil. It is thus difficult to draw general conclusions about ‘diversity’ as such and in  
253 particular with respect to naturally co-evolved communities. The results of such ‘un-natural’  
254 experiments may however be more applicable to agricultural systems that in one sense can be  
255 said to have been assembled in a similar way.

#### 256 **4.3 The minimum diversity required within a functional group**

257 One potentially valuable interpretation of the Vitousek-Hooper relationship has been that the  
258 minimal level of diversity required to maximise the production function consists of  
259 representatives of an essential set of ‘functional groups’ of plants (Schultze and Chapin,  
260 1987). A functional group may be defined ‘a set of species that have similar effects on a  
261 specific ecosystem-level biogeochemical process’. As Vitousek and Hooper put it the  
262 ‘essential’ plant species are those that contribute in different ways to the key ecosystem  
263 functions – in the case of primary production by exploiting different components of the  
264 available resources by differences in canopy structure to maximise light capture or symbionts  
265 and root architecture to optimise capture of water and nutrients. Drawing together the threads  
266 of this discussion we hypothesise that ‘the minimum diversity essential to maintain any given  
267 ecosystem function can be represented by one or a few functionally distinct species i.e. one or  
268 a few representatives of a small range of functional groups’ is a useful null-hypothesis to  
269 guide investigations of the functional significance of biological diversity in agricultural  
270 systems. It may need further operationalization for specific ecosystem contexts, however. The  
271 total diversity required then depends on the number of functions that are recognized and to  
272 the degree of overlap in ‘functional groups’ between these different functions.

#### 273 **5. WHICH FUNCTIONAL GROUPS OF ORGANISMS ARE ESSENTIAL?**

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

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

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

294 The dominant biological properties regulating water flow and storage in the soil are the plant  
295 cover, the soil organic matter content and soil biological activity. Macrofauna such as  
296 earthworms, termites and other invertebrates influence the pore structure. Bacteria and fungi  
297 modify the extent of aggregation of soil particles. All these organisms and an additional  
298 range of decomposer organisms influence synthesis and decomposition of soil organic matter.  
299 Control of erosion and trapping of sediment is regulated by the architecture of the plants at  
300 and below the soil surface, the amount (and hence the rate of decomposition and movement)  
301 of surface litter, and the physical quality and organic matter content of the soil.

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

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

317 The earth's climate is regulated by the content of 'greenhouse' gases in the atmosphere –  
318 (CO<sub>2</sub>, CH<sub>4</sub>, NO<sub>x</sub>, etc). Carbon dioxide is emitted or taken up under one circumstance or other  
319 by the majority of living organisms and is thus a phenomenon of such generality as to defy  
320 attempts to relate its dynamics to changes in diversity other than the totally catastrophic.

321 Methane and the nitrous oxides are however the product and/or substrate for a relatively  
322 small number of bacterial species in the soil associated with soil, decomposing organic matter  
323 or the gut flora of animals. Diversity change may thus be more significant in these cases.

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

327 **5.1 What is the significance of diversity within functional groups?**

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

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

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

349 It is valuable to note that these are not necessarily mutually exclusive hypotheses, as they  
350 may refer to different space and/or time aspects of the system and the function of specific  
351 concern. We need to clearly separate the question of how the current diversity came into

352 being (the 'self organization' of the system, based on the success in the evolutionary history  
353 of all component species) from the human or teleological perspective of the relevance of this  
354 diversity. Just as we have to distinguish between 'diversity per se' and 'diversity of actual  
355 systems', we have also to recognize that not all components of a system have the same  
356 probability of being lost as a result of simplification of agro-ecosystems and some functions  
357 may therefore be more resilient than others. Differences in life histories of the key groups of  
358 organisms confer different temporal and spatial contexts to their role in the ecosystem and  
359 their responsiveness to its self-organising properties.

360 The third of Vandermeer et al's (1998) hypotheses is extremely pertinent to the question of  
361 how much of this diversity is needed to maintain ecosystem goods and services in the face of  
362 agricultural intensification and other aspects of ongoing 'global change'. There is certainly  
363 substantial experimental evidence that the many key functions can be maintained by only  
364 small numbers of species within a particular functional group. For example monotypic cover  
365 by perennial plants can be as effective as a diverse community in controlling erosion.

366 Although the decomposer community of a particular soil may be very diverse only a minority  
367 of the hundreds of species of fungi, bacteria or invertebrates participate in the decomposition  
368 process at a given time and place. The extent of redundancy implied by this can be  
369 demonstrated under laboratory conditions where decomposition can be fully mediated by  
370 single species cultures of enzymatically-diverse organisms such as white-rot basidiomycete  
371 fungi whilst in nature the same process may be carried out by several species of fungi,  
372 bacteria and animals (Swift 1976, Giller et al 1997).

373 The third hypothesis raises questions whether key functions can be maintained by one (and  
374 the same) species under all circumstances. This addresses the issue of the capacity of  
375 ecosystems to adapt to changing circumstances that result from elements of stress and  
376 disturbance. The capacity of a system to respond to and recover from disturbance is termed

377 its resilience. This property has been attributed to the degree of connectivity within an  
378 ecosystem, a feature that depends at least in part on the composition and diversity (Holling  
379 1973, 1986; Allen and Starr 1982). Diversity within functional groups may provide an  
380 important means for increasing the probability that ecosystem performance can be maintained  
381 or regained in the face of changing conditions. For the below-ground community for instance  
382 there is evidence that the same enzymatic function is carried out by different species of  
383 bacteria or fungi from the same soil under different, and even fluctuating, conditions of  
384 moisture stress or pH (see Griffin 1972 for discussion of this). In the case of plants different  
385 species may play a similar functional role in different seasons, under varying conditions of  
386 climatic or edaphic stress and in different stages of patch-level succession.

## 387 **6. RESILIENCE AND DIVERSITY THRESHOLDS**

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

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

402 **7. MANAGING BIODIVERSITY AND ECOSYSTEM SERVICES IN**  
403 **AGRICULTURAL LANDSCAPES**

404 **7.1 What is the impact of agricultural intensification on biodiversity and ecosystem**  
405 **functions?**

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

426 immediate negative impact but also kill non-target organisms with other functions such as  
427 pollination or soil fertility enhancement.

428 During agricultural intensification the diversity of crops and livestock is reduced to one or a  
429 very few species of usually genetically homogenous species. The varieties are selected or  
430 bred for yield (e.g. high plant harvest index), taste and nutritional quality. Plant arrangement  
431 is commonly in rows, fallow periods are bare, sequences may be monospecific (varietal) or of  
432 two or rarely more species. This is in contrast to natural ecosystems where the genetic  
433 diversity of plants (both within and among functional groups) is high but varies in relation to  
434 environment. The effects of land use change and agricultural intensification on biodiversity  
435 and associated functions are still poorly understood but conversion to agriculture almost  
436 always results in fewer species of both planned and associated biota with lower genetic  
437 variation and representing less functional groups. Nonetheless the extent of diversity in even  
438 so-called monocultures may be underestimated by plot-level assessment of diversity at any  
439 point in time. A rapid interannual turnover of the germplasm is often employed to stay ahead  
440 of the evolutionary race with pests and diseases, adding a time dimension to diversity that  
441 may exceed evolution in natural systems, albeit with respect to a narrow genetic base. This  
442 varietal turnover depends however on ‘externalized’ functions of maintaining genetic  
443 diversity in gene banks, and on the mechanisms of rapid multiplication and transfer of such  
444 germplasm. This situation contrasts with that of extensive agricultural systems where  
445 diversity is deliberately maintained within the system with or without external exchange.

446 Here a plot-level assessment may have more relevant boundaries of measurement, although  
447 lateral flows of organisms exist here as well. Production systems based on perennial crops  
448 and trees provide less opportunity for rapid turnover of varieties for obvious reasons, and  
449 there clearly is a much stronger need here for maintaining plot-level diversity as a risk  
450 management strategy (Van Noordwijk and Ong, 1999).

## 451 **7.2 Primary production**

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

## 470 **7.3 Nutrient cycling**

471 Nutrient cycles become more open in agricultural systems with losses of nutrient through  
472 offtake in harvest, run-off from compact surfaces, increased volatilisation through a changed  
473 surface environment and increased leaching associated with decreased soil organic matter  
474 content. These losses can be substituted by inorganic inputs but the efficiency of return to the  
475 plant is often low and fertilisation is usually required at levels far in excess of direct crop

476 demand, which further exacerbates the losses and can leads to pollution of groundwater etc.  
477 There is substantial evidence demonstrating gains in crop productivity from nutrient additions  
478 through mixtures of organic and inorganic sources of nutrients compared with either alone  
479 (e.g. Swift et al 1994). Maintenance of organic inputs to the soil is thus an important  
480 management strategy for efficient use of external inputs. Advantages in utilising a variety of  
481 such inputs have also been demonstrated because of the strong influence of input chemistry  
482 ('resource quality') on patterns of mineralisation. The diversity of organisms involved in  
483 nutrient cycling may be substantially reduced under agricultural intensification but there is  
484 little evidence of significant effects on decomposition and mineralisation processes which has  
485 been attributed to a high level of functional redundancy among decomposer fungi, bacteria  
486 and microregulators such as nematodes or collembola (Beare et al 1994, 1997; Giller et al  
487 1997). The significance of this loss of diversity should not however be assumed to be  
488 inconsequential. In particular it is unclear how the resilience of the system under conditions  
489 of change is influenced by such loss. Organisms with very specific functions, such as those  
490 exhibited by some bacteria of the nitrogen cycle, often show specialisation to particular soil  
491 conditions such as pH and specific genotypes may be lost as a result of soil degradation.  
492 Specific strains of dinitrogen-fixing bacteria may also be lost as a result of agricultural  
493 intensification resulting in the need for subsequent inoculation (Kahindi et al 1997).

#### 494 **7.4 Organic matter dynamics**

495 Soil organic matter (SOM) is a keystone component of the ecosystem in the sense that its  
496 impact on overall system performance exceeds its relative share in the energy flow through  
497 the system. Soil organic matter (SOM) stores and buffers nutrient concentrations, influences  
498 water storage in the soil and is a major factor in determining soil structure and thence  
499 erosivity. Above all it is a store of energy in the soil that drives many of the soil-based  
500 processes. SOM synthesis and decomposition is brought about by much the same community

501 of organisms as those involved in decomposition of plant litter. A well-charted phenomenon  
502 is the decline in SOM as a result of conversion of natural ecosystems to agriculture. Farmers  
503 utilize the nutrients mineralised as part of this decline of the SOM capital to support high  
504 initial levels of crop production after clearance. Soil tillage is also an effective additional way  
505 of stimulating the breakdown of SOM and plays a key role in promoting crop yields after  
506 land conversion to agriculture, until a new and lower equilibrium between breakdown and  
507 formation of SOM is reached. The level of the new SOM equilibrium, with its consequent  
508 impact on nutrient cycling, soil water regimes and erosivity, is related to the quantity of plant  
509 litter input, which is almost invariably lower than that of natural systems. Crops in intensive  
510 systems are usually selected for high harvest indices, and there may be uses for crop residues  
511 other than soil fertility maintenance (e.g. fodder or fuel). The SOM content is thus related to  
512 the quantity, diversity and mode of management of organic input to soil. A key feature of  
513 agroecosystem management is thus the trade-off between the gains in production from  
514 ‘mining’ the SOM versus the potential negative impact on its other ecosystem services and in  
515 particular on system resilience. This ‘trade-off’ between the different values of SOM has  
516 been rarely recognised but become a matter of greater interest as society has begun to realize  
517 the potential value of sequestering carbon in soil as a means to slow down the rate of global  
518 climate change. A research question of continuing interest is whether the functional  
519 properties of SOM are in any way influenced by the diversity of organic materials from  
520 which it is synthesised.

## 521 **7.5 Watershed functions**

522 The most important factors regulating water infiltration and retention are the extent of ground  
523 cover by plants and/or plant litter. The reduction in these, including interposing of periods  
524 when ground is bare, leads to greater run-off and diminished infiltration as well as increasing  
525 the risk of erosion. Substitution by mechanical tillage can ameliorate as well as aggravate

526 these effects. Monospecific cover can be just as effective as a diverse one with respect to  
527 limiting run-off and erosion, trapping sediment and promoting infiltration, but to be effective  
528 it has to be present year round. Diversity of organic inputs is likely to have a positive effect  
529 by widening the probability of differences in timing of litterfall and rates of disappearance  
530 from the soil surface. As soil protection on slopes depends more on partially decomposed  
531 litter with good ground contact than on fresh leaves that can be easily washed away, the role  
532 of plant diversity on slopes is likely to be greater than on flat lands. The macrofauna moving  
533 between litter layer and soil strongly influence partitioning of water between surface runoff  
534 and infiltration as well as modifying water movement within soil. Interesting examples of the  
535 influence of these ‘ecosystem engineers’ show how circumstance-specific diversity effects  
536 may be. Soil engineers making macropores in the soil are not welcome in all circumstances.  
537 In banded rice fields, farmers make an effort to destroy soil structure by puddling to reduce  
538 the porosity of the soil and building dykes to contain the water. These earthworks may be  
539 destroyed by the actions of earthworms and surveys by Joshi et al. (1999) in the Ifugao Rice  
540 Terraces (IRT), in the Philippines showed that 125 out of 150 farmers interviewed ranked  
541 earthworms as the most destructive pest of terraced rice fields. In a second example the  
542 conversion of Amazonian rainforest to pastures has been shown to lead to extinction of the  
543 natural earthworm community, which have been replaced in some circumstances by a single  
544 exotic species, Pontoscolex corethrurus. This has a negative effect on pasture productivity  
545 because the introduced worms compact the soil, whereas the native species improve soil  
546 structure (Chauvel et al 1999). Inoculation with species from the forest might reverse this  
547 effect, but remains to be tested.

#### 548 **7.6 Risks of pests and diseases**

549 As already indicated the decreased genetic diversity of plant cover increases the risk of pest  
550 attack. Simplification of the ecosystem and in particular the use of broad-spectrum pesticides

551 also decreases the diversity of natural enemies and increase risks of pest attack (Lawton and  
552 Brown 1993). Pesticides also have negative effects on non-target beneficial organisms  
553 including pollinators and beneficial soil biota.

#### 554 **7.7 Greenhouse gas emissions**

555 Land-use change alters the balance of gas emissions and thence influences global climates.  
556 There are very large increases in the CO<sub>2</sub> output during clearing from natural vegetation and  
557 break down of soil organic matter reserves that are rarely if ever balanced by regrowth. The  
558 output of methane may be significantly increased in systems such as paddy rice and intensive  
559 cattle production and of nitrous oxides by N-fertilisation. These changes are linked to  
560 alterations in soil structure that dominate changes in the activity of a variety of soil organisms  
561 (e.g. methanogenic and methanotrophic bacteria) but we are not aware of any documented  
562 case where such effects are linked to the absence of functional groups or to biodiversity  
563 change per se.

#### 564 **7.8 A hierarchy of functions**

565 There are a few general conclusions that may be drawn from this brief review of the impacts  
566 of agricultural intensification on the relationship between biodiversity and ecosystem  
567 services. First that whilst there are a number of clear examples where changes in diversity  
568 have threatened the provision of ecosystem services, especially relating to the regulation of  
569 pests and diseases, there are also others where the changes in biodiversity seem to be  
570 functionally neutral, at least within relatively stable environmental conditions. Second there  
571 may be some functional groups, particularly micro-organisms such as the decomposers,  
572 where the degree of functional redundancy is such that the resilience of the function is very  
573 high. These two observations may be generalised by stating that there are no rules to be  
574 derived for agricultural systems concerning the importance of biodiversity with respect to the  
575 maintenance of ecosystem services that apply across all functional groups and environmental

576 circumstances. Both the concept of ‘diversity’ and that of ‘ecosystem function’ are too broad  
577 to make generalizations at this level testable. There is a need and potential however to  
578 investigate the issues of thresholds of diversity-function relationship within specific  
579 functional groups and under circumstances of change in stress and/or disturbance.  
580 Finally we should re-emphasise the importance of the hierarchical control exerted by the  
581 plants over the other functional groups (Figure 4, Appendix).  
582 This is a particularly important feature when determining management options, not only at  
583 the field and farm scale but also at that of the landscape. The plant, decomposer and  
584 herbivore subsystems of the biological community interact in a variety of ways but the  
585 productivity, mass, chemical diversity (resource quality) and physical complexity of the plant  
586 component exerts the strongest influence and is the single most important determinant of both  
587 the diversity and the functional efficiency of the other two subsystems. Wardle et al (1999a  
588 and b) and Yeates et al (1999) showed for example that arthropod and microbial communities  
589 were not adversely affected by agricultural intensification provided the type of management  
590 (eg. mulching) provided for increases in the quantity and quality of the organic inputs. The  
591 maintenance of total system diversity and of the major part of the ecosystem services is thus  
592 predominantly determined by the nature of the plant community. This is also of course the  
593 main point at which humans intervene in the agroecosystem – to decide the species richness,  
594 the genetic variability and the organisation in space and time of the planned biota in the  
595 vegetation subsystem.

## 596 **8 IMPLICATIONS FOR THE DESIGN AND MANAGEMENT OF AGRICULTURAL** 597 **LANDSCAPES**

598 A substantial research investment has been made into agricultural systems that fall short of  
599 the full extent of genetic homogenisation and petro-chemical substitution. Examples are  
600 agroforestry and other inter-crops, rotations, mulch-based, minimum tillage and integrated

601 livestock-arable systems. All these systems are characterised by maintenance of diversity of  
602 plant functional groups above the level of monocropping. The scientific justification for such  
603 approaches has generally been made on grounds of greater functional sustainability and the  
604 wider spread of risk associated with more diverse products as well as on the recognition that  
605 it is in line with the management choices of the majority of the rural poor in the tropics. For  
606 farmers labour saving and low investment and risk may be the preferred attributes of these  
607 systems. It is interesting to note however that, whereas scientists had introduced single-  
608 species fallow systems to farmers in Western Kenya, these farmers decided on their own to  
609 diversify tree species in these improved fallow systems (Bashir Jama, pers. com., 2001).

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

618 Ewel (1986) and Moreno and Hart (1979) are among those who have advocated using plant  
619 functional groups as a basis for the (plot level) design of multi-plant agroecosystems. These  
620 designs also rely, explicitly or implicitly, on the impact that the effect of increasing the  
621 diversity of the vegetation system will have in enhancing the associated biodiversity both  
622 above- and below-ground and thence the probability of maintaining ecosystem services over  
623 a wider range of stress and disturbance. The evidence comparing such systems is almost  
624 entirely however based on assessments of yield, Vandermeer et al (1998) reviewed the  
625 literature on inter-cropping of all types and concluded that yield gains in comparison with

626 mono-crops depends on the specific complementarities in resource use and seasonal  
627 development of the components. As risks for the farmer depend on farm level diversity of  
628 potentially productive resources rather than on plot-level diversity, the focus of much  
629 agroecological research may have been too narrow.

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

636 **9 . DOES THE RELATIONSHIP BETWEEN DIVERSITY AND ECOSYSTEM**  
637 **SERVICES CHANGE ACROSS SCALES?**

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

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

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

671 It can be further hypothesised that at the higher scales of landscape and region the frequency  
672 and intensity of disturbance and stress (both natural and anthropogenic) is greater than those  
673 at the plot or farm scale and increasingly beyond the control of the land users. Prevention of  
674 decreases in the stability of agroecosystems and management of restoration become more

675 difficult and costly and eventually become impossible from both biological and economic  
676 perspectives because connectivity is too high and disturbances too large. The ecosystem  
677 services that enhance the resilience and adaptation of systems, such as biodiversity, thus  
678 become more and more important a feature of sustainable management as the scale of  
679 operation widens.

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

689 Curves 1 and 2 of Figure 3 deal with this case of diversity management at the plot to farm (ie.  
690 land-use) scale and are therefore concerned with alpha diversity – that is within these  
691 boundaries. (Curves 3 and 4 refer to higher landscape scales and are discussed in the next  
692 section). The arrow linking Curve 1 to Curve 2 represents the capacity of farmers to maintain  
693 the ecosystem services necessary for their production goals whilst sacrificing diversity., This  
694 shift thus hypothesises that at the plot and farm scale management interventions can  
695 compensate for losses of diversity, although of course both the economic and off-site  
696 ecological consequences of this remain unstated and will be very circumstantial. We know, as  
697 shown for small-scale farms in Kenya by Osgood (1998), that many farmers do value genetic  
698 and species diversity on their farms, as they are aware that it minimises economic risk by  
699 enhancing on-farm diversification of plant and animal production. The history of agriculture

700 provides many examples of how even extreme reductions in biodiversity can be managed,  
701 through periods of disturbance, by individual land users by substitution (e.g. chemicals,  
702 labour). Therefore, even though biodiversity has important ecological functions at the farm  
703 scale, it is nevertheless possible to decrease biodiversity levels very substantially at that scale  
704 while maintaining the productivity and resilience of agroecosystems. We hypothesize below  
705 however that at higher scales the control and management of disturbances and stresses  
706 becomes more and more problematic and costly and the resilience function of biodiversity  
707 thus becomes an increasingly important issue in management.

### 708 **9.1 Keep it simple: maintain ground cover**

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

### 721 **9.2 Landscape mosaics**

722 The majority of agricultural landscapes in the tropics, in contrast with most of the northern  
723 temperate zones, are mosaics of different land uses. How does this influence the biodiversity-  
724 ecosystem service relationship? At the plot scale the ecosystem services which is probably

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

745 The third hypothesis of Vandermeer et al (1998) predicts that a higher diversity of species  
746 will be required to provide a buffer against stress and disturbance at the landscape scale than  
747 will be the case for any single patch within it (i.e. gamma diversity will be higher than the  
748 sum of alpha diversity). This is pictured in Figure 3 by the difference between curves 1 and 3.  
749 Humans can intervene relatively easily (although not necessarily cost-effectively) at the plot

750 scale to substitute for diversity loss – as represented by the difference between curves 1 and  
751 2. At the landscape scale however intervention by humans, including these substitutive  
752 actions, will tend to widen the range of stress and increase the frequency of disturbance. We  
753 therefore hypothesise that this will result in yet greater need for diversity to ensure the  
754 maintenance of ecosystem services and resilience. This is shown by the arrow linking Curves  
755 3 and 4 in figure 3.

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

767 This model is of course simplistic and does not provide any guide to other features such as  
768 the size, shape and position (pattern) of patches on the landscape or on the temporal  
769 relationships between them. The hierarchical relationship between ecosystem services should  
770 assist in developing rules for these aspects. The regulation of erosion and water flows  
771 operates at a higher level in the hierarchy of controls than do aspects of nutrient cycling, soil  
772 structure and gas emissions or pest controls. The next part of this volume takes up these  
773 higher-level aspects of landscape management under the title of ‘watershed services’. The  
774 lower level services such as nutrient cycles and biological control activities may then be built

775 in through focus on aspects such as the degree of connection between the patches and the  
776 location, direction and intensity of the flows between them. It may be useful to classify land-  
777 use types into ‘functional groups’ in a manner analogous with that for species in order to  
778 develop more meaningful relationships between diversity and function at the landscape scale.

## 779 **10. POLICY IMPLICATIONS**

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

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

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

820 Second, the higher the scale under consideration, the more difficult it is for the increased  
821 numbers of individual land users to develop an effective management strategy for  
822 agroecosystem disturbances, that takes ecological interactions and connectivity into  
823 consideration. Even at the scale of small watersheds, it is not often the case that land users  
824 have been successful in developing collective and effective means of control and

825 management of disturbances. Furthermore, even if these land users have full knowledge of  
826 the relevant level of connectivity necessary to ensure resilience at the watershed scale,  
827 different sectors of society place differing levels of importance on ecosystem services and  
828 diversity. Farmers in tropical countries are unlikely to place as high a value on these  
829 functions of landscape diversity as does the community at large or the national society. They  
830 are furthermore highly unlikely to value the serpendic (i.e. future) value of diversity, which  
831 is much more likely to be valued by national and global communities.

832 In economic terms, farmers value some of the on-farm benefits of diversity and very few of  
833 the off-farm benefits, for the usual reasons that costs and benefits outside of the managers'  
834 domain (i.e. externalities) are generally not taken into account by individual decision-makers.  
835 The argument is however not simply about off-farm effects of biodiversity being ignored.

836 Farmer knowledge varies greatly. There may be many on-farm ecosystem services of which  
837 farmers are unaware (e.g., the role of micro-organisms), and thus cannot value, as well as  
838 services they may be aware of but will not consider important (e.g., reduction of greenhouse  
839 gas emissions). The same services may be valued by other groups in society, with a different  
840 perspective and set of interests. What is a beneficial service for one group may also be a cost  
841 for another (e.g. the perception of earthworms as 'pests' for paddy rice farmers, the trade-off  
842 between carbon sequestration and SOM mining). For these reasons, management of  
843 ecosystem services, and of biodiversity at the landscape scale, as well as management of  
844 disturbances in agroecosystems in land use mosaics, is unlikely to be optimal, from either an  
845 ecological or an economic perspective, in the absence of specific policy or institutional  
846 interventions. Lack of knowledge of threshold levels in connectivity at different scales,  
847 different perspectives on the value of biodiversity, externalities and difficulties in large  
848 groups of land users coming together in developing effective means of controlling

849 disturbances at the landscape scale thus result in biodiversity being managed by individual  
850 farmers in a sub-optimal manner.

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

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

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

## 879 **11. CONCLUDING REMARKS**

880 In the above discussion we have quoted or proposed a range of hypotheses concerning the  
881 relationships between biological diversity and ecosystem functions, and their implications for  
882 the management of agricultural landscapes. The general relationships that have been  
883 proposed may have to be replaced by more specific hypotheses of the relation between  
884 components of overall biodiversity and specific environmental functions, bounded in space  
885 and time. Sweeping generalizations from experiments that are necessarily restricted in space  
886 and time, and for example do not include major parts of the diversity-generating processes  
887 (including ‘lateral flows’ of dispersal and migration for re-establishment), are unlikely to be  
888 helpful in guiding the development of agro-ecosystems that have to provide for short,  
889 medium and long term service functions. Future investigations should utilise co-evolved  
890 communities, be structured to investigate the distinct roles of clearly defined functional  
891 groups, separate the effects of between- and within-group diversity and be conducted over a  
892 range of stress and disturbance to identify threshold levels of irreversibility of functional  
893 losses. This might include: testing the basic functional-biodiversity rule by experimentally  
894 determining the minimal level of diversity between and within functional groups that is  
895 necessary to maintain productivity, integrity and perpetuation of ecosystems; characterising  
896 the functional groups of organisms necessary to maintain specific ecosystem services;  
897 determining the ecosystem function and service effects that ensue from elimination or  
898 substitution of key functional groups, including particular investigation of controls over

899 below-ground diversity and function exerted by particular plant functional groups and other  
900 keystone organisms; and determining (and developing indicators for) the biodiversity  
901 thresholds for different ecosystem services. An interesting extension of the latter study might  
902 be to investigate whether similar thresholds exist for the intrinsic, utilitarian and serendipitous  
903 values of biodiversity.

904 Society as a whole has an interest in ecosystem services that are manifested substantially at  
905 scales above that of the field, plot or farm. At the scale of the watershed or landscapes there  
906 is, in comparison with any single patch, a greater range of environmental stress and higher  
907 frequency of disturbance, including of extreme events. The maintenance of ecosystem  
908 services at these scales thus requires either a higher diversity of species within functional  
909 groups or a greater investment in substitutive management to maintain ecosystem services.

910 These increments in diversity and/or investment are unlikely to be simply additive in view of  
911 the significant shifts in complexity that occur with shifts across scale. Optimal maintenance  
912 of ecosystem services at the landscape scale may be most readily achieved by a mosaic of a  
913 relatively few land-use types. This model is however likely to be overly simple because of:  
914 (a) differences in functional impact of different land-use types; and (b) the importance of  
915 organisation at the landscape scale in terms of the size, shape and location pattern of the  
916 constituent land-uses.

917 In developing appropriate land-use scenarios landscapes should be compared with respect to  
918 the aggregate values of their component land-uses for intrinsic, utilitarian and functional  
919 (ecosystem service) values of biodiversity. This would be assisted by establishing a typology  
920 of land-uses in terms of their efficiency in maintaining ecosystem service and in the trade-  
921 offs between this and profitability. The results of the ASB project provide a model for this  
922 approach with respect to the interactions between carbon sequestration potential and  
923 profitability. The relative costs and benefits of segregating the intrinsic, utilitarian and

924 functional uses of biodiversity between different land-use or landscape units compared with  
925 integrating them within such units is another parameter that should be of significant value for  
926 policy development.

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

933 We have indicated a number of biological and socio-economic issues that need to be clarified  
934 in order to provide more explicit advice to policy makers. No single optimal value can be  
935 placed on the biodiversity within a landscape. Land-use decisions are likely to be optimised if  
936 decision makers can be provided with scenarios showing how various land-use combinations  
937 result in different levels of diversity and the efficiency of different ecosystem services, and  
938 the associated values of biodiversity. In so-doing it will be important to include aspects of  
939 temporal change as well as pattern on the landscape as both these factors influence the  
940 resilience of the landscapes which should be regarded as a factor of over-riding importance.

941 These scenarios can then be used to identify policy interventions and institutional  
942 arrangements necessary to achieve the desired objective, whether it is one dominated by  
943 agricultural productivity targets or the maintenance of ecosystem services or the conservation  
944 of biodiversity, or a combination of all three.

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1108

1108 **Table 1:** Relationship between key functional groups of organisms, the ecosystem level  
 1109 functions they perform and the ecosystem goods and services they provide

<b>ECOSYSTEM GOODS AND SERVICES</b>	<b>ECOSYSTEM FUNCTIONS</b>	<b>KEY FUNCTIONAL GROUPS</b>
<b>Ecosystem goods including:</b>		
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)
<b>Ecosystem services including:</b>		
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 <sup>1</sup> Herbivores <sup>1</sup> Parasites <sup>1</sup> Micro-symbionts <sup>1</sup> Hyper-parasites <sup>2</sup> Predators <sup>2</sup>
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

1110 Notes to Table 1.

1111 Primary Production

1112 In some ecosystems photosynthetic micro-organisms may constitute as significant group eg.  
1113 rice ecosystems). Here we deal only with plants.

1114 Note 1.

1115 Plants. There is a long history of classification of plants into functional groups. The  
1116 groupings have been based on a variety of reproductive, architectural and physiological  
1117 criteria. For the purposes of this paper the efficiency of resource capture is suggested as the  
1118 main criterion. This will be determined by features of both architecture (eg. position and  
1119 shape of the canopy and depth and pattern of the rooting system) and physiological  
1120 efficiency. A very simple classification could for instance distinguish the roles of trees,  
1121 shrubs, vines and cover plants etc. and then subdivisions within each of these groups. Much  
1122 more detailed consideration of these aspects is given by Smith et al (1997).

1123 Primary Regulation (Note 1).

1124 These are a set of functional groups which have a significant regulatory effect on primary  
1125 production and therefore influence the goods and services provided by the plants.

1126 Pollinators. This is a taxonomically very disparate group of organisms including many insect  
1127 groups and vertebrates such as birds and bats. However there does not appear to be any  
1128 generally accepted categorisation based on feeding behaviour or similar criteria (Barbara  
1129 Gemmill, personal communication).

1130 Herbivores: A great variety of organisms feed directly on primary producers. Vertebrate  
1131 grazers and browsers are readily distinguished from invertebrate pests although their impacts  
1132 on the plants may have similar functional significance at the ecosystem level. Each of these  
1133 major groups are sub-divisible in terms of, for instance, feeding habits. The balance between  
1134 different types of browser for instance can influence the structure of the canopy.

1135 Parasites: Microbial infections of plants may limit primary production in analogous manner  
1136 to herbivory. Parasitic associations can also influence the growth pattern of the plants and  
1137 thence their architecture and physiological efficiency.

1138 Micro-symbionts: There is a wide range of microbial infections that are beneficial rather than  
1139 destructive of which the most familiar are di-nitrogen fixing bacteria and mycorrhizal fungi.  
1140 Service Provision.

1141 The functional groups within this category also strongly influence primary production but not  
1142 in the directly destructive or stimulatory way of the primary regulators. They also provide a  
1143 set of ecosystem services distinct to those deriving mainly from the primary producers.

1144 Decomposers: This is a group of great diversity which can be sub-divided taxonomically  
1145 (bacteria, fungi, invertebrates etc) and in relation to size both of which correlate somewhat  
1146 with functional roles in the breakdown (eg. detritivorous invertebrates) and mineralisation  
1147 (fungi and bacteria) of organic materials of plant or animal origin (Swift et al 1979, Lavelle  
1148 and Spain 2001).

1149 Ecosystem Engineers: These are organisms that change the structure of soil by burrowing,  
1150 transport of soil particles and formation of aggregate structures. The term is often confined to  
1151 the macrofauna such as earthworms and termites but fungi and bacteria also play a key role in  
1152 the binding of soil aggregates. Many of these organisms also contribute to the processes of  
1153 decomposition.

1154 Elemental Transformers: This may be the most diverse group of all and deserving of  
1155 substantial subdivision. It includes a range of autotrophic bacteria that utilise sources of  
1156 energy other than organic matter (and therefore not classifiable as decomposers) that play  
1157 key roles in nutrient cycles as transformers of C, N, S etc. In addition there are heterotrophs  
1158 that thus have a decomposer function but also carry out elemental transformations beyond  
1159 mineralisation (eg. free-living di-nitrogen fixers).

1160 Secondary Regulators (Note 2)

1161 Hyper-Parasites and Predators: This is diverse group of microbial parasites and vertebrate and  
1162 invertebrate predators that feed on decomposers, herbivore, pollinators etc. They have  
1163 particular significance in agriculture because of the service of biological control of pests and  
1164 diseases that they play.

1165 **FIGURE LEGENDS**

1166 Figure 1: Possible relationships between biological diversity and ecosystem functions for the  
1167 plant subsystem (from Vitousek and Hooper 1993). The authors hypothesised that curve 2  
1168 was the most probable of the three propositions.

1169 Figure 2: Hypothesised relationship between the diversity of ecosystem or land-use types and  
1170 the efficiency of function of (the totality of) ecosystem services at the landscape scale.

1171 Figure 3: Hypothesised relationships between diversity (as measured by species richness) and  
1172 the efficiency of function of ecosystem services at the patch-ecosystem (i.e. plot) scale

1173 (Curves 1 and 2) and the scale of the landscape (Curves 3 and 4). Curve 1 repeats hypothesis

1174 2 of Figure 1: Curve 2 shows how in an intensively managed agricultural plot ecosystem

1175 services may be maintained by substitution of diversity by inputs derived from human and

1176 petro-chemical energy. Curve 3 shows, by comparison with curve 1, that the threshold of

1177 ‘essential’ diversity is greater as the land area increases. Curve 4 represents circumstances of

1178 high disturbance of the landscape by human intervention.

1179 Figure 4: Hierarchical relationships between different categories of Functional Group – see

1180 Table 1 and Notes

## Appendix

### 1181 **KEY FUNCTIONAL GROUPS: A PRELIMINARY CLASSIFICATION**

1182 We have defined a Functional Group in the text as ‘ a set of species that have similar effects  
1183 on a specific ecosystem-level biogeochemical process’. There are many examples of  
1184 classification of species in this way within specific taxonomic or trophic groups (e.g. for  
1185 plants or pests). . There is no single classification to suit all purposes. In each case it is clear  
1186 that the number of functional groups that is recognised, the criteria that are used to classify  
1187 them and the degree of sub-division that is applied is a function of the question that is being  
1188 addressed. We propose here a classification into the ten major groups that are briefly  
1189 described below, together with such sub-division as may be necessary, for the purposes  
1190 addressed in this paper, i.e. the relationships between biodiversity and function with  
1191 particular respect to agriculture and ecosystem services. These Key Functional Groups are  
1192 listed in Table 1 in relation to the ecosystem services they provide. The relationships between  
1193 them are pictured in Figure 4. We suggest that this could provide a useful framework for  
1194 investigating and testing key questions on this topic. A hierarchical structure is suggested  
1195 (Figure 4). At the highest level are four major categories related to major trophic functions at  
1196 the ecosystem scale i.e. Primary Production, Primary Regulation, Service Provision and  
1197 Secondary Regulation. At the next level are the ten groups listed in Table 1 that perform  
1198 distinct ecosystem functions; and at the third level are sub-divisions which it may be  
1199 functionally and/or taxonomically useful to distinguish (e.g. vertebrate grazers versus  
1200 invertebrate pests among the herbivores). Further levels of subdivision may also be useful or  
1201 necessary in some cases.