The functioning of European grassland ecosystems: potential benefits of biodiversity to agriculture

Asher Minns, John Finn, Andy Hector, Maria Caldeira, Jasmin Joshi, Cecillia Palmborg, Bernhard Schmid, Michael Scherer-Lorenzen, Eva Spehn, Andreas Troumbis and the BIODEPTH project

Asher Minns and Andy Hector are with the Natural Environmental Research Council (NERC) Centre for Population Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, UK. E-mail: a.hector01@ic.ac.uk. John A. Finn is with the Department of Agriculture, University of Reading, Earley Gate, PO Box 236, Reading, Berkshire RG6 6AT, UK. Maria C. Caldeira is with Departmento de Engenharia Florestal, Universidade Tecnica de Lisboa, Tapada da Ajuda, Lisboa PT-1399, Portugal. Jasmin Joshi and Bernhard Schmid are with Institut für Umweltwissenschaften, Universität Zürich, Winterthurerstrasse 190, Zürich CH-8057, Switzerland. Cecilia Palmborg is with the Department of Agriculture for Northern Sweden, Swedish University of Agricultural Sciences, Box 4097, S-90403 Umeå, Sweden. Eva Spehn is with the Institute of Botany, University of Basel, Schoenbeinstrasse 6, Basel CH-4056, Switzerland. Michael Scherer-Lorenzen is with the Max-Planck-Institute for Biogeochemistry, Postfach 10 01 64, Jena D-07701, Germany. Andreas Troumbis is with the Biodiversity Conservation Laboratory, Department of Environmental Studies, University of the Aegean, Karadoni 17, Mytilene, Lesbos GR-811 00, Greece. Others involved in the BIODEPTH project include: C. Beierkuhnlein, P.G. Dimitrakopoulos, K. Huss-Danell, A. Jumpponen, M. Loreau, C.P.H. Mulder, G. O'Donovan, J.S. Pereira, E-D. Schulze, A.C. Terry and F.I. Woodward.

The BIODEPTH project was funded by the EC Framework IV Environment and Climate Programme from 1996–99. The network is still active both in publishing results from the project and conducting further research on the plots. Asher Minns was a member of the BIODEPTH project based at the Centre for Population Biology. He is now Public Affairs Officer of the Environmental Change Institute at the University of Oxford.

About half the farmland of Europe is grassland pasture or hay meadow, and much is impoverished in plant species due to the addition of fertilizers and pesticides, agricultural re-sowing, habitat fragmentation, land abandonment and changes in grazing and mowing regimes. Given this widespread reduction, it is important to understand the effect that loss of biodiversity is having upon our wider environment. Here the authors summarize the main results from the BIODEPTH project, the first multinational, large-scale experiment to examine directly the relationship between plant diversity and the processes that determine the functioning of ecosystems. The results suggest that preserving and restoring grassland diversity may be beneficial to maintaining desirable levels of several ecosystem processes, and may therefore have applications in land management and agriculture.

The functioning of ecosystems provides many types of benefits to mankind, as so-called 'ecosystem services'.[1] Services provided by particular ecosystem processes include, among many others, the provision of harvestable goods (production), purification of freshwater, as well as the provision of clean air and the regulation of weather and climate. Economists have recently valued the benefits supplied to human society by ecosystem services at US$33 trillion per year, approximately double the estimated value of global gross national product (GNP).[2] However, ecosystem processes can be affected by the activities of microbes, plants and animals and changes in their biodiversity. In response to concerns about the loss of biodiversity, ecologists have begun to investigate the impacts on the beneficial services that humans derive from ecosystems. Modern intensive agriculture is typically of low diversity, but has achieved very high levels of productivity largely through the combination of monocultures of selected crop varieties and high inputs of fertilizers, biocides and energy. However, in addition to the direct costs of inputs, associated environmental problems can arise from intensive agricultural practices. Hence, there is a demand for alternative management practices that reduce these associated costs while maintaining productivity and other ecosystem services. In this article we discuss the role of species diversity in affecting ecosystem functioning, ie how the diversity of components (eg genetic and species diversity) in an ecosystem affects the way it functions. We summarize the findings of the BIODEPTH project, a major international collaboration that experimentally varied plant diversity and monitored effects on ecological processes, and discuss potential applications to agricultural systems.

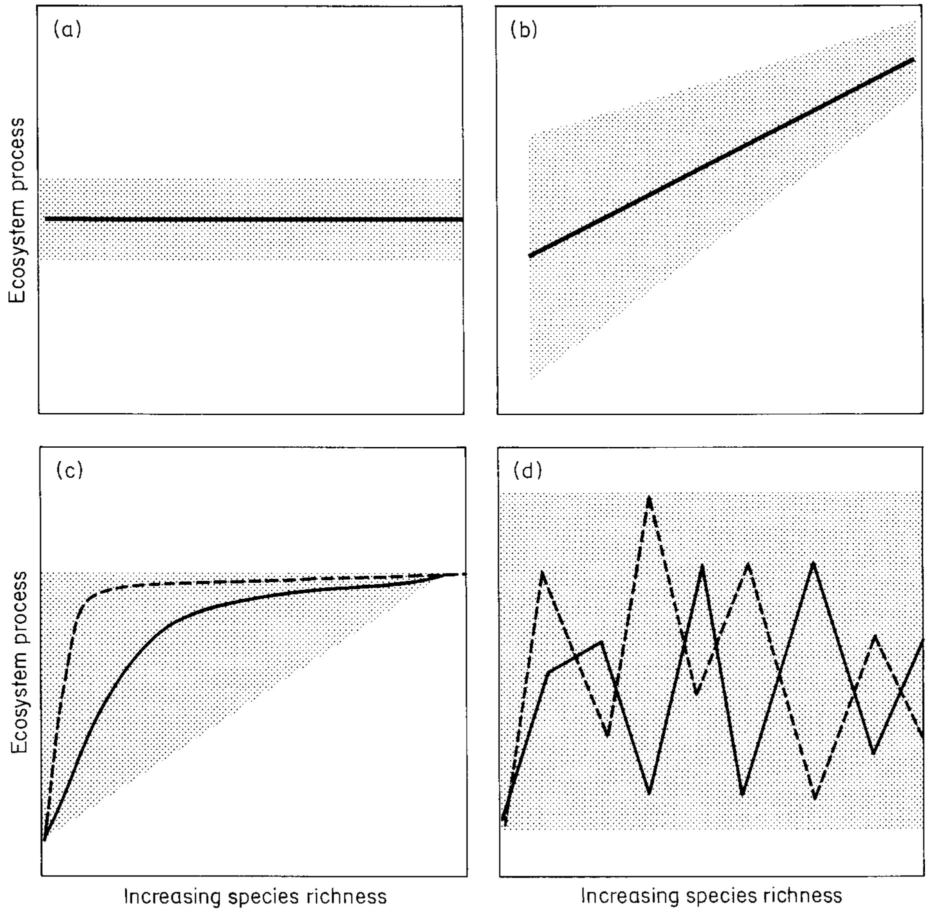

Figure 1. Hypotheses on the relationship of biodiversity and ecosystem functioning. In each panel, solid and broken lines show average responses of a given ecosystem process, with variance shown by the shaded area. Suggested relationships include: (a) flat null response, (b) linear, (c) curvilinear, saturating at variable numbers of species, and (d) idiosyncratic.

Background

A number of conceptual hypotheses have been proposed to predict the effects of a decline in species richness on ecosystem functioning (Figure 1). However, in addition to describing the patterns, we also want to gain an understanding of the underlying mechanisms that act to produce biodiversity effects when species are combined in diverse mixtures. Biodiversity effects partly arise from the intrinsic properties of species and the likelihood of their being present in a community. For example, the 'selection' or 'sampling' effect of biodiversity[3] predicts that more diverse communities have a higher probability of including species with any given trait, including high productivity, drought tolerance, etc. However, species in communities interact and additional biodiversity effects can arise from these positive or negative interactions. In addition to sampling effects, potential benefits of biodiversity arise from positive species interactions or from niche complementarity — in which ecological differences between species in intact communities lead to a more complete use of resources relative to their impoverished versions. In plant communities such ecological differences include specialized ways of exploiting resources, deterring pests and tolerating diseases.

The BIODEPTH experiment

The BIODEPTH project (BIODiversity and Ecological Processes in Terrestrial Herbaceous Ecosystems) tested whether ecosystem processes were affected by a decline in plant diversity in European grasslands. The approach and results are summarized in Hector *et al*[4] and more recent comprehensive lists of associated publications are available elsewhere.[5] Our eight field sites included a range of grassland types and spanned Europe from Ireland to Greece and from Portugal to Sweden (Figure 2). To mimic the gradual loss of plant species from grasslands, we created experimental plant communities in plots at each site by ploughing to remove the existing vegetation, and then neutralizing the seed banks. We re-established plant communities in experimental plots (each of area 2 m × 2 m) by sowing grasses and forbs of local origin, varying the highest level of diversity to reflect natural differences in grassland diversity. At each field site, a gradient of five

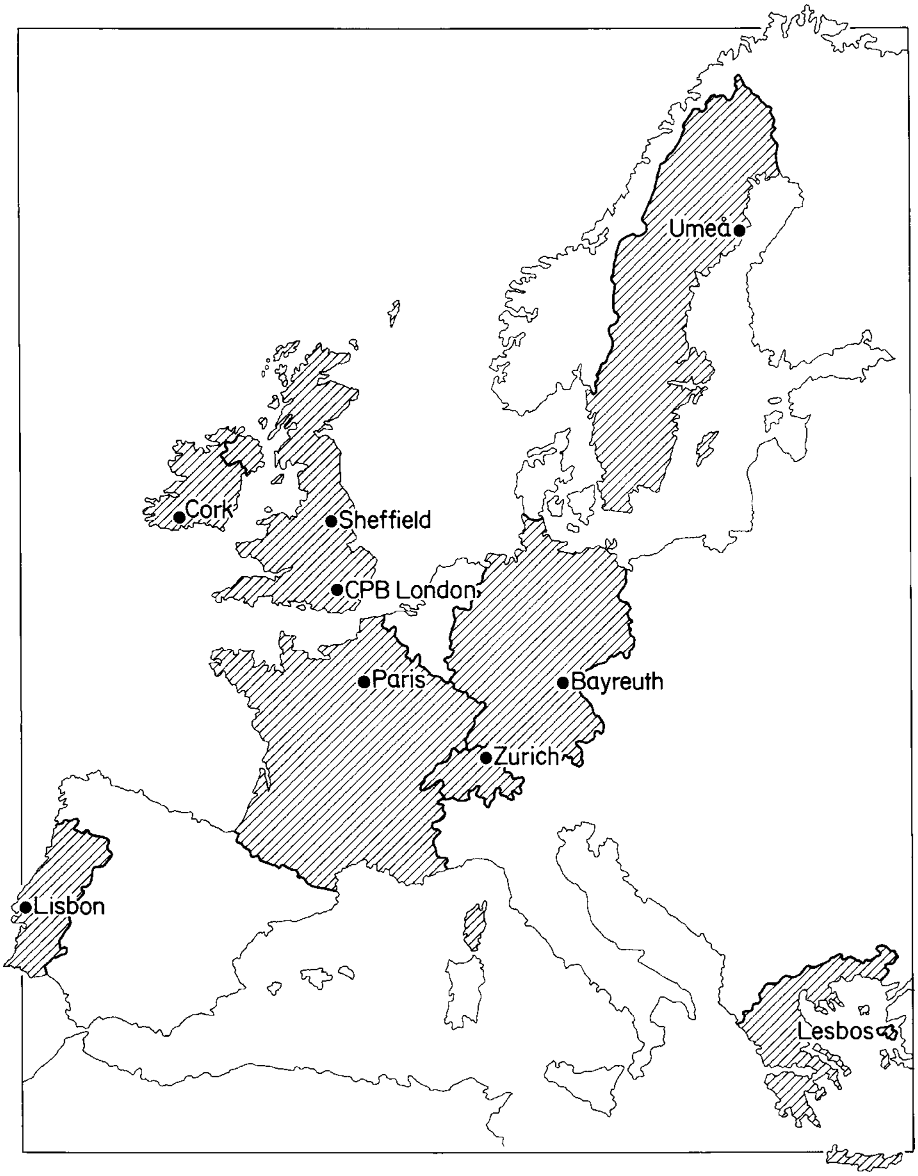

Figure 2. Map of BIODEPTH sites within Europe.

levels of sown diversity reduced this baseline diversity down to single-species monoculture plots of a variety of species. To facilitate across-site comparisons, a similar experimental methodology was adopted at each of the eight BIODEPTH field sites, creating a total of 480 plots containing 200 different plant communities. Ecologists often classify plants into 'functional groups', according to the role they perform in an ecosystem: eg legumes can be distinguished by their ability symbiotically to fix atmospheric nitrogen. One contention in the research of biodiversity and ecosystem functioning is whether observed changes in processes, for example productivity, are due to loss of species richness, or a reduction of functional group richness. However, to some degree the two go hand in hand — clearly, a more species-rich community is more likely to contain a range of functional groups, whereas an impoverished community contains fewer species and functional groups.

When designing the BIODEPTH experiment, we categorized species into three broad functional groups: grasses, nitrogen-fixing legumes, and other herbaceous plant species (herbs). In addition to manipulating plant species richness, we manipulated the sown communities so that a particular level of species richness could independently vary in the number of functional groups, eg different four-species communities might be composed of one, two or three functional groups. We represented each level of species richness and functional richness by several different communities at each site, with each assemblage containing a different species or a mixture of species. Excluding monocultures, each community contained at least one grass, with each community duplicated at a site to replicate composition (the particular mixture of species). We monitored key ecological processes such as plant growth and harvest yield (using above-ground biomass as a surrogate for productivity), the breakdown of dead plant material (decomposition) and the amounts of nutrients in plants and soils (nutrient cycling and retention). We used standardized methods to take 'core' measurements at all sites, and monitored other processes at selected sites, reflecting local interests and expertise of the researchers.

Species richness and grassland productivity

The BIODEPTH experiment reveals the relative roles of species richness, geographic location and community composition as determinants of grassland productivity, with these three variables accounting for about 20, 30 and 40% of the overall variation in productivity, respectively.[6] Species composition of the experimental communities, although not statistically significant, was important since it accounted for a large amount of the variation in yield. We found that both species richness and functional group richness had highly significant effects on above-ground productivity, measured as biomass yield at times of harvest. Overall, analysing all 480 plots as a single experiment, communities with lower diversity were, on average, less productive (Figure 3). We can best describe the overall effect of decreasing species richness by a simple linear relationship between productivity and the number of plant species on a log scale ($\log_2$ examines successive halving or doubling of species numbers). This log–linear relationship describes an initially weak but increasing reduction of productivity of approximately

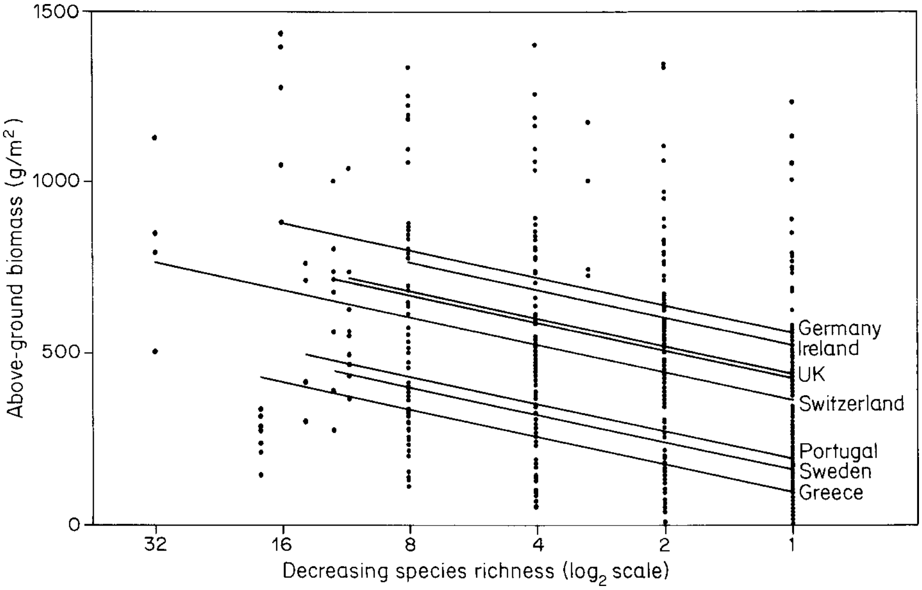

Figure 3. Productivity declines with the loss of plant diversity: across sites there is a reduction of harvest yield with decreasing species richness. Each halving of the number of plant species reduces yield by approximately 80 g/m^2. Points are total above-ground biomass for individual plots; lines are slopes from the multiple regression model using species richness on a log–linear scale. Silwood (southern England) and Sheffield (northern England) are labelled as UK. Based on a figure from Hector *et al*, 'No consistent effect of plant diversity on productivity? Response', *Science,* Vol 289, 2000.

80 g/m^2 per year for every halving of species richness. Twenty-nine out of 71 commonly occurring species in the experiment contributed significantly to the effect of composition on productivity, most small, but some large. For a given number of species, communities with fewer functional groups were less productive and, on average, the omission of a single functional group reduced productivity by approximately 100 g/m^2 per year. When the data for individual sites are plotted separately (Figure 4), they produce a variety of patterns compared with the single overall analysis. Hence, when looking at any single site we might see a variety of relationships between species richness and biomass, but on average we would expect to see a log–linear decline in productivity. Not surprisingly, there are highly significant effects on productivity due to the presence of the legume and herb functional groups. One species, the nitrogen-fixing red clover, *Trifolium pratense*, had particularly marked effects, increasing productivity in the second year of the experiment by about 360 g/m^2 when present. Legumes may have 'keystone' effects on many ecosystem processes due to their nitrogen-fixing ability. Consequently, the effects of the loss of biodiversity will vary depending on which species are lost. In particular, when legumes are lost, especially *T. pratense*, we would expect the reductions in productivity and related processes to be greater than when legumes remain and species of other functional groups are lost.

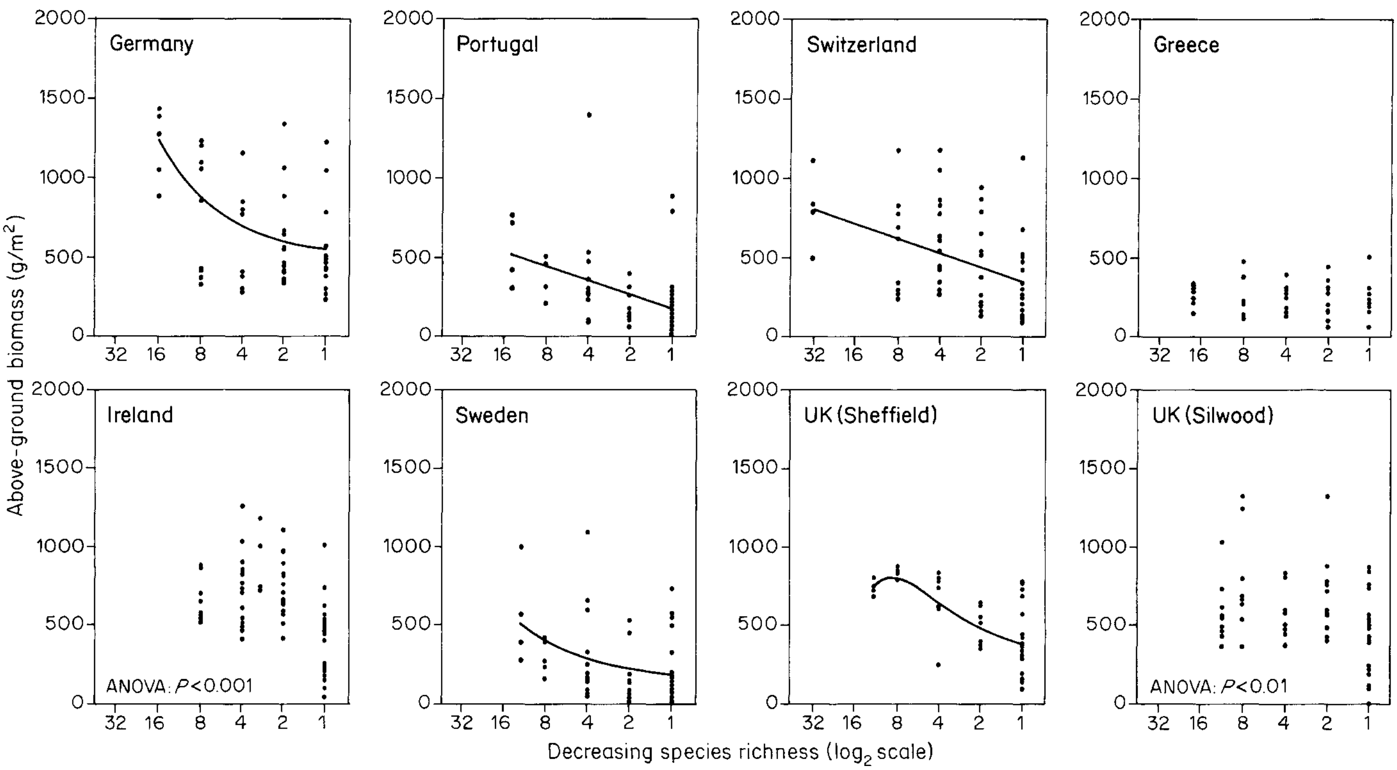

Figure 4. Different productivity responses seen at individual sites. When the same data used for Figure 3 are analysed for individual locations, different 'best' relationships are found at different sites, despite the overall log–linear trend. Based on a figure from Hector *et al*, 'No consistent effect of plant diversity on productivity? Response', *Science,* Vol 289, 2000.

In summary, the productivity patterns observed in our experiment arose from a variety of different biodiversity effects. Productivity is partly determined by the intrinsic traits of the species present in a community (ie by 'selection' or 'sampling' effects) but also by species interactions. For example, when we analysed individual species performances, fewer species declined in performance in our multi-species communities than increased. This result is consistent with reduced interspecific competition between some species in mixtures, compared with intraspecific competition in our single-species monocultures and with niche complementarity and positive species interactions as contributory mechanisms producing greater productivity in our diverse grassland communities.

Nitrogen retention and leaching

In general, nitrogen pools in above-ground vegetation increased with diversity, although the results varied between sites. This result was most likely driven by the presence of legume species and the uptake of fixed nitrogen by non-legume species. The effect of legumes probably comes via two mechanisms: reduced competition with the non-legumes for soil nitrogen and the addition of fixed nitrogen to the soil through fast decomposition of legume litter. Analysis of decomposition rates of cotton strips at four of the northern BIODEPTH sites indicates that nutrient cycling may be more efficient in communities with legumes due to strong competition for nitrogen between soil microbes and plants, especially in pure grass communities.[7] Interestingly, the increase in nitrogen pools was driven mainly by the increase in productivity with diversity, ie vegetation quantity not quality. In other words, given more nitrogen our plant communities tended to hold a constant percentage of nitrogen in the vegetation, but produced more biomass.

Contamination with nitrate leached from the soil is a serious threat for groundwater quality in regions with intensive agriculture. Measurements of nitrate leaching across plant communities with different diversities were conducted at the field site in Bayreuth, Germany[8] and at the Swedish site in Umeå. A variety of factors influence nitrate leaching from ecosystems, including climate, soil properties, agricultural management practices, crop species or the presence of grazing animals. Complementary resource use predicts that systems that have lost species should be less effective in the uptake of available soil nitrogen and other soil resources. Thus, available inorganic nitrogen in the soil should increase with loss of diversity, and because nitrate ions are highly mobile in soil, they are easily leached into groundwater.

In our experiments, nitrate leaching was highly variable depending on the species composition of the plant communities. In Germany, communities with nitrogen-fixing legumes lost significantly more nitrate than communities without legumes, causing a high variation within each diversity level (Figure 5). In several low-diversity mixtures containing legumes, nitrate concentrations in the soil solution were higher than the official EU threshold value for drinking water, at 50 ml/l. In Umeå, this threshold was also exceeded, but only after frost damage to pure legume mixtures. In the extreme, 350 mg/l from the Bayreuth clover monocultures predicts a loss of 100 kg nitrogen per hectare per year. In accordance with the complementarity hypothesis, leaching increased with decreasing diversity, but this pattern was only significant in communities containing legumes. On average, we found that communities with four or fewer species were relatively 'leaky', while communities composed of eight or more species might be regarded as relatively 'impermeable' due to the effects of diversity on the balance

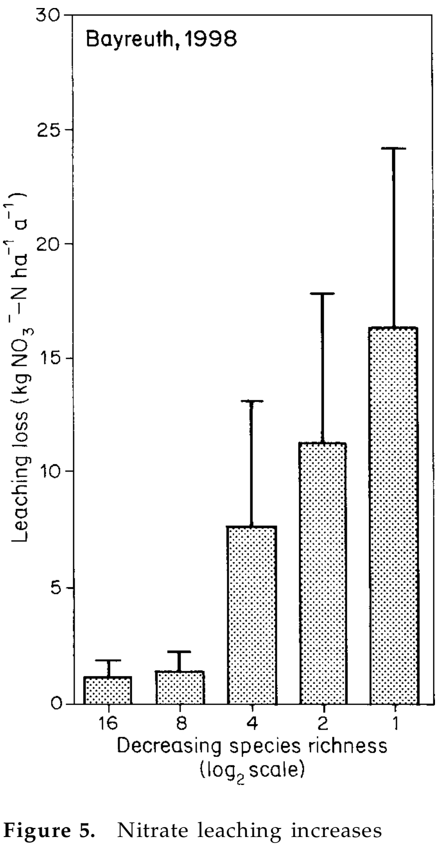

Figure 5. Nitrate leaching increases with loss of plant species (means ± SE per species richness level). Low-diversity mixtures containing nitrogen-fixing legumes are particularly vulnerable to leaching; nitrate concentrations in the soil solution may be substantially higher than the official EU threshold value for drinking water.

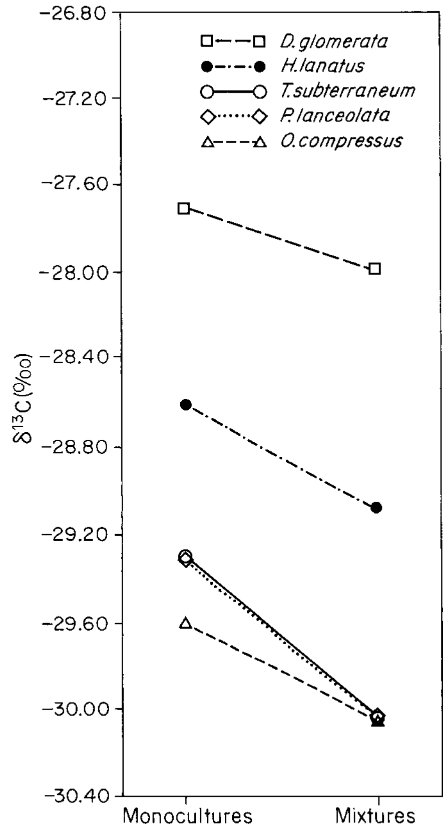

Figure 6. Leaf carbon isotope ratio ($\delta^{13}C$) of *Plantago lanceolata, Holcus lanatus, Dactylis glomerata, Trifolium subterraneum* and *Ornithopus compressus* in monocultures and in species-rich mixtures (8 and 14 sown species). Plots are means of 1997 and 1998 measurements.

between nitrogen fixation and uptake (Figure 5). There was a negative correlation between root biomass and leaching — this underlines the importance of well developed root systems for the avoidance of nitrate leaching losses and the use of species that rapidly develop an extensive root system as 'catch crops' to reduce nitrate leaching after the harvest of annual crops. Enhanced nitrate leaching during and after the cultivation of legume crops is well known, and there is strong evidence of nitrate leaching in grass–clover pastures. In our experiments, the risk of nitrate leaching was very low without the additional input from fixed atmospheric nitrogen by legumes. Recommendations for grassland management aiming at a reduction in nitrogen losses focus on fertilization regimes, grazing intensities and the avoidance of pasture conversion, but not on a control of legume abundance. In summary, the results of nitrate monitoring of the experimental communities at the Bayreuth and Umeå field sites suggest that low-diversity grass–clover mixtures (probably the most common types of agricultural sward in Europe) can be detrimental to groundwater quality. This is especially the case if the grass species are poorly established in their root structures or have a short annual period of vegetative growth.

Water use efficiency in southern European grasslands

Plant productivity in Mediterranean systems is often limited by water availability. Changes in community water use appear to explain some of the effects of diversity at the Portuguese BIODEPTH site. Cover and productivity were higher in more diverse plant communities. This partly arose due to better establishment of some species in diverse communities and poor performance in low-diversity plots. Early season differences in cover and biomass in diverse communities then facilitated reduced water loss to evaporation after rain events. Water content in the upper soil layer of diverse communities was higher than in monocultures after rainfall. Stable carbon isotope ratios ($^{13}C/^{12}C$) in leaves indicated that several plant species growing in diverse plots had less limitation to photosynthesis by stomatal diffusion than when grown alone (Figure 6).[9] Overall, photosynthesis in more diverse communities was less limited by water deficits due to a complex combination of diversity effects, thus increasing community productivity.

Genetic diversity and local adaptation

There are increasing trends towards standardization of seed sources and loss of local varieties. If species and varieties are adapted to local conditions, this standardization could lead to a loss of potentially important benefits of genetic diversity. We tested for local adaptation of three forage species: the grass *Dactylis glomerata*, the legume *Trifolium pratense* and the forb *Plantago lanceolata*, which occurred at the majority of our field sites. We collected local seed of these species and performed a European-wide reciprocal re-plant (planting seedlings of local origin) and transplant (seed from the other sites) experiment, utilizing the BIODEPTH network. Although there was some variation due to species identity, site of origin and site of planting, the important general result was that over all three species, plant performance (assessed through basic measures of plant growth, survival and reproduction) was generally best at the site of origin and declined significantly with distance from the site of origin. The results suggest that these three widespread forage species were all locally adapted and that this form of biodiversity should be preserved to maintain productivity.

Potential relevance to agriculture

Agriculturists and farmers have obviously long known the importance of the identity of species and varieties with a long history of selection for the most productive variety. This is reflected in the importance of species composition in our results. This may mean that in certain situations, the agricultural monoculture may be the most productive option. However, evidence for complementary and positive interactions in our species mixtures suggests that a monoculture may not always maximize productivity. Application of the log–linear effect of species loss on the yield of the BIODEPTH plots to grasslands in Switzerland predicts that losses in productivity could cost around 100 million Swiss francs for every halving of diversity.[10] Furthermore, in monocultures ecosystem functioning in traits other than productivity may be non-optimal compared with a multispecies mixture. This could come about through undesirable effects associated with high productivity; high levels of nitrate leaching from low-diversity grass–legume mixtures provide an example from our work. Additionally, in some situations mixtures may not increase yield compared with monocultures, but may have improved ability to withstand environmental fluctuation, for example. Differential frost damage to high- and low-diversity mixtures provides an example of this type of insurance effect from BIODEPTH.

Farmers in 'traditional' agriculture frequently practise intercropping, in which different crops are grown together to get a better yield from the land because of, for example, improved utilization of sunlight and nutrients. The BIODEPTH project demonstrates that similar effects may also occur in semi-natural plant communities, with potential applications in the management of land for forage crops, for example. Traditional Indian cropping systems have also been used as hypothetical examples of agriculture imitating the multispecies characters of natural ecosystems.[11] Modelling their productivity and dynamics suggests that these agricultural systems have potential advantages in production, stability of output, resilience to perturbation, and ecological stability. Multiple cropping is also often associated with better maintenance of soil fertility, greater protection from soil erosion, enhanced stability of output, improved dietary nutrition and beneficial effects for wildlife. Why then do we not see the use of intercropping more often? It is important to emphasize the costs as well as benefits of multicropping systems: they can sometimes be harder to manage than conventional mechanized agriculture. These costs do not necessarily arise in developing countries, where hand-harvesting is often common, as illustrated by the recent example of mixed rice varieties.[12]

Under the direction of a team of scientists, thousands of rice farmers from the Yunnan province of China increased their yields by 89% and reduced the severity of rice blast by 94% by complementary planting of two rice varieties.[13] Rice blast is the most severe fungal disease of the staple crop of about half the population of the world. In the largest agricultural study ever, the farmers planted two rice varieties together, instead of single-variety monocultures: a standard, mainly disease-resistant variety and a more valuable rice that is susceptible to rice blast. This experiment was so successful that by the end of the two-year programme farmers were no longer applying fungicidal sprays. Although these farmers and researchers looked at mixtures of varieties, not mixtures of species, these impressive results nevertheless provide an example of real benefits of diversity in agriculture.

Insurance values of biodiversity

New theory and evidence suggest that impoverished ecosystems are less resistant to changes in the environment.[14] The 'Insurance Hypothesis' proposes that when environmental conditions change, more diverse communities have a greater probability of containing species that are adapted to the environmental change and can more easily maintain ecosystem functioning compared with an impoverished community. For example, an intact community may better maintain productivity despite conditions of drought, frost or other extreme environmental change, compared with an impoverished version. If a community has a full complement of species, then previously subordinate species may be better adapted to the changed conditions and occupy a dominant role previously occupied by another species. We are currently in the process of experimentally testing this Insurance Hypothesis. Investigating the science behind ways that European agriculture might be able to cope with environmental change is extremely relevant for sustainable management of the environment and our agricultural economy, particularly given predictions of global climate change.

In summary, results from the BIODEPTH project suggest that the maintenance or restoration of plant species and genetic diversity in European grasslands may bring benefits to agriculture through effects on productivity, retention of soil nutrients and water use. More generally, our work illustrates how agricultural systems can be viewed in the wider framework of their biodiversity and the ecosystem services they provide, rather than just in terms of maximizing productivity in the short term.

Acknowledgments

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