

# Relationships between biodiversity and production in grasslands at local and regional scales

A. Hector<sup>1</sup> and M. Loreau<sup>2</sup>

<sup>1</sup>*Institute for Environmental Sciences, University of Zürich, CH-8057, Zürich, Switzerland*

*Email: ahector@uwinst.unizh.ch*

<sup>2</sup>*Laboratoire d'Ecologie, UMR 7625, Ecole Normale Supérieure, 46 Rue d'Ulm, F-75230 Paris Cedex 05, France*

## Key points

1. Experimental manipulations of plant species diversity in unfertilised prairies and meadows has revealed that increasing diversity often leads to increased productivity (range of observed relationships varies from flat to log-linearly positive); driven by a combination of facilitation, niche-partitioning and sampling/selection effects.
2. The longer-term effects of diversity on ecosystem stability are not as clear and in need of further work.
3. Recent applied work, and a new review of the grassland literature, both show the potential for biodiversity to increase productivity under realistic field conditions.
4. The longer-term feedback of grazers on biodiversity gradients is unknown, and grassland biodiversity experiments that incorporate grazers will be needed to test whether patterns differ from those seen in ungrazed prairies and meadows.
5. The relationship between diversity and productivity seen in local experiments is often different from regional-scale correlations, and the scaling-up of experimental results remains a research priority.

**Keywords:** grazing, ecosystem functioning

## Local and regional relationships

One of the main debates in ecology during the last few years has focused on the relationship between diversity and productivity, largely based on data from grasslands. A major factor contributing to this so-called 'biodiversity debate' is a failure to clearly distinguish between patterns and processes that act at local, versus regional scales. In trying to explain large-scale patterns in diversity, many ecologists have focused on productivity as a key factor; generations of ecologists are used to seeing graphs in which diversity is plotted as a function of productivity. While the frequency of different types of patterns (positive, negative, unimodal etc.) and their causes are still open to debate (Grace 1999; Mittelbach *et al.*, 2001), diversity is often correlated with productivity at large-scales (from regional to global). What has been less well researched is the biotic feedback: can local diversity itself influence productivity? The newer question - how does biodiversity influence productivity and ecosystem functioning - was prompted by concern over the ongoing loss of species from ecosystems. The potential for confusion is immediately obvious since now the scale has changed and the graph is reversed: productivity is now the response variable and diversity the explanatory variable. In larger-scale patterns, productivity and diversity are both covarying with environmental factors that change from place to place, while the local influence of diversity on ecosystem functioning will depend on the traits of the species present and their ecological interactions (Loreau 1998; Loreau *et al.*, 2001). The methodologies employed to study these two questions also vary. Larger-scale patterns are usually investigated with the analysis of collected observational data while the local influence of diversity on productivity

has been investigated by the controlled experimental manipulation of diversity, both by removal experiments and with experimentally controlled diversity gradients ('biodiversity experiments'). While the relationship between biodiversity and ecosystem functioning has only existed as a focused research area for about a decade (since the book edited by Schulze & Mooney, 1993), the conceptual link can be traced all the way back to Darwin (Hector & Hooper 2002). The correlation between diversity and productivity at larger scales is the subject of several reviews (Ricklefs & Schuler 1993; Grace 1999; Mittelbach *et al.*, 2001), consequently this paper will focus on how changes in local diversity within grasslands can affect productivity and other ecosystem processes and services. This area has been comprehensively reviewed by Loreau *et al.* (2001); Kinzig *et al.* (2002); Loreau *et al.* (2002b); Hooper *et al.* (in press), and so the focus will be on the most important ideas, experiments and results. Major stages in the development of pure research in this area are reviewed before looking at more applied studies on the potential value of biodiversity in grasslands.

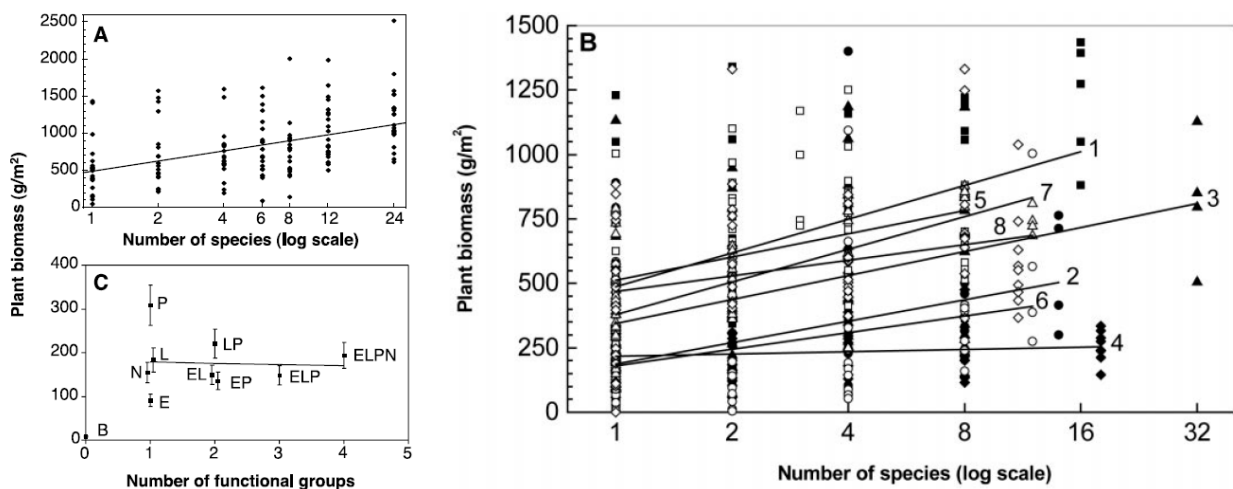
### **Grassland biodiversity and production**

The first controlled experiment deliberately designed to test the relationship between biodiversity and ecosystem functioning was carried out not in grassland, but with experimental communities of annual species grown in an Ecotron controlled environment facility (Naeem *et al.*, 1994). The experiment compared ecosystem processes measured in a hypothetical intact community with those in two depauperate versions that had species omitted at random. Diversity was simultaneously reduced at four trophic levels. The key result from this experiment was that the depauperate communities were less productive. However, since only a single intact community and two increasingly depauperate versions were compared the generality of the result was not clear - the results could have been specific to the particular order of species extinction examined. It was also impossible to separate effects at different trophic levels and so the mechanism generating the patterns was not clear.

In response to these limitations, Tilman *et al.* (1996) conducted a field experiment on Minnesota prairie grassland at Cedar Creek where they established an experimental diversity gradient, but where each level of diversity (a given number of species) was replicated with different mixtures of species selected at random from the species pool. Productivity was again positively related to diversity, the longer diversity gradient producing an asymptotic curve (on a log scale the pattern proved to be linear, see Figure 1A). While the random selection of species mixtures within diversity levels produced a more general result, the mechanism was still unclear. Interpretations had tended to focus on ecological 'niche differentiation' as the likely underlying mechanism, but a simpler 'sampling' effect had been initially missed. When combined in mixed communities some species in these experiments increased in abundance while others decreased. The sampling effect hypothesis (Huston, 1997) proposed that if relative abundance in a mixture is positively related to productivity in monoculture, then productive species would come to dominate mixtures and this effect will be stronger at higher diversity since there is a greater chance of randomly selecting the most productive species. Simple models demonstrated that with these assumptions, dominance of mixtures by productive species could generate a positive asymptotic curve in the absence of other ecological differences between species.

However Hooper & Vitousek (1997) performed a further biodiversity experiment on Californian grassland at Jasper Ridge, in which they combined different functional groups of species (early season annuals, late season annuals, nitrogen fixing legumes and perennial

bunchgrasses). In this instance the results were more complex: there was evidence for resource partitioning and facilitation between the different groups of species, but the overall pattern was flat - no significant effect of diversity (Figure 1C). It subsequently transpired that in this system the experimental communities were dominated not by the high-biomass perennial bunchgrasses, but by low-biomass early season annuals. Competition appeared to be largely for nitrogen and the early season annuals were somehow the best nitrogen competitors despite their small shoot and root systems. Dominance of communities by low-biomass species resulted in the opposite of the early sampling effect models - a negative sampling effect. This negative sampling effect cancelled out the effects of resource partitioning and positive interactions to produce the flat relationship between diversity and productivity on average.



**Figure 1** Examples of responses of total (A) or aboveground (B and C) plant biomass (in  $\text{g/m}^2$ ) to experimental manipulations of plant species richness (A, B) or functional-group richness (C) in grasslands in Minnesota (A) (Tilman *et al.*, 1996), across Europe (B) (Hector *et al.*, 1999), and in California (C) (Hooper & Vitousek, 1997). Points in (A) and (B) are data for individual plots. In (B) different regression slopes are shown for the eight sites to focus on between-location differences rather than the general log-linear relationship reported elsewhere (Hector *et al.*, 1999). Closed squares = Germany, line 1; closed circles = Portugal, line 2; closed triangles = Switzerland, line 3; solid diamonds = Greece, line 4; open squares = Ireland, line 5; open circles = Sweden, line 6; open diamonds = Sheffield (UK), line 7; open diamonds = Silwood Park (UK), line 8. Symbols in (C) correspond to functional groups and their combinations: B = bare ground, E = early-season annuals, L = late-season annuals, P = perennial bunchgrasses, N = N fixers. Reproduced from Loreau *et al.*, (2001) with permission.

At this point in time, there were only small numbers of data from single locations available, and it was unclear whether the relationship was highly idiosyncratic or whether some patterns tended to be more common than others. The EC-funded BIODEPTH project (BIODiversity and Ecosystem Processes in Terrestrial Herbaceous communities) deliberately set out to test the generality of relationships between biodiversity and ecosystem processes in European grasslands. The same biodiversity experiment was conducted at eight different grassland sites using standardised methodologies. In the main, ecological studies are carried out by individual research groups at individual locations, and it is interesting to speculate how results

would have been interpreted had the experiments been conducted individually? When viewed in this way, patterns varied from site to site between the extremes seen in the Cedar Creek and Jasper Ridge studies (Figure 1B). The Greek BIODDEPTH site showed no significant effect of diversity on productivity while other sites showed the positive log-linear curve. At other sites effects were nonlinear. However, when combined in a single analysis the interaction between sites and species richness was not significant, producing a final statistical model with eight parallel log-linear curves. Thus, all else being equal, a progressive loss of diversity from European grasslands can be expected, resulting in accelerating declines in productivity - with variation around the average expectation that includes both stronger and weaker (flat) relationships. No negative effect of diversity on production was found in this study (or from any other study to date).

While the range of different patterns and the typical result was now better understood, the contribution of different underlying mechanisms was still unknown. What was needed was a method that could take the overall pattern and divide it into the portion due to sampling-type effects and the portion due to niche-partitioning and facilitative effects. Loreau & Hector (2001) devised a new methodology to do just this. The methodology extends relative yield approaches previously used in intercropping and plant ecology. It defines a net effect of biodiversity, which is the difference between the observed yield of a mixture and that of the average monoculture. This net effect is then partitioned into two additive components: the selection and complementarity effects. The selection effect is the standard statistical measure of covariance applied to the relationship between yield in monoculture and relative yield in mixture. Selection effects will be positive when species with higher-than-average yield dominate communities and negative when species with lower-than-average yield dominate. The complementarity effect uses relative yields to ask whether increases in the abundance of some species exactly cancel declines in others. When this is the case, resource partitioning is a zero-sum game with some species taking more of a fixed total pool of resources and others taking less. Positive complementarity effects occur when decreases in the abundances of some species do not compensate for the increases in the abundance of other species, and could result from facilitation, resource partitioning or decreased impact of natural enemies in more diverse communities. When applied to the BIODDEPTH productivity data, the additive partitioning equation revealed that the complementarity effect drives the relationships more than the selection effect. Selection effects were sometimes positive and sometimes negative. Negative selection effects have since emerged as a widespread result, even though ecologists predicting the results of biodiversity experiments did not anticipate them. One consequence is that complementarity effects are effectively partly 'hidden' by negative selection effects that counter and mask them.

While the patterns and contribution of selection and complementarity effects had now become clearer, the biological mechanisms behind these effects were still largely untested. In particular, complementarity effects could be driven entirely by facilitation between nitrogen-fixing legumes and other species (note that this effect can also be seen as resource partitioning in which nitrogen is accessed from the soil or atmosphere). The existing studies had not been designed to isolate the effects of legumes and were limited in how well they could address this question. The problem was that more diverse plots were also more likely to contain legumes, and to contain more species of legumes. The effects of different components of biodiversity are collinear and whichever is entered first into statistical models often takes the greater portion of the shared variation (Schmid *et al.*, 2002). To better test whether positive biodiversity effects hinged on the presence of legumes, van Ruijven & Berendse (2003), established a new biodiversity experiment using many of the species found in the BIODDEPTH

project but omitting legumes from all communities. To their surprise the experiment produced a strong positive relationship similar to those seen in the earlier studies. It appears that while legumes play an important role in generating relationships between biodiversity and productivity, they may also sometimes mask the effects of other aspects of diversity. For example, natural enemies play a role in generating the biodiversity effects seen in the work by van Ruijven & Berendse (2003), effects that may have been hidden had legumes been included.

The main Cedar Creek biodiversity experiment (Tilman *et al.*, 2001), the Jasper Ridge experiment (Hooper & Dukes, 2004) and the BIODEPTH project fieldsites (Hector *et al.*, *in press*; Spehn *et al.*, *in press*) have all been monitored in the longer term. In general, the strength of the relationship between biodiversity and ecosystem processes in these studies became stronger, with complementarity effects playing a greater role. A wide range of ecosystem processes in addition to primary production are also affected by diversity.

### **How many species?**

To determine how many species are important in biodiversity effects is difficult both in principle and in practice. When there is a positive relationship between diversity and productivity it is often asymptotic, and so the difficulty then is to decide where on the continuum is the cut-off point at which there are enough species to provide the appropriate level of an ecosystem process. An alternative would be to quantify how many species provide different levels of productivity. Tilman *et al.* (2001, 2002) addressed this question by ranking species from most to least productive in their high-diversity community. They then constructed diversity indices that quantified how many of the 2, 3, etc, most productive species were present in a plot. When above and belowground biomass was analysed as a function of the different diversity indices, they found that indices with between 9 and 13 of the most productive species produced the highest  $r^2$ s. Thus, in these analyses, a large proportion of the species present were needed to best explain the productivity of a plot. Additional analyses of species-specific contributions suggest that much of the biodiversity effects can be explained by legumes and C4 grasses, but with additional species coexisting alongside them and contributing to total productivity (Lambers *et al.*, 2004). In contrast, the BioCON experiment at Cedar Creek (a combination of biodiversity gradients, elevated carbon dioxide and nitrogen fertilisation) suggests that the greater range of conditions present in this experiment provides opportunities for a greater range of species to contribute to the biodiversity effect (Reich *et al.*, 2004).

### **Functional groups**

Can species be amalgamated into functional groups that impact ecosystem processes in similar ways? The experiments discussed above used traditional functional group schemes based on traits expected to impact ecosystem processes. Legumes are grouped due to their ability to fix nitrogen from the atmosphere, and C4 and C3 grasses are separated on the basis of their different photosynthetic pathways. Other herbs (forbs) are more difficult to group but can be divided with respect to growth form (rosette versus tall), rooting depth etc. In many cases these groups do capture many of the functionally important differences between species, but frequently additional significant effects of species richness remain after controlling for the effects of functional groups. In particular, this may be the case when there is a high degree of environmental heterogeneity. In the BioCON experiment (which examined the same biodiversity gradient under different conditions of CO<sub>2</sub> and N enrichment), species and

functional group richness had largely independent effects across the whole range of conditions, such that species within groups were not functionally redundant but made separate contributions (Reich *et al.*, 2004). In situations like this a more appropriate approach may not be to force species into groups, but to search for continuous measures of functional diversity (Petchey, 2002; Petchey *et al.*, 2004).

