How Plant Population Processes Mediate Biodiversity Effects on Ecosystem Functioning

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

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aus

Deutschland

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Zürich 2007
Contents

1. General Introduction 4
   1.1 Background 5
   1.2 Research framework 6
   1.3 Outline of the thesis 7

2. Overyielding in experimental grassland communities –irrespective of species pool or spatial scale 11

3. Density and evenness effects on biodiversity–ecosystem functioning relationships 42

4. Removing less-abundant plant species across a randomly assembled biodiversity gradient increases productivity 74

5. Niche pre-emption increases with species richness in experimental plant communities 97

6. General discussion 125

7. Summary 132

8. Zusammenfassung 135

9. Literature 139

10. Acknowledgments 146

11. Curriculum vitae 147
Chapter 1

General Introduction
**Background**

Several billions of years of evolutionary history have formed life on our planet. The outcome of this ongoing process is the development of diverse life forms in diverse ecosystems. The term biodiversity wants to encompass this variety of plants, animals and microorganisms occurring in different environments, landscapes and habitats. Thus, biodiversity is not only understood as the variety of species but also includes the genetic differences within species on the population level, as well as the diversity of ecosystems.

Since biodiversity covers many aspects of life on earth it is not surprising that it also provides a large number of goods (e.g. food, construction material, medicines) and services (e.g. cleansing air and water, pollination, nutrient cycling) sustaining our lives (Hooper et al. 2005). Thus, at the 1992 Earth Summit in Rio de Janeiro world leaders agreed on a “sustainable development” to ensure a viable world for future generations. One of those key agreements in Rio was the “Convention on Biological Diversity”. The Convention establishes three main goals: the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits from the use of genetic resources (Secretariat of the Convention on Biological Diversity 2000). Since then biodiversity has become a priority topic not only for policy makers but also for scientists in ecological research.

The exploitation of natural resources, changing patterns of land use, the introduction of exotic species and global climate change have caused a tremendous loss of biological diversity. The loss of habitats and ecosystem changes are accompanied by the extinction of species. Although the loss of species is a natural process, extinction rates today increased by 50–100 times the natural rate and are predicted to increase even further (Millennium Ecosystem Assessment 2005). A consequential question therefore is: how will this loss of biodiversity influence ecosystem functions and the services they provide to human life on earth?

During the last decade much of ecological research has focused on the effects of biodiversity loss on ecosystem functioning (i.e. ecosystem properties, ecosystem goods and services) (Schulze & Mooney 1993, Kinzig et al. 2002, Loreau et al. 2002, Hooper et al. 2005, Scherer-Lorenzen et al. 2005). This includes numerous observational and experimental studies. Observational studies,
however, have the disadvantage that environmental conditions, species interactions and the available species pool are not controlled and thus may affect species diversity and ecosystem properties (Lepš 2004). In contrast, biodiversity experiments provide deeper insights by manipulating certain aspects of diversity, while keeping environmental conditions constant among treatments (Pfisterer et al. 2004, Schmid & Hector 2004). They thus treat diversity as the independent variable and ecosystem processes or properties as the dependent variable. Despite the number of studies and the advances made in design and analysis, many aspects of how biodiversity loss affects ecosystem functioning are still not well understood (Schmid et al. 2002, Hooper et al. 2005).

**Research framework**

Biodiversity experiments working with synthetic plant communities drawn from a local or regional species pool started in the 1990s in England (Naeem et al. 1995, 1996), Switzerland (Leadley and Körner 1996) and USA (Tilman et al. 1996). Follow-up projects were the pan-European “BIODEPTH” project with 8 field sides spanning all over Europe (Hector et al. 1999, Spehn et al. 2005) and “The Jena Experiment” which started in 2002. “The Jena Experiment” (The role of biodiversity for element cycling and trophic interactions – an experimental approach in a grassland community) located in Jena, Germany is an ongoing long-term research project (Roscher et al. 2004) and provides the platform for all research presented in this thesis. This experiment, currently the largest in grassland worldwide, is comprised of 90 large plots of 20 x 20 m and almost 400 small plots of 3.5 x 3.5 m. Mainly a subset of the latter plots were used for the studies presented here. The site is located on a former agricultural field in the floodplain of the Saale River and contains experimental plant communities assembled by constrained random selection from a pool of 60 typical grassland species of Central Europe (Roscher et al. 2004). The gradient of plant species richness ranges from 1, 2, 4, 8, to 16 species, which belong to 1–4 functional groups (grasses, legumes, small herbs, tall herbs). At each level of species richness, 16 replicates with a different species composition were established, except at the highest richness level with only 14 replicates. Four additional replicates contain the full mixture of all 60 species. In addition, all possible combinations of functional group
mixtures were represented. More detailed information on the experimental design will be presented in the Method sections of the following chapters.

The field site provides the basis to study interactions not only among individual plants or plant species, but also between different trophic levels and to trace elements on their cycle. Thus “The Jena Experiment” serves as a platform for 13 research groups joined in a collaborative research group funded by the German Science Foundation (DFG, Forschergruppe FOR 456). Topics reach from hydrology and soil over plant population biology to invertebrates and mammals. Major goals of the project can be summarized as follows:

i) investigation of the relation between plant species diversity and diversity at other trophic levels
ii) inquiry about the relationship between carbon storage and diversity
iii) test the extent to which plant diversity contributes to closed element cycles and productivity
iv) identification of the components of diversity which control C-storage and element cycling
v) find factors which contribute to the stability of plant communities (see http://www.the-jena-experiment.de)

Outline of this thesis

A major argument for the conservation of biological diversity is its conceivable role for a sustainable life on earth. Thus a key to the protection of biodiversity should be the well-founded knowledge about its influence on ecosystem functioning and their properties (goods and services). Since many studies about the relationship between biodiversity and ecosystem functioning provide increasing evidence for the hypothesis that species loss affects ecosystem functioning negatively (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006), it seems now important to know how this process is ruled.

Previous biodiversity experiments generally measured ecosystem properties in an aggregated way, thus they could not be related directly to the performance of the individual species within the ecosystem. Major problems in the current understanding of ecosystem functioning may be resolved if the responses of plants to species loss are also tested at the population level, the species level and the
level of the individual plant. For example, variable population dynamics of species could lead to temporal niche complementarity and thus increase ecosystem productivity and enhance stability over time (Miles 1979, Tilman et al. 1997). To bridge this gap between community ecology and population biology as pointed out by Bazzaz (1996) and Lawton (2000) I tested how plant population processes mediate biodiversity effects on ecosystem functioning.

Studying the influence of biodiversity on ecosystem functioning from the individual plant level to the level of the community also raises the question about the relevance of space. The ability of extrapolating the relationship between plant species richness and biomass production across space was one additional aspect tested with other experimental factors in this study. In this supplementary part several experimental factors were changed, which are usually not manipulated in biodiversity experiments (e.g. evenness, type of species loss).

Chapter 2 starts with the basic question if the positive relationship between plant species richness and biomass productivity found in other experiments also applies to “The Jena Experiment”. Then the relevance of the spatial scale for this relationship is added-on by comparing different plot sizes. To examine the importance of the experimental species pool for the species richness–productivity relationship, plots with randomly selected species were compared with plots whose species composition was based on a pool of potentially dominant species. Both experimental pools were tested and compared for overyielding. Additive partitioning and analyses of relative yield totals (RYTs) were used to reveal different contributions of complementarity and selection effects to the net biodiversity effect.

Chapter 3. In the experiment reported here, not only the numbers of species but also population densities were manipulated. This was done by using different total amounts of seeds and changing the proportions of seeds in the mixture. Thus, subplots of low and high sowing density combined with even and uneven species abundance distribution were established along the experimental gradient of plant species richness with given species composition. The study showed to what extend species evenness, which is usually not manipulated in plant biodiversity experiments (but see Wilsey and Potvin 2000), did affect the species richness–productivity relationship. Thus, the manipulation of
density and evenness revealed population-dynamic processes behind the common ecosystem responses.

Chapter 4. This chapter provides another test of the importance of species identity for the species richness–productivity relationship. In a removal experiment less abundant species were removed from half of each plot leaving only dominant species in this half of the plot. Thus this study superimposed a non-random species loss (removal) on an existing biodiversity experiment with simulated random species loss, which had been running for 2 years.

Chapter 5 assesses the effects of both species richness and functional group composition on the performance of introduced “phytometer” species in the experimental communities. Using native species as transplant phytometer, this experiment was designed to control for the extrinsic factors that may confound the effect of plant diversity. In particular, it was tested if diverse communities are less susceptible to invasions of species, because of less empty niche space.

References


Chapter 2

Overyielding in experimental grassland communities – irrespective of species pool or spatial scale

with
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Ecology Letters, 8: 419–429, 2005
Abstract

In a large integrated biodiversity project ("The Jena Experiment" in Germany) we established two experiments, one with a pool of 60 plant species that ranged broadly from dominant to subordinate competitors on large 20 × 20 m and small 3.5 × 3.5 m plots (= main experiment), and one with a pool of nine potentially dominant species on small 3.5 × 3.5 m plots (= dominance experiment). We found identical positive species richness–aboveground productivity relationships in the main experiment at both scales. This result suggests that scaling up, at least over the short term, is appropriate in interpreting the implications of such experiments for larger-scale patterns. The species richness–productivity relationship was more pronounced in the experiment with dominant species (46.7 % and 82.6 % yield increase compared to mean monoculture, respectively). Additionally, transgressive overyielding occurred more frequently in the dominance experiment (67.7 % of cases) than in the main experiment (23.4 % of cases). Additive partitioning and relative yield total analyses showed that both complementarity and selection effects contributed to the positive net biodiversity effect.
INTRODUCTION

A central issue in current ecological research is the potential influence of biodiversity on ecosystem functioning (Chapin et al. 1998; Loreau et al. 2001). Environmental conditions, species interactions and the available species pool all influence species diversity and ecosystem properties (Lepš 2004). As such, observational studies cannot provide the same insights as biodiversity experiments, where either diversity or ecosystem properties are experimentally manipulated (Pfisterer et al. 2004; Schmid & Hector 2004). For example, clear causal relationships between species richness and ecosystem productivity can be examined only with experimental approaches, keeping environmental conditions constant among treatments (“within-site comparisons”). Such experiments can best be done in ecosystems that allow easy manipulation of species richness and rapid measurement of productivity, such as perennial grassland communities (Loreau et al. 2002). Experiments with this system have often, but not always found a positive, asymptotic relationship between plant species richness on the x-axis and aboveground plant biomass production on the y-axis (e.g., Tilman et al. 1997; Hector et al. 1999; further references in Schmid et al. 2002b). Initial disputes about the possible explanations for the positive relationship have been addressed with the newly developed additive partitioning analysis method that allows separating a net biodiversity effect into contributions of complementarity and selection effects (Loreau & Hector 2001; Hector et al. 2002a). Complementarity occurs if performance of species in mixture is on average higher than expected from their monoculture yields, while the selection effect explains higher productivity of mixtures by the dominance of individual, highly-productive species.

Despite the advances in experimental design and statistical analysis (Schmid et al. 2002a), major questions remain about the ability to extrapolate the relationship between plant species richness and biomass production across time, space, environments, species pools and other
factors. Analyses of data from the Cedar Creek experiment in Minnesota and theoretical considerations suggest that complementarity effects increase over time whereas positive selection effects decrease (Tilman et al. 2001; Pacala & Tilman 2002). The BIODEPTH multi-site experiment has shown that diversity effects on biomass production can vary to some extent across localities, but a general pattern was found if all sites were analysed together (Hector et al. 2002b). Several studies found that increasing CO₂ or nutrient levels can accentuate diversity effects (Stocker et al. 1999; Reich et al. 2001; He et al. 2002; Fridley 2002, 2003).

Experimental studies often simulate random species loss, but in natural communities, rare and uncommon species are subject to higher risk of extinction because of smaller population sizes (MacArthur & Wilson 1967; Pimm et al. 1988). Recent results of removal experiments reducing species number in a non-random fashion provided evidence that dominant species can sometimes control ecosystem functioning (Smith & Knapp 2003; Zavaleta & Hulvey 2004). It may be that the drop in productivity with random species loss, observed in experiments, would be less strong if subordinate species were not included in the species pool from the beginning (equivalent to subordinate species going extinct first). If selection effects in such a pool of only dominant species are the major cause for the relationship, then productivity would be expected to increase less with species richness in this case, because averaging only across highly productive species in monocultures or low-diversity mixtures will not yield the low values expected with averaging across monocultures or low-diversity mixtures of both dominant and subordinate species.

In addition to using different species pools, the spatial scale of previous biodiversity experiments varied considerably, with plot sizes from about one to more than 100 m², such that the experimental effects might have been confounded with scale effects (Schmid et al. 2002a). Scale effects may be caused by abiotic factors (e.g. different intensity of exchange
processes with the surrounding environment of large versus small stands), biotic factors (e.g. smaller population sizes and reduced fitness, higher or lower visitation rates of plants by herbivores or pollinators in small plots), or increasing environmental heterogeneity with increasing plot size and other, presently unknown factors. In the literature these effects are often related to an increasing amount of edge relative to central parts in smaller plots (see e.g. Groppe et al. 2001; Fahrig 2003 and references in these).

To examine these issues, we manipulated two factors. First, we manipulated plot size to examine scale effects. Second, we manipulated the relative abundance of dominant species in the species pool to determine the extent to which the exclusion of minor species changes the richness–productivity relationships. The experimental set-up of this integrated project (“The Jena Experiment”), carried out near the Saale river in Jena (Germany), comprises a total of more than 480 plots, arranged on a single large field with four blocks (Roscher et al. 2004). The main experiment uses a large species pool of 60 species, on either plots of 20 × 20 m or of 3.5 × 3.5 m. A second experiment (dominance experiment) uses a species pool of nine dominant species and plots of 3.5 × 3.5 m. These experiments serve as a platform for a number of studies evaluating biodiversity effects on ecosystem functioning.

In this paper, we present the first results of The Jena Experiment obtained by measuring peak biomass at the end of May in the second year of the project (2003), comparable to the main measurements analysed in the European BIODEPTH project (Hector et al. 1999, 2002a, 2002b). First, we ask if a positive relationship between plant species richness and productivity (henceforth species richness-productivity relationship) also applies in The Jena Experiment. Second, we test if the relationship differs between large and small plots of the main experiment. If the relationship is independent of plot size, this may indicate that scaling up from small-plot studies is possible, at least in the short term. Third, we compare the relationship from the main experiment with the large species pool with the dominance
experiment.

MATERIALS AND METHODS

Study system

Our study system is a typical Central European mesophilic grassland community as was traditionally used for haymaking (Ellenberg 1988) before the intensification of agriculture and the shift to fast rotation, low-diversity seed mixes and high fertilizer inputs. We selected 60 species on the basis of their frequent occurrence in the original grassland community on floodplains such as along the river Saale near Jena, Germany (Roscher et al. 2004). For the main experiment species were divided into four functional groups corresponding to graminoids, legumes, tall herbs, and small herbs, which were obtained by ordination of 17 species traits (see Roscher et al. 2004 for details). A subset of nine species known to become dominant in semi-natural grassland vegetation (Roscher 1999) and expected to be highly productive also in monocultures was selected as species pool for the second experiment: five graminoids (Alopecurus pratensis, Arrhenatherum elatius, Dactylis glomerata, Phleum pratense, Poa trivialis), two tall herbs (Anthriscus sylvestris, Geranium pratense), and two legumes (Trifolium pratense, T. repens). Two of these species, Anthriscus sylvestris and Geranium pratense, are known to establish more slowly (Roberts 1979; Nikolaeva et al. 1985), which should be considered in the interpretation of the corresponding experiment. The selection of species for the dominance experiment was independent of their allocation to the four functional groups, because the design of the dominance experiment focuses on effects of particular species.
Experimental design

Details of the experimental design are given in Roscher et al. (2004) and summarized in Table 1. For the experiment with the large species pool (= main experiment), replications of the same species richness level comprised all possible numbers of functional groups. Random selection (with replacement) of species for mixtures was subject to the additional constraint that all functional groups are evenly represented at each level of species richness. Species mixtures were grown on large 20 × 20 m plots and identically replicated on smaller 3.5 × 3.5 m plots to test for the effect of scale. In addition, mixtures composed of the complete pool of 60 species were established as controls, with four replicates at both large and small plot sizes. The experiment with the dominant-species pool (= dominance experiment) was established on small 3.5 × 3.5 m plots. In the dominance experiment species richness levels were more densely spaced from monocultures to nine-species mixture (Table 1) and every species and every species pair was represented with the same frequency at each particular level of species richness. Furthermore, in the dominance experiment each particular species mixture was replicated on a second plot of the same size. We grew all species in two single-species plots of 3.5 × 3.5 m to estimate monoculture yields. This was necessary for analyses involving expected relative yields in mixtures.

The field site on the floodplain of the river Saale in Jena (Thuringia, Germany, 51°N, 11°E, 135 m a.s.l.) has a mean annual air temperature of 9.3 °C, and average annual precipitation is 587 mm (Kluge & Müller-Westermeier 2000). The experimental area was partitioned into four blocks, following a gradient of soil characteristics due to fluvial dynamics of the river Saale. Each block contained an equal number of large plots on one side with diversity treatments assigned randomly; the small plots were similarly arranged along a strip on the other side.

The plots were sown from 11 to 16 May 2002. Seed material was mixed with groats of
soya as a bulking agent to ensure an even distribution of seed mixtures over the whole plot in spite of the high variability of seed sizes and shapes among species. We used total seedling densities of 1,000 seeds per m². In all mixtures, species were grown at maximum evenness. As additional experimental treatments, sowing density and evenness were manipulated in three of four quadrats in the small plots of the main experiment (Roscher et al. 2004), but data are not reported here. We thus only analyse the data obtained from the normal-density, maximum-evenness treatment of these small plots. All plots were weeded regularly, thus maintaining species richness at the planned levels or slightly below in cases where a species did not establish. The experimental communities were mown twice in 2002.

**Data collection**

The first harvest in 2003 was taken at estimated maximum biomass during 26 May–5 June, one year after sowing. The plants were cut 3 cm above ground on randomly selected sample areas of 20 × 50 cm, excluding the outer margin (50 cm) of the plot. Two samples were harvested in the dominance experiment and all small-area monocultures. To account for the expected higher within-plot heterogeneity of soil conditions in large-area plots, these were sampled with four replicates per plot, which were combined to yield mean biomass per plot. All samples were sorted to species. One sample was taken in small-area plots of the main experiment, and only community biomass was determined without sorting into species because of time constraints. All samples were dried (48 h, 70 °C) to constant mass and weighed.

**Data analyses**

The community biomass data were analysed with general linear models (Schmid et al. 2002a). First, “geographic” variation was eliminated as a block effect. Second, we fitted
species richness as three contrasts, the first to separate monocultures from mixtures, the second for the linear and the third for the quadratic trend with increasing species number. Then, we fitted dominant versus large species pool (main experiment versus dominance experiment), the interaction between species richness and experiment, small versus large plots (within the main experiment), the interaction of the latter with species richness, the particular species mixture, the interaction of experiment with mixture, and the interaction of small versus large plots with mixture (within the main experiment). In this overall analysis, we excluded the 16-species mixtures to make the range of species-richness levels comparable between the main and the dominance experiment. Furthermore, we sometimes omitted the monocultures and varied the particular treatment terms and their sequence to test alternative models. We restricted our comparative analysis of both experiments to species richness effects, but individual analysis testing for either functional group effects (main experiment) or species identity effects (dominance experiment) is ongoing.

We used different measures to compare the yields of mixtures relative to their component monocultures. The additive partitioning method (Loreau & Hector 2001) was used to calculate complementarity (CE) and selection effects (SE), along with net biodiversity effects (NE), for both experiments. Because average yield of monocultures enters the calculation of the complementarity effect, this measure of complementarity is sensitively dependent on absolute yields and over-weights the contributions of higher-yielding species (Loreau & Hector 2001; Fridley 2003). To assess complementarity also in relative terms, we calculated relative yield totals (RYT, Hector 1998). The relative yield (RY) of a species considers its biomass in mixture as a proportion of its yield in monoculture, and the relative yield total (RYT) of the mixture is the sum of relative yields of all component species (Harper 1977). RYT is directly linked to “non-transgressive” overyielding, where a mixture outperforms the average biomass of its component monocultures (Fridley 2001; or D_{mean} = RYT–1 > 0, Loreau
1998). We additionally tested for “transgressive” overyielding, where a mixture obtains higher productivity per unit area than its most productive component monoculture ($D_{\text{max}} > 0$, Loreau 1998). These derived measures were then themselves analysed with general linear models, although these derived variables have more complicated theoretical distribution functions than the normal distribution assumed in general linear models.

**RESULTS**

**Biomass production of individual species in monocultures and mixtures**

Based on aboveground biomass production in monocultures, *Onobrychis viciifolia*, *Bromus erectus*, *Leucanthemum vulgare*, *Centaurea jacea* and *Arrhenatherum elatius* were the five most productive species in the second year of the experiment (Fig. 1a). However, in mixtures containing the complete pool of 60 species, *Arrhenatherum elatius* reached the highest productivity and had twice the yield of the second-most productive species *Dactylis glomerata* (Fig. 1b). Species chosen for the dominance experiment had a wide range of productivities in monoculture, but a consistently high relative productivity in the 60-species mixture. Five species (*Arrhenatherum elatius*, *Dactylis glomerata*, *Phleum pratense*, *Poa trivialis*, *Trifolium pratense*) out of the nine species chosen for the dominance experiment ranked among the ten most productive species in the 60-species mixtures (Fig. 1b), confirming the appropriateness of their a priori selection.

Aboveground biomass production of mixtures ranged from 18 to 1096 g m$^{-2}$. The relationship between biomass production in monoculture and relative yield of a species in mixtures differed between the two experiments. In the dominance experiment, all species were located above or close to the line predicting their biomass in mixture from their yield in monoculture (Fig. 2). This pattern was consistent across all diversity levels. *Arrhenatherum*
elatius showed the greatest relative increase of all species in mixtures. Species of the main experiment with the large species pool were expected to include both, species performing better and species performing worse in mixtures compared with monocultures. However, the majority of species had a higher observed than expected relative yield in mixtures. Even some of the less productive monoculture species reached higher relative yields in mixtures (e.g. Plantago lanceolata, Trifolium pratense). Among the highly productive monoculture species a notable exception to this finding was Bromus erectus in 4- and 8-species mixtures.

**Species richness–productivity relationships**

Statistical analysis of aboveground biomass indicated a positive relationship between species richness and biomass production in both experiments (Table 2, Fig. 3a). Altogether, species richness explained 19 % of the total variation of biomass among plots. The contrast between monocultures and mixtures explained 13 % of the total variation (F\(1,155 = 36.61, p < 0.001\)). Within mixtures, the linear (F\(1,155 = 6.80, p = 0.010\)) and quadratic (F\(1,155 = 8.73, p = 0.004\)) contrasts of species richness together explained an additional 6 % (= 19 % − 13 %) of the total variation, leaving a negligible amount to any deviations from the second-degree polynomial. Overall, and as expected, biomass production was higher in the dominance experiment (F\(1,155 = 26.61; p < 0.001; \) Table 2), species pool explaining 10 % of the total variation. However, contrary to expectation, the difference between species pools was larger for mixtures than for monocultures (F\(1,155 = 4.26, p = 0.041\)), and this interaction of monoculture vs. mixture contrast and experiment explained a further 1.5 % of the variation. In total, average yield increase in comparison to monocultures amounted to 82.6 % in the dominance experiment, and to 46.7 % in the main experiment. The difference in biomass production between 20 × 20 m and 3.5 × 3.5 m plots in the main experiment was extremely small (F\(1,155 = 0.01, p = 0.937\)). The effect of particular monoculture species and of particular
species compositions of mixtures was large (Table 2), as observed in previous studies, accounting for 55% of the total variation. This latter result is not surprising when the large number of degrees of freedom is taken into account.

**Tests for overyielding and niche complementarity**

Using the additive partitioning method of Loreau & Hector (2001), we analysed the relative contributions of selection and complementarity effects to the positive net biodiversity effect (Fig. 3b-d). The net biodiversity effect increased significantly with species richness (Table 3), and was stronger in the dominance experiment than in the main experiment. The complementarity effect was positive across the whole range of species richness levels (test for overall mean $\neq 0$: $F_{1,132} = 182.64, p < 0.001$) but curvilinear (linear contrast $F_{1,132} = 2.78, p = 0.098$; quadratic contrast $F_{1,132} = 7.01, p = 0.009$), reaching a maximum at the richness level of four species in the main experiment and six species in the dominance experiment (Fig. 3c). The selection effect was also positive across the whole range of species richness levels (test for overall mean $\neq 0$: $F_{1,132} = 172.06, p < 0.001$) and increased linearly ($F_{1,132} = 10.54, p = 0.001$; Fig. 3d). Selection and complementarity effects were significantly larger in the dominance experiment. Furthermore, a large amount of variation in selection and complementarity effects was due to differences between particular monoculture species and particular species compositions of mixtures.

The comparison of mixtures with the most productive component monoculture indicated transgressive overyielding for 67.6% of the plots in the dominance experiment, and a smaller ($F_{1,132} = 15.53, p < 0.001$) proportion of 23.4% of the plots in the main experiment. The mean values of RYT were greater than one in both experiments, supporting our findings of significant complementarity effects (Fig. 3e). In both experiments, transgressive overyielding linearly declined with species richness (Fig. 3f, Table 4). In the dominance experiment,
85.6% (161 out of 188 plots) and in the main experiment with the large species pool 72.9% (35 out of 48 plots) of all plots showed RYT > 1, indicating non-transgressive overyielding. Again, values were significantly higher in the dominance experiment (F<sub>1,132</sub> = 5.51, p = 0.020).

**DISCUSSION**

Our analysis confirms a positive relationship between plant species richness and biomass productivity in experiments at different spatial scales and with different species pools. Both, complementarity and selection effects, had significantly positive contributions to the observed net biodiversity effect.

**Importance of scale**

The analysis of the main experiment with a large species pool and randomly assembled species mixtures on large- (20.0 × 20.0 m) and small-area (3.5 × 3.5 m) plots resulted in no significant difference of biomass production. This indicates that results from small-scale experiments can be scaled up and are not biased by effects caused by the small plot size, at least in the short term. In the long run in which multiple-generation population dynamics of the different plant species start to play a role (sexual reproduction, seed dispersal, seedling recruitment), additional effects could result from smaller population sizes, reduced fitness of some plant species and changed visitation rates of associated animal and fungal species in small plots (see Ouborg et al. 1991; Fischer & Matthies 1998; Groppe et al. 2001 for examples and further references). By following the population dynamics within the different plots we will in future be able to analyse these longer-term effects.

Most previous experiments that found a positive relationship between plant diversity and productivity were done in very different plot sizes, ranging across four orders of magnitude,
from 0.03 m² (Naeem et al. 1996), 1 m² (van Ruijven & Berendse 2003), 4 m² (Hector et al. 1999) to 169 m² (Tilman et al. 1997). The extension to 400 m² in our main experiment still does not indicate a barrier to extrapolation of this major result. This shows that the caveat of inappropriate scale of biodiversity experiments for field-scale predictions may be unwarranted and reinforces the view that other results from small-scale experiments should be taken seriously in developing larger-scale ecosystem management applications. Additional effects may start to play a more important role only if enlarging scale inevitably leads to the crossing of habitat boundaries (see Bengtsson et al. 2002).

**Importance of species pool**

While the species richness–productivity relationships had similar shapes in the two experiments, one with a large pool of 60 species and the other with a small pool of nine potentially dominant species, the dominance experiment did exhibit a stronger productivity response. This demonstrates that species richness–productivity relationships can depend on the selected species pool, in particular the inclusion or exclusion of sub-dominant species. Some authors have proposed that the positive biodiversity–productivity relationship often found in experiments such as the one described here, can be explained by the selection effect, in the sense that the likelihood of including dominant and therefore productive species rises with increasing number of species sown in a plot (see Tilman & Lehmann 2002 for an overview). If such a mechanism had been the predominant cause for the relationships found in the current study, we would have expected the opposite from the observed results, i.e. a less pronounced increase, starting at higher values in the dominance experiment. This is because averaging across highly productive species in monocultures or low-diversity mixtures will produce much higher values than averaging across monocultures of both dominant and sub-dominant species. An explanation for the stronger biodiversity effect could be a greater
degree of niche complementarity among dominant species (Fargione et al. 2003) than among sub-dominant ones. Sub-dominant species may be able to coexist due to competition / colonization trade-offs (Levine & Rees 2002) or due to stochastic processes (Hubbell 2001); these are mechanisms that are less likely than niche complementarity to result in increased productivity of high-diversity mixtures.

Complementary resource use and facilitation (combined under the term complementarity effects in the additive partitioning method of Loreau & Hector 2001) are often considered as primary mechanisms behind overyielding accompanied by varying contributions of selection effects ranging from predominantly negative (e.g. van Ruijven & Berendse 2003; Hooper & Dukes 2004) to positive (e.g. Dimitrakopoulos & Schmid 2004) or being of minor importance (Loreau & Hector 2001). In this study, we found a positive net biodiversity effect comprising positive selection and complementarity effects in both experiments. In the dominance experiment, however, these measures were on average higher than in the main experiment with the large species pool, and the majority of mixtures overyielded both transgressively and non-transgressively in the dominance experiment. One reason for this can be seen by simple visual comparison of monoculture versus mixture biomasses (Fig. 2). Even considering the delayed establishment of two species (Anthriscus sylvestris, Geranium pratense) it remains obvious that the dominant species, especially Arrhenatherum elatius and Dactylis glomerata, often increased in relative yields in mixture compared to monoculture, indicating stronger intraspecific than interspecific competition.

Our findings that complementarity effects reach a maximum at lower diversity levels, whereas selection effects increase linearly with species richness, support a hypothesis that needs to be tested in further analyses. The prevailing importance of reduced intraspecific competition, which increases the likelihood of complementarity, seems to reach a limit beyond which further species additions do not increase the total niche space taken up by the
community (Dimitrakopoulos & Schmid 2004), but rather lead to suppression of some species by others as measured by the selection effect. Furthermore, adding more and more species reduces the proportional densities of all species, including the potentially high-yielding ones, perhaps to a level where some of them require considerable time to establish dominance.

To summarize, with our experimental approach we found a positive within-site relationship between plant species richness and aboveground biomass production. This relationship was very robust, independent of spatial scales or species pools. In addition, in our experimental temperate grasslands, the complementarity effect seems to operate most strongly between dominant species and at low species richness, where it is the prominent driver for the observed increase in ecosystem functioning with increasing plant diversity.

ACKNOWLEDGEMENTS

We thank S. Naeem, D.U. Hooper and two anonymous reviewers for critical comments that helped to improve the manuscript. The Jena Experiment is funded by the Deutsche Forschungsgemeinschaft (DFG, FOR 456), with additional support from the Friedrich Schiller University of Jena and the Max Planck Society. We are grateful to the many people who helped with the management of the experiment, in particular the gardeners S. Eismann, S. Junghans, B. Lenk, H. Scheffler and U. Wehmeier, and many student helpers, especially M. Bärwolf, J. Janeček, E. Machalett, N. Mitschunas, C. Möller, A. Rinck, F. Walther and K. Würfel, assisting in the biomass harvests. Thanks also to all the helpers during the weeding campaigns.

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Overyielding in experimental grassland communities


FIGURES

Fig. 1: Rank-dominance relationship of all 60 plant species used in both experiments. Values are aboveground biomass means (± s.e.). For the monocultures (a), means were calculated from two identical replicates in small-area plots, whereas means of the 60-species mixture (b) were derived from four identical replicates in the large-area plots.

Grey bars indicate species used in the dominance experiment. Species abbreviations are: Alo pra = Alopecurus pratensis; Ant syl = Anthriscus sylvestris; Arr ela = Arrhenatherum elatius; Dac glo = Dactylis glomerata; Ger pra = Geranium pratense; Phl pra = Phleum pratense; Poa tri = Poa trivialis; Tri pra = Trifolium pratense; Tri rep = Trifolium repens.

Fig. 2: Species-specific biomass in monocultures and mixtures.

Values are means (± s.d.), calculated from two replicates of small-area monoculture plots, and from different mixtures per diversity level for the mixture plots. The line represents the mixture biomass of species predicted from their yield in monoculture (monoculture biomass divided by species richness level).

Fig. 3: Aboveground productivity (a), net biodiversity effect (b), complementarity effect (c), selection effect (d), relative yield total (e), and transgressive overyielding $D_{\text{max}}$ (f), as functions of sown species richness. Note that overyielding analyses (b – f) were restricted to the dominance experiment and the large plots of the main experiment.

Symbols are aboveground biomasses for individual plots: ○ main experiment on large-area plots (a–f); ● identical replicates of the main experiment on small-area plots (a); ▲ dominance experiment (a–f). Lines show predicted values from the regression model: solid line = main experiment on large-area plots; dashed line = main experiment on small-area plots.
plots; dash-dot line = dominance experiment.
Figure 1

(a) Aboveground biomass > 3 cm (g m$^{-2}$) for Monocultures and 60-species mixtures. Species rank includes Alo pra, Ar. elia, Phi pra, Dec glo, Alo pra, Tri rep, Phl pra, Poa tri, Tri pra, Ger pra, Ant syl.

(b) Aboveground biomass > 3 cm (g m$^{-2}$) for 60-species mixtures. Species rank includes Alo pra, Poa tri, Tri pra, Tri rep, Ger pra, Ant syl.
Figure 2

Jena, May 2003
Main experiment

Dominance experiment

Aboveground biomass in mixture

Aboveground biomass in monoculture

2-species mixtures

4-species mixtures

8-species mixtures

2-species mixtures

4-species mixtures

9-species mixtures

Aboveground biomass in mixture

Aboveground biomass in monoculture

> 3cm (g m⁻²)

0 200 400 600 800 1000 1200 1400

0 200 400 600 800 1000 1200 1400

Aboveground biomass in mixture

Aboveground biomass in monoculture

> 3cm (g m⁻²)

0 200 400 600 800 1000 1200 1400
Figure 3

(a) Biomass yield (g m$^{-2}$, corrected for block) vs. species richness.
(b) Net effect (g m$^{-2}$, corrected for block) vs. species richness.
(c) Complementarity effect (g m$^{-2}$, corrected for block) vs. species richness.
(d) Selection effect (g m$^{-2}$, corrected for block) vs. species richness.
(e) Relative yield total (corrected for block) vs. species richness.
(f) Dmax (corrected for block) vs. species richness.
Table 1: Summary of the experimental design. The main experiment is replicated with identical species mixtures on large and small plots. The number of plots per species richness level represents replications with different species compositions, except at the 60-species level in the main experiment and the 9-species level in the dominance experiment where plots have identical species compositions. Plots with mixtures of 16 and 60 species are not included in the analysis to make species richness ranges of the main and dominance experiment comparable.

<table>
<thead>
<tr>
<th>Experiment</th>
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<th>Species richness levels</th>
<th>Number of plots per species richness level</th>
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Table 2: Summary of statistical analysis comparing aboveground biomass production in mixtures assembled from a large species pool on large- and small-area plots or from a pool of potentially dominant species on small-area plots. Model terms were added sequentially and tested against the species composition term.

<table>
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<tr>
<th>Source</th>
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<th>p</th>
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<td>12.27</td>
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Overyielding in experimental grassland communities 39
Table 3: Summary of statistical analysis comparing net biodiversity effect (NE), selection effect (SE) and complementarity effect (CE) calculated for aboveground biomass production in mixtures assembled from a large species pool on large-area plots or from a pool of potentially dominant species on small-area plots. Model terms were added sequentially and tested against the species composition term.

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Table 4: Summary of statistical analysis comparing relative yield total (RYT) or non-transgressive overyielding (D_{\text{mean}} = \text{RYT}-1), and transgressive overyielding (D_{\text{max}}) calculated for aboveground biomass production in mixtures assembled from a large species pool on large-area plots or from a pool of potentially dominant species on small-area plots. Model terms were added sequentially and tested against the species composition term.

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<th>Source</th>
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Chapter 3

Density and evenness effects on biodiversity–ecosystem functioning relationships

with

Peter N. Mwangi, Michael Scherer-Lorenzen, Wolfgang W. Weisser and Bernhard Schmid
Abstract

1 Grassland biodiversity experiments commonly manipulate species richness but not density and evenness. It is conceivable that different values of community biomass production could be obtained if density and evenness would be varied as well and thus the generality of reported richness–productivity relationships could be compromised. We tested this in an experiment.

2 We simulated random species loss from a pool of 60 common grassland species down to 16, 8, 4, 2 or 1 species. The richness gradient was factorially crossed with a density (total planting density 1000 or 2000 seeds/m²) and an evenness treatment (all species with equal initial abundances or one functional group initially dominant).

3 Aboveground plant biomass increased linearly with the logarithm of species richness in all density and evenness treatments during all three years of the experiment. This was due to a convergence of realized density and evenness within species richness levels.

4 Between species richness levels, realized density increased and realized evenness decreased with species richness. This suggests that more individuals could coexist if they belonged to different species but that at the same time abundance distributions became more skewed due to increased interspecific competition at high richness.

5 Within the initial species richness x density x evenness treatment combinations, high biomass values were correlated with low density, suggesting an underlying thinning process. However, communities with low realized evenness within treatment combinations also had low biomass values; that is, biomass increases were not due to an increase of species dominance during thinning.

6 We conclude that species richness is the more important driver of the investigated aboveground processes in plant communities than variation in total density and species abundance distributions. In our experiments, realized density and evenness were determined
by species richness; initial differences in these variables did not lead to different “stable states” in biomass production within given species richness levels or species compositions.

Our results also suggest that simply varying species richness can be a sufficient manipulation to study general patterns of biodiversity–ecosystem functioning relationships in experiments.
**Introduction**

Major drivers of global environmental change such as changing patterns of land use, global climate change, nitrogen depositions and biotic exchange influence the distribution and abundance of species (Sala et al. 2000). Thus, environmental change, in addition to affecting ecosystems directly, may affect them indirectly via changes in species diversity and composition (Chapin et al. 2000). To address the question of whether changes in biodiversity influence ecosystem functioning, scientists have been manipulating species and functional group richness mainly in experimental studies with plant communities (e.g. Naeem et al. 1994, Tilman et al. 1996, Tilman, Knops, Wedin, Reich, Ritchie & Siemann 1997, Hooper & Vitousek 1997, Symstad et al. 1998, Hector et al. 1999, Stocker et al. 1999, Van der Putten et al. 2000). These and subsequent experiments often showed a positive relationship between species richness and ecosystem productivity (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). One interpretation of these results suggests that there is a complementary resource use between species (Naeem et al. 1994, Tilman, Lehman & Thomson 1997, Loreau 2000). An alternative interpretation suggests that the positive effects of species number on ecosystem properties result from a so-called sampling effect (Aarssen 1997, Huston 1997, Tilman, Lehman & Thomson 1997): mixtures of many species have a higher probability of becoming dominated by a single or a few species that demonstrate higher performance.

In plant communities, evenness is the similarity of the proportions of component species and it is inversely related to dominance (Whittaker 1975). This community attribute is often held constant in plant diversity–productivity studies. However, Wilsey & Potvin (2000) experimentally varied the evenness of mixtures of three plant species commonly occurring in old-field communities. They found that productivity in those mixtures decreased as the relative initial densities of species became uneven by experimentally making any one of the
three species numerically dominant. Mulder et al. (2004) analyzed data of a multi-site grassland biodiversity experiment (BIODEPTH) for the relationship between evenness of species composition and biomass production. They found that plots with the same species composition, but lower evenness produced more biomass and that higher species richness decreased evenness, but increased biomass production.

Like evenness, total density may also influence the diversity–productivity relationship in experimental plant communities. For example, He et al. (2005) showed that, over the time-course of their experiment, at low sowing density, constant final yield was only reached in plant communities with high species richness, while at high-sowing density, communities reached constant final yield at any level of species richness. From basic research in plant population biology it is known that size-distributions of individuals in monocultures are more skewed at higher density (Harper 1977). By extrapolation it might be predicted that in mixtures, species abundance distributions become more rapidly uneven in high than in low community density. However, this prediction has not been tested so far. Species deliberately made dominant or gaining dominance due to high community density may subsequently determine aggregated ecosystem measures as suggested by the sampling effect.

To study density and evenness effects in connection with species richness, we manipulated these three variables in a factorial biodiversity experiment. This experiment was part of a large integrated biodiversity project (The Jena Experiment, Roscher et al. 2004). To compare the initial differences in community density and evenness with realized density and evenness values, we recorded plant densities for each species in each treatment combination over time. We expected the initial evenness and density in mixed populations to affect the diversity–productivity relationship of the plant community. However, we also expected that the effects of initial evenness and density might disappear over time if realized density and
evenness converged. This would suggest that in the long term only the species presences or absences are relevant for ecosystem functioning.

**Materials and Methods**

**Experimental design**

The experiment was part of The Jena Experiment, a large-scale facility to study the relationship between plant diversity and ecosystem processes (Roscher et al. 2004). The site is located on a former agricultural field in the floodplain of the Saale river near the city of Jena, Germany (50°55’ N, 11°35’ E, 130 m above sea level; mean annual temperature 9.3 °C, mean annual precipitation 587 mm). We created a gradient of plant species richness with mixtures of 1, 2, 4, 8, and 16 species, stratified into 1–4 functional groups (grasses, legumes, small herbs, tall herbs) which were obtained by ordination of species traits (Roscher et al. 2004). We assembled experimental plant communities from seeds in May 2002 by random selection from a pool of 60 typical grassland species of Central Europe. Random selection was constrained by the requirement for even representation of all functional groups at each level of species richness. In addition, we avoided confounding of species richness and functional group richness as far as possible. For example, communities with one functional group varied in species richness from 1–16, communities with two functional groups from 2–16 and communities with three or four functional groups from 4–16 (see Roscher et al. 2004 for details). For the additional manipulation of density and evenness, we divided plots of 3.5 x 3.5 m into four subplots of 1.75 x 1.75 m. Subplots within a plot had the same species composition, but differed in sowing density and evenness. In total, the experiment consisted of 280 subplots because we could not impose evenness treatments in monocultures. The density and evenness treatments were (see also Table 1):
i) **Low sowing density** and **even abundance distribution** (control). In these subplots the total density of 1000 viable seeds per m² was divided equally among the component species (same as in a parallel set of 20 x 20 m plots of The Jena Experiment, see Roscher et al. 2004). The number of viable seeds was adjusted according to germination pre-tests.

ii) **Low sowing density**, **uneven abundance distribution** (for monocultures ii = i). These subplots had the same total density as (i), and we obtained uneven species abundance distributions by increasing the density of only one species or functional group and decreasing the density of all others. The uneven distributions were 3:1 (2-species mixtures), 5:1:1:1 (4-species mixtures), 5:5:1:1:1:1:1 (8-species mixtures), 5:5:5:1:1:1:1:1:1:1:1:1:1:1:1:1:1:1 (16-species mixtures). In the 8- and 16-species mixtures the two and four dominant species, respectively, belonged to the same functional group. The reason for making more than one species numerically dominant in the high diversity mixtures (the 8 and 16 species mixtures) was to maintain a fixed ratio between the numbers of dominant and subordinate species. The functional group and the species within functional groups which were made numerically dominant were selected randomly, with the restriction that every functional group was made dominant in the same number of replicates at each species richness level (Table 1; a few exceptions to this rule occurred at the 2- and 16-species richness level).

iii) **High sowing density**, **even abundance distribution**. In these subplots, the component density of each species was doubled, yielding a total density of 2000 viable seeds per m².

iv) **High sowing density**, **uneven abundance distribution** (for monocultures iv = iii). These subplots had the same total density as (iii) and the same uneven species abundance distribution as (ii). The dominants were also the same as in (ii).

The initial proportion of a species was the number of seeds of that species divided by the total number of viable seeds in the subplot. Later, during the course of the experiment, we calculated the proportion of a species from the relative densities of surviving individuals. We
removed weeds twice a year in April and July. After establishment in fall 2002, we mowed the experimental plots twice a year in June and September simulating the traditional management as hay meadows (see Roscher et al. 2004). The high sowing density treatments were monitored from 2002–2003, while the other treatments were observed until late summer 2004.

We assessed population dynamics of all species by recording population densities (number of individuals per species) and sampling individual species biomass along transects of 10 x 100 cm (0.1 m²). These assessments were done twice in late spring of 2003 and 2004. Plants were cut at ground level, dried at 70 °C for about 48 h to constant mass and weighed. In accordance with the harvest protocols of other subprojects of The Jena Experiment, we also harvested community biomass in 20 x 50-cm (0.1 m²) quadrats at 3 cm above ground (see Roscher et al. 2005) in late summer 2002 and 2003 (all subplots), in late spring 2003 and 2004 (subplots with low sowing density and even abundance distribution) and in late summer 2004 (subplots with low sowing density).

**Calculation of evenness**

We used either initial seed proportions (initial evenness as experimental factor) or the number of individuals of each species (realized evenness) as the basis for calculations of evenness. We assigned all monocultures to the initial low evenness treatment category in a statistical model. If realized evenness was included in a model, monocultures were given missing values, because by definition they cannot vary in evenness. To separate effects of evenness from effects of species richness we used the index \( E_{1/D} \), which is mathematically independent of species richness (Williams 1964, Smith & Wilson 1996). The index is based on Simpson’s dominance index \( D \) (Simpson 1949), and is calculated as follows:
Here $p_i$ is the proportion of individuals from species $i$ and $S$ is the number of sown species in the sample. The index is zero when all species except one in a mixture have no individuals. It is one when individuals are equally distributed among all species of the sample. The disadvantage of the index is that it is also one for monocultures, which in fact we considered as most uneven (one species fully dominant).

**Statistical analysis**

We analyzed the data using general linear models, with the design variables used as treatment factors (Schmid, Hector, Huston, Inchausti, Nijs, Leadley & Tilman 2002). We eliminated environmental heterogeneity of the field site by block and plot effects using a split-plot design with the error strata plot and subplot (cf. Roscher et al. 2004). Species richness was tested in the plot stratum (plots as error term), whereas density and evenness were tested in the subplot stratum (subplots as error term). Corresponding interactions were also tested in these error strata. Log-linear contrasts were fitted for species richness and its interactions. Changes in biomass (2002–2004) and evenness (2003–2004) between years were tested using a repeated-measures analysis of variance (ANOVA) for the data obtained in the low sowing density subplots (Meyer & Schmid 1999). The high sowing density treatment was discontinued after the second harvest in spring 2003 and used for a different experimental study. Data were log-transformed where necessary to achieve normality and homoscedasticity of residuals. All calculations were done using GenStat statistical software (Payne et al. 1993).
Results

Species richness effects

Aboveground biomass production, recorded for all subplots until late spring 2003 and for low sowing density subplots until 2004, increased linearly with the logarithm of plant species richness in all analyses (all subplots 2002/2003: F_{1,70} = 22.80, p < 0.001; low sowing density subplots 2002–2004: Table 2; Fig. 1a–g). A repeated-measures ANOVA of the biomass data from the low sowing density treatment showed that the positive effect of species richness did not significantly change over the years (non-significant interaction between log species richness and year in Table 2; Fig. 1a, c, e, g, h) or between harvest methods (harvest at 3 vs. 0 cm above ground; interaction between log species richness and harvest with F_{1,66} = 1.98 and p = 0.164, in Table 2 pooled with residual). However, the species richness effect on aboveground biomass production was stronger at the time of peak biomass in late spring than in late summer (significant interaction between log species richness and season in Table 2).

Species richness positively affected realized community density (counts of individuals that survived into the second year, 2003, in high and low sowing density subplots: F_{1,73} = 28.35, p < 0.001; counts of individuals that survived into the third year, 2004, in low sowing density subplots only: F_{1,72} = 4.15, p = 0.045; Fig. 2a–c). At the same time, species richness negatively affected realized evenness, E_{1/D}, calculated with the number of surviving individuals in low sowing density subplots (2003/2004 without monocultures: F_{1,57} = 130.87, p < 0.001, Fig. 3a–c).

Density effects

The sowing density treatment affected aboveground biomass production of the entire plant communities only in the first year (2002) where all treatment categories were analyzed (F_{1,176}}
In the first year (2002) subplots with high sowing density produced an average of 10% more biomass than subplots with low sowing density. By the second year (2003) sowing density no longer influenced biomass production ($F_{1,198} = 0.24$, $p = 0.625$). Realized community density was, however, still different between the two sowing density treatments. An average of 294 (SE $\pm 13.69$) individuals occurred per m$^2$ in subplots with low sowing density (initially 1000 seeds m$^{-2}$) and 383 (SE $\pm 14.78$) individuals in subplots with high sowing density (initially 2000 seeds m$^{-2}$; $F_{1,73} = 53.55$, $p < 0.001$; Fig. 2a, b).

Using realized density instead of sowing density as an explanatory variable showed a reversal of the density effect on aboveground biomass in the second year, 2003. Subplots with high realized community density actually had significantly lower aboveground biomass production than subplots with lower community density (Table 3, Fig. 1c, d). This would be expected if self-thinning of communities allowed surviving individuals to increase in biomass by a larger amount than the biomass lost from dying individuals. The negative relation between realized community density and aboveground biomass production did not occur at the highest diversity levels (significant interaction between log species richness and realized density, Table 3), indicating that even at high community biomass more individuals could be maintained in species-rich than in species-poor experimental communities.

In contrast to our prediction, high sowing density did not decrease the realized evenness calculated with the number of surviving individuals (2003: $F_{1,183} = 0.222$, $p = 0.638$; Fig. 3a, b). This suggests that species with small individuals did not suffer higher mortality in subplots with high initial community density, i.e. self-thinning in communities did not affect species differentially. Furthermore, there was no significant relationship between realized density and realized evenness in low sowing density treatment, we had data for both 2003 and 2004 (2003/2004: $F_{1,62} = 0.14$, $p = 0.712$). However, considering only the data for 2004 in the low density treatment, the relationship was positive at high species richness and negative at
low species richness (interaction between log species richness and realized density in repeated-measures analysis for 2003/2004 with realized evenness as dependent variable: $F_{1,62} = 4.47, p = 0.039$).

**Evenness effects**

Analyzing the available data from the low sowing density treatment from 2002–2004 in a repeated-measures ANOVA showed that subplots sown with an even initial species abundance distribution produced significantly more aboveground biomass (14%) than subplots sown with an uneven initial species abundance distribution (Table 2; Fig. 1a, c, e, g, h). Although separate analyses for each year suggested that this positive effect of initial evenness on biomass production declined over time (being significant in the first but not in the second and third year), interactions between year, season or harvest type and evenness were not significant in the repeated-measures ANOVA (Table 2). This indicates that, initial evenness had a longer-lasting effect on biomass production than did the sowing density.

As a dependent variable, the realized evenness ($E_{1/D}$) was strongly influenced by initial evenness in summer 2003 ($F_{1,123} = 16.97, p < 0.001$; Fig. 3a, b). However, compared with the index value based on the sowing proportions the realized evenness was reduced in all treatments, although least in the low species richness with uneven sowing combinations (Fig. 3a, b). After two years, in spring 2004, subplots with even and uneven sowing had converged to essentially the same realized evenness (low sowing density subplots: $F_{1,121} = 0.94, p = 0.337$) which was almost perfectly linearly related to the log of species richness (low sowing density subplots: $F_{1,60} = 109.74, p < 0.001$; Fig. 3c). In the repeated-measures ANOVA of the years 2003 and 2004 the corresponding year by evenness interaction was highly significant (low sowing density subplots: $F_{1,59} = 8.80, p = 0.004$).
As an explanatory variable, the realized evenness had a consistent positive effect on aboveground biomass in 2003 and 2004 (F\(_{1,62} = 6.40, p = 0.014\) in repeated-measures analysis of the two harvests in 2003 and 2004; Fig. 4). This indicates that sampling effects, which would coincide with reduction in realized evenness, were not the major cause of high aboveground biomass production. The slope of the relationship increased with the log of species richness (interaction between log species richness and realized evenness F\(_{1,62} = 6.89, p = 0.011\); Fig 4), indicating that evenness plays a greater role in species-rich communities. At the same time, the mean of realized evenness in species-rich communities was less variable and lower than the mean of realized evenness in species-poor communities (Figs. 3a–c, 4). This indicates that there is a trade-off or balance between the effects of species richness and realized evenness on aboveground biomass production of plant communities.

**Discussion**

**Similar species richness–productivity relationships under different evenness and density treatments**

This study confirms the general finding of a positive relationship between plant species richness and aboveground community biomass in biodiversity experiments with grassland plant communities (e.g. Hector et al. 1999, van Ruijven & Berendse 2003, Roscher et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). This positive relationship between richness and biomass production was not affected by the additional experimental manipulations of density and evenness beyond the establishment phase of experimental communities. As in most biodiversity experiments, we theoretically maximized evenness by sowing equal proportions of the species in the even treatments. By the end of the project the resulting communities were not at maximum evenness. In fact, by the first year they showed
rank-dominance patterns similar to semi-natural grasslands (Roscher et al. 2005). Similar patterns of species abundance distributions were also obtained in the uneven treatments. This means that experimental communities sown at maximum evenness have a more realistic species abundance distribution than previously thought (e.g. Houston 1997, Grime 1998, Mulder et al. 2004, Wilsey & Polley 2004). It also suggests that varying only species richness is possibly a sufficient manipulation to study general patterns of biodiversity–ecosystem functioning relationships in experiments. In fact, if different starting proportions and densities of the same species always converge to similar species abundance distributions after the initial phase of an experiment, other designs that vary species proportions, e.g. so-called simplex designs (Cornell 2002, Ramseier et al. 2005), may not be more realistic than designs that simply vary species richness to study biodiversity effects.

**Density effects**

The loss of the initial effect of the density treatment on species richness–productivity relationship suggests that the communities were below constant yield during the establishment phase. Thus, higher community densities yielded a higher biomass production (Harper 1977, He et al. 2005). Although initial density did not affect community biomass production in the longer term, the realized density remained somewhat higher in plots with high sowing density than in plots with lower sowing density in the second year after establishment (2003). Thus, the community must have been around constant yield in the second year, because on average the low sowing density treatment yielded the same community biomass with fewer individuals as the high sowing density treatment. In fact, within treatments there was a negative correlation between realized density and community biomass at low species richness levels. This indicates that some degree of community-level thinning may allow higher community biomass, which would be in accordance with the self-
thinning rule in single-species stands (Harper 1977). Apparently, such community-level thinning was more pronounced in low- than in high-species richness plots: plant species richness had a positive effect on the realized density of individuals in the community. This suggests that high species richness enhances establishment and survival of individual plants. Thus, species-rich communities used local resources more efficiently, which suggests a mechanism for complementarity effects in biodiversity experiments (Naeem et al. 1994, Tilman, Lehman & Thomson 1997, Loreau 2000, Silvertown 2004).

Extrapolating constant-yield and self-thinning rules from single- to multispecies stands (Bazzaz & Harper 1976, He et al. 2005) would also lead to the prediction that community-level thinning should remove subordinate species and thus high sowing density should lead to faster gains of dominant species than low sowing density. Interestingly, however, varying initial community density did not affect realized evenness in our communities. This demonstrates that the self-thinning rule cannot be directly extrapolated to multispecies communities because the effects of community-level thinning are not indifferent to species identities. This contradicts the results of a two-species self-thinning experiment of Bazzaz & Harper (1976), which to our knowledge was the only multi-species thinning experiment carried out so far.

**Evenness effects**

The experimental communities were sown in May 2002 and first harvested in late summer 2002. Thus, there was not much time for single species to develop dominance according to their competitive abilities. Nevertheless, the analysis of the realized evenness using the index $E_{1/D}$ showed that both evenness treatments had already departed from their initial sowing proportions. Yet, the treatment with even initial proportions still had a higher realized
evenness than the treatment with uneven initial proportions (see Fig. 3a, b). This was combined with a positive effect of evenness on biomass production at the time of the first harvest in 2002. Wilsey & Polley (2004) also found short-term benefits of evenness on productivity, but only for deep-rooting plants.

As the two evenness treatments continued to converge in realized evenness, differences in initial evenness no longer affected community biomass production in the second and third years. The continuous decline of the evenness index $E_{1/D}$ over time indicates that some species were still gaining dominance in the experimental communities. Mulder et al. (2004) showed in a path analysis that such dominance developments can eventually weaken the positive effect of evenness on biomass production as suggested by Nijs and Roy (2000) with a simulation model. However, Mulder et al. (2004) found no evidence for a consistent decline in evenness over two years in their analysis of a multi-site biodiversity experiment. Although they found their results difficult to interpret without knowing to what extent growing conditions may have differed over time, the results indicate that dominance and complementarity may reach some balance in the longer term. Such a balance between dominance and complementarity may also be inferred from the fact that community biomass production increased with realized evenness at each level of species richness, but realized evenness decreased with increasing species richness (see Fig. 3a–c, 4). Thus, higher biomass production was reached at lower levels of realized evenness if the community contained more species. The more species a community has, the higher is the chance that the community will incorporate highly productive species, which will then gain dominance and thereby reduce realized evenness. It is conceivable that the species gaining dominance at high diversity are not those that perform best in monocultures or in low diversity mixtures (see e.g. Lamberts et al. 2004, Schläpfer et al. 2005). Lamberts et al. (2004) and Mulder et al. (2004) also showed
that these dominant species with high yield in mixtures generally do not displace species with lower yield over time.

The positive effect of realized evenness on community biomass production within the different species-richness levels suggests that complementarity effects also contributed to the positive species richness–biomass production relationship between species-richness levels in our experimental communities. However, the lower realized evenness in species-rich communities (see Fig. 3a–c) also indicates that there were tradeoffs between achieving complementarity effects through high realized evenness within species richness levels and by high species richness itself. In a previous analysis of plots started with low sowing density and high evenness (Roscher et al. 2005) we had shown that the selection effect indeed increased in importance relative to the complementarity effