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Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies

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Biodiversity and ecosystem functioning research has been some of the most controversial of the last decade but rapid progress has been made by deriving hypotheses from the differing view points and challenging them with appropriate experimental and analytical tests (Loreau *et al.* 2001). Here we address some recent criticisms of the BIODEPTH project (Thompson *et al.* 2005) and show that:

1. While legume species play an important role in the BIODEPTH results, patterns are not generally consistent with the multispecies sampling effect for legumes proposed by Huston & McBride (2002) as suggested in Thompson *et al.* (2005).

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2. The BIODEPTH results are also not consistent with transient biodiversity effects. Levels of species diversity were generally maintained over the 3 years of the project (i.e. little competitive exclusion) and diversity-productivity relationships in BIODEPTH generally strengthened during the experiments.

The role of legume/non-legume interactions

Thompson *et al.* (2005) suggest that the effects of diversity on biomass production seen in the BIODEPTH project can be explained adequately by the mechanisms described by Huston & McBride (2002). Huston & McBride's proposed explanation is a complex multispecies sampling effect in which more diverse plots have a higher chance of simultaneously containing legume species, productive non-legume species and of occurring on nitrogen-limited patches. We cannot address initial soil nitrogen heterogeneity much in our experiment except at the Sheffield site where nutrients were evenly applied in solution on a sand substrate. Here, the presence of a positive diversity-productivity relationship (Fig. 1g) in the absence of soil nitrogen heterogeneity does not seem to be consistent with Huston & McBride (2002). To further examine the role of legume and non-legume species we briefly report the relationship between diversity and total plant biomass at the end of the BIODEPTH project for communities with

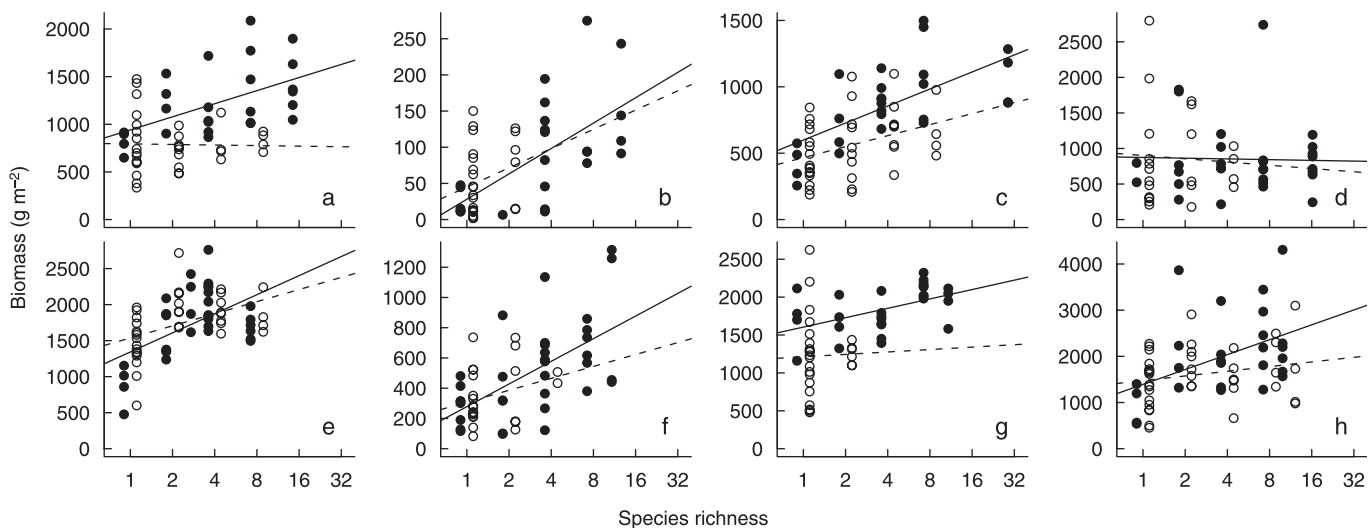


Fig. 1. The relationship between sown species richness and total biomass (sum of above- and below-ground biomass at the end of the third growing season) for communities with (closed symbols, solid lines) and without legumes (open symbols, broken lines) in (a) Germany, (b) Portugal, (c) Switzerland, (d) Greece, (e) Ireland, (f) Sweden, (g) Sheffield, UK and (h) Silwood Park, UK. Lines are linear regression slopes from the statistical model with significant site-by-legume interaction that is presented in Supplementary Table S1. Note differences in Y axis limits and that symbols have been staggered to avoid overlap.

and without nitrogen fixers (Supplementary Tables S1 and S2; data from Spehn *et al.* 2005). The BIODEPTH design is limited in how far it can distinguish between different aspects of diversity (including legume species) because these different aspects are collinear (Schmid *et al.* 2002). In a sequential statistical model the presence of legumes can be fitted before testing for additional effects of diversity although this runs the risk of attributing to legumes some of the effects of collinear aspects of diversity. Nonetheless, when we do this conservative analysis we usually do find additional significant effects of other aspects of diversity such as numbers of species and plant functional groups (Loreau & Hector 2001; Spehn *et al.* 2005). For total plant biomass (Fig. 1) there is a highly-significant interaction between the effects of species richness and legumes ($F_{1,159} = 10.7$, $P < 0.001$; Supplementary Table S1). Main effects are of limited interest and use in the presence of an interaction (but here it may be justified to cautiously examine them since they generally explain more variation than the interaction) but even when tested after legumes the residual main effect of species richness is of similar size to that of this group (Supplementary Tables S1a vs S1b). Individual site relationships vary (Supplementary Table S2) but only in Germany does the species richness effect depend on the presence of legumes (Fig. 1a; but see Scherer-Lorenzen *et al.* (2003) for consideration of effects on nitrate leaching as well as productivity). At other sites the species richness effects for communities with and without legumes are similar to each other (e.g. Ireland, Fig. 1e) and in Greece there is no effect of species richness on total biomass whether legumes are present or not (Fig. 1d). Therefore, with the possible exception of one site our results are not consistent with the

multispecies sampling effect proposed by Huston & McBride (2002). Further detailed information on the complex effects of legume species in BIODEPTH can be found in many previously published papers (see Hector *et al.* 1999; Loreau & Hector 2001; Jumpponen *et al.* 2002; Mulder *et al.* 2002; Spehn *et al.* 2002; Gastine, Scherer-Lorenzen & Leadley 2003; Scherer-Lorenzen *et al.* 2003; Palmberg *et al.* 2005; Spehn *et al.* 2005).

More generally, a biodiversity experiment that deliberately omitted legumes produced results that were similar to the overall pattern from BIODEPTH: a loglinear relationship between diversity and productivity that strengthened over time and which was largely driven by complementarity effects (Van Ruijven & Berendse 2005). To date only one other biodiversity experiment without legumes exists. Grime (2001, p. 309) and colleagues found that a 12-species mixture, and a particular subset of three species that it contained, showed strong complementary nitrogen uptake (long-term results for productivity and other ecosystem processes are currently unpublished).

Are the results of biodiversity experiments transient?

If the results of biodiversity experiments are a feature of the first year or two as Thompson *et al.* suggest then they should weaken in the longer-term. While we could only maintain weeded communities at all sites for 3 years (but for up to eight at some) patterns were generally weakest in the first year and strengthened or maintained thereafter (Pfisterer *et al.* 2004; Spehn *et al.* 2005), as were those from comparable studies (Tilman *et al.* 2001; Hooper & Dukes 2004; Van Ruijven &

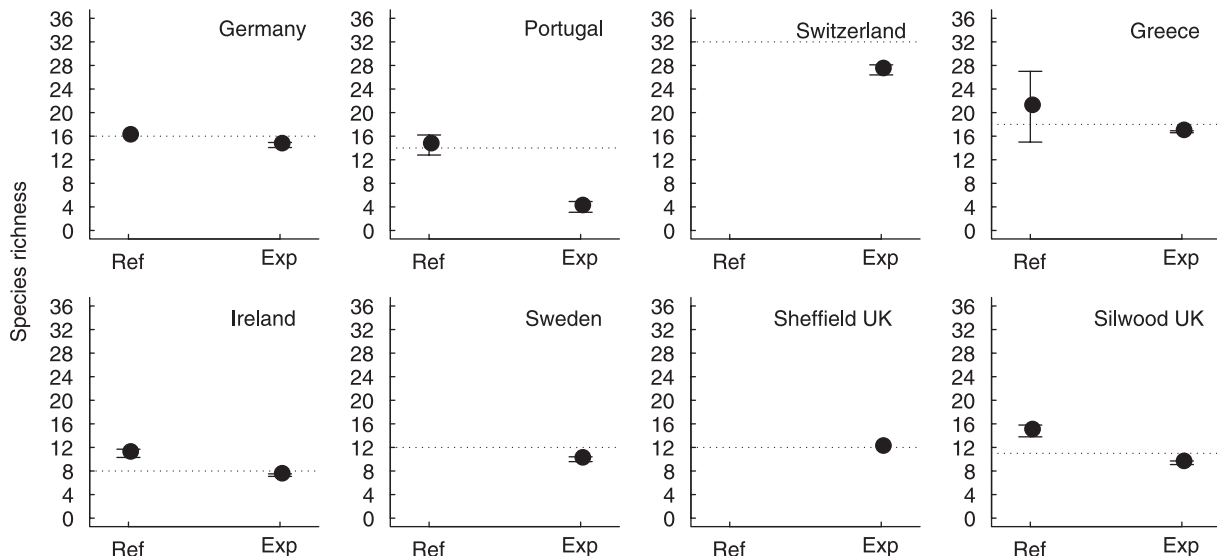


Fig. 2. Target, observed and reference diversity levels at individual BIODEPTH fieldsites. Horizontal lines show the target (sown) levels for the highest level of diversity, 'Exp' shows average observed diversities of the same experimental plots in the third year of the experiments (with SEMs) and 'Ref' shows average diversity levels in neighbouring unmanipulated reference plots in the same year. Note that all experimental communities were at or below levels observed in the reference communities.

Berendse 2005; Tilman, Reich & Knops 2006). The relationship between biodiversity and many ecosystem processes observed from these experiments therefore appears to strengthen over time, not weaken.

Thompson *et al.* also argue that high diversity and productivity only coincide in biodiversity experiments in the first year or two before competitive exclusion erodes the high-diversity mixtures. In BIODEPTH we generally aimed to set our highest level of diversity at each site to approximate levels of diversity seen in unmanipulated 'reference' plots in neighbouring grasslands, in anticipation that these realistic levels of species richness would be maintained (Spehn *et al.* 2005). For four of the five sites with reference plots levels did indeed match relatively well (Fig. 2) and we did not observe substantial reductions in species richness. The main exception comes from the Portuguese experiment where diversity did decline substantially in the final year but due to an unusually extreme winter (see Caldeira *et al.* 2005). Another minor exception is the Swiss site where, although there were no reference plots, the highest level of diversity was apparently set slightly above that which could be maintained (at 32 species to complete the \log_2 diversity gradient) and declined slightly during the main weeded period of the experiment (Pfisterer *et al.* 2004).

Reconciling observational and experimental approaches

We propose that the apparent conflict in the results of biodiversity experiments and observational biodiversity studies arises because they use different approaches (experimental *vs* correlational) to address different questions (within- *vs* across-habitat relationships) (Loreau

et al. 2001; Schmid 2002). It is because the direct influence of diversity on ecosystem processes can be obscured by variation in environmental conditions (Fridley 2002; Mulder *et al.* 2002; Dimitrakopoulos & Schmid 2004) that it is necessary to perform biodiversity experiments and why it is not surprising that observational surveys and biodiversity manipulation experiments sometimes show different relationships (e.g. Wardle *et al.* 1997 *vs.* Wardle & Zackrisson 2005; Levine 2000). However, there are ways in which observational and experimental studies could be made more comparable.

First, biodiversity experiments like BIODEPTH become more comparable to observational studies like the one at Bibury reported in Thompson *et al.* (2005) once the designed experiment is over and the weeding treatment that maintained the differences in diversity and composition is stopped, as has now happened at all of the BIODEPTH sites (Troumbis, Galanidis & Kokkoris 2002; Pfisterer *et al.* 2004; Dimitrakopoulos *et al.* 2005). Once weeding ceases (i.e. the simulation of species loss is stopped) the diversity-productivity relationship degrades as the diversity gradient decays through low-diversity plots gaining species and high-diversity plots losing species following exclusion by invaders. As biodiversity experiments generally attempt to remove underlying environmental heterogeneity (like soil depth at Bibury) no clear environmentally-driven pattern emerges in our experiments and species richness and productivity appear to be unrelated, at least in the first few years following the cessation of weeding (e.g. Pfisterer *et al.* 2004; Neßhöver 2005).

On the other hand, Bibury could be made more closely comparable with BIODEPTH by creating an

experimentally-controlled diversity gradient (by removing species from plots – cf. Symstad & Tilman 2001 – or by synthesizing communities of differing diversity from the Bibury species pool). Indeed the herbicide application experiments that existed at Bibury prior to 1990 could serve as a removal experiment as long as the herbicide reduced diversity of the treatment plots relative to controls.

More generally, comparison of experimental and observational studies may reveal something about the processes influencing diversity at different scales because biodiversity experiments show the effects of dispersal limitation in homogeneous environments while observational surveys show the effects of environmental heterogeneity in sites with presumably little variation in the propagule pool. If natural plant communities are mainly limited by dispersal of species from the pool into local areas, and competitive interactions amongst species are small and equal, we would expect surveys to show that plots with many species also have high biomass. At the largest scales plant diversity and productivity are often positively associated but the fact that regional surveys sometimes show negative or unimodal relationships suggests that interactions between environmental conditions and competition have played an important role in shaping these patterns. Such comparisons could inspire a new generation of biodiversity experiments in which the size of the effects of biodiversity are compared to those of other factors (fertility, soil depth, dispersal limitation, etc.).

Nevertheless, biodiversity experiments may indicate the future impacts of species loss through processes that may impose dispersal limitation (habitat fragmentation, over-harvesting, climate change, etc.). The results of biodiversity experiments like BIODEPTH have turned out to be highly repeatable and have established that changes in biodiversity (both richness and composition) do have the potential to impact many different ecosystem processes (Loreau *et al.* 2001; Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006; Worm *et al.* 2006). More generally, the first generation of biodiversity experiments has also led to new advances in relative-yield and covariance-based analytical methods (Loreau 1998; Loreau & Hector 2001), has added to the previously limited evidence for niche differentiation and complementarity effects in plant communities and has produced some unexpected results on the relationship between species traits and dominance (e.g. widespread negative selection effects (Hector *et al.* 2002)).

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Supplementary material

The following supplementary material is available for this article.

Table S1. Analysis of variance summary for the combined site analysis of species richness and legume presence/absence.

Table S2 (a) and (b). Analysis of variance summary for the individual site analyses of species richness and legume presence/absence.

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