Another point of debate is whether the functional traits and groups that distinguish species across large-scale gradients are the same traits that are functionally relevant within a particular ecosystem. For example, specific leaf area seems to provide a distinguishing trait when analysing patterns across different ecosystems, or the same type of ecosystem in different geographic locations. However, it is not clear if this is a particularly useful functional trait when looking at a particular community of species in one location.

### **Other ecosystem processes**

Most of the biodiversity experiments to date, particularly those with plants, have tended to focus on biomass production as a key ecosystem process. While production is of high interest, particularly in grasslands, other ecosystem processes have received less attention than they deserve. Some ecosystem processes can be integrated with biomass production in a logical fashion. For example, in some biodiversity experiments a positive relationship between diversity and biomass is mirrored by a negative relationship with soil nitrogen (Tilman *et al.*, 1996; Scherer-Lorenzen *et al.*, 2003). Lower levels of free resources would be expected if production is higher due to more complete resource capture in high-diversity plots. However, the relationship between plants and soil resources can be complex - particularly when nitrogen fixers are included in communities. Decomposition rates often appear to be less sensitive to changes in diversity, at least in the short-term, than is production (Hector *et al.*, 2000; Knops *et al.*, 2001), which matches with build up of biomass in many studies (Reich *et al.*, 2001). One of the new areas of development in biodiversity experiments is the intention to take a broader whole-system view focusing on element cycles (Roscher *et al.*, 2004).

### **Diversity and stability**

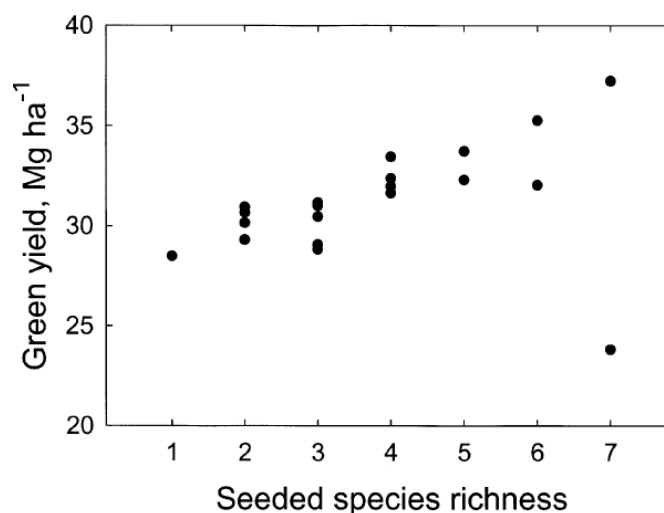
Theory predicts that biodiversity should have a 'portfolio' or 'insurance' effect if asynchronies in the fluctuations of species populations serve to average out fluctuations at the ecosystem level (e.g. total community biomass) (Loreau *et al.*, 2002a). Unfortunately, experimentation has not kept pace with the development of new theory, and to date only a single experimental test exists for grasslands. Pfisterer & Schmid (2002) subjected the Swiss BIODEPTH biodiversity gradient to an artificial drought. Unexpectedly, they found that in absolute terms high diversity communities showed a greater reduction in biomass than did lower diversity communities. However, it must be kept in mind that the relationship between diversity and productivity before drought was already positive. When looked at in relative terms all communities suffered a similar proportional reduction in biomass. Work from the Portuguese BIODEPTH experiment (Caldeira *et al.*, in press) shows similar patterns. Thus, so far there is no strong experimental evidence that biodiversity acts as insurance in natural ecosystems. This lack of evidence, however, may be due to the small number and limited length of studies performed on this issue.

## Management strategies, sustainability and ecosystem services in grasslands

All of the experiments reviewed above are from basic ecology. They were intended to perform the first general tests on the influence of biodiversity on ecosystem functioning. However, results from pure science do not always translate into more applied situations in the real world. Bullock *et al.* (2001) set out to perform a more realistic biodiversity experiment. They selected six field sites in the South East of England with similar soil type. The UK Ministry of Agriculture, Fisheries and Food (MAFF) recommended particular seed mixtures as appropriate for these site conditions. At each field site, Bullock and colleagues compared the performance of the recommended seed mixtures with higher-diversity mixtures where they supplemented the recommended mixtures with extra appropriate species. The result was a linear increase in yield with the extra species, a result consistent across the six field sites. The economic assessment obviously depends on the worth of the extra hay produced, how long this effect persists and the price of the seed. Nonetheless, under realistic conditions Bullock and colleagues showed that notwithstanding the recommendations of an expert organisation, increasing biodiversity lead to increased production.

### Grazing

All of the grassland biodiversity experiments to date have excluded large grazers. The study systems have been prairies where periodic fires maintain the grassland or meadows where humans act as the main grazer by swathing hay. Sanderson *et al.* (2004) reviewed the grazing literature and suggest that biodiversity experiments incorporating grazers are the next area awaiting good experimentation. Their review of the relevant applied literature produced some old results showing that at least some grassland mixtures designed for pastures exhibit a positive relationship between diversity and production (Figure 2). The untested aspect is what effect grazing would have on diversity; the feasibility of maintaining a diversity gradient once grazers have been added, is not known. While difficult to perform, grassland biodiversity experiments that include grazers will be needed to determine whether relationships differ from those observed in ungrazed prairies and meadows.



**Figure 2** Positive relationship between diversity and yield of fresh green forage in selected grass-legume mixtures grown under grazing and irrigation at Logan, Utah, from 1947 to 1951. Data points are averages of 5 years (Reproduced from Sanderson *et al.*, (2004) with permission).

## Scaling-up

One of the major objections to the positive relationships found in experiments is the apparent conflict with correlational patterns found at regional scales (Grace 1999; Mittelbach *et al.*, 2001). A suggested resolution to this apparent conflict is that in experiments the direct effect of biodiversity on ecosystem processes is isolated, whereas in larger-scale surveys both diversity and ecosystem processes are driven by changes in other environmental variables (Loreau, 1998; Loreau *et al.*, 2001). Levine (2000) provides an enlightening example of how local and regional relationships can vary in relation to different ecological processes acting at these different scales.

However, this poses a common problem in ecology: how to scale-up small-scale experimental results to the larger landscape and regional scales? There have been few attempts to do this. Tilman *et al.* (2002) used the empirical species-area approach to predict how many species would be needed to maintain ecosystem processes within the Great Plains prairies (based on work at the Cedar Creek site). This empirical approach is useful as an order-of-magnitude guess about the functional consequences of biodiversity at larger spatial scales. However, it ignores the dynamics of both diversity and ecosystem processes at these scales. Recent theoretical work on metacommunities (sets of communities connected by dispersal of organisms) shows that landscape connectivity can have dramatic influences on diversity and productivity, and predicts that local species diversity, productivity and ecosystem stability will all be highest at intermediate rates of dispersal across communities (Loreau *et al.*, 2003). Thus, investigating processes at landscape and regional scales becomes an urgent need to predict the changes and functional consequences of biodiversity, at the scales where human influences are strongest.

## Conclusions

Experimental manipulations of diversity in unfertilised prairies and meadows has revealed that increasing diversity often leads to increased productivity, although the range of observed relationship varies from flat to linearly positive. The effects are driven by a combination of facilitation, niche-partitioning and sampling/selection effects. The longer-term effects of diversity on ecosystem stability are not as clear and in need of further work. The local patterns revealed by biodiversity experiments often differ from regional-scale correlations between diversity and productivity, and the scaling-up of experimental results remains an important challenge.

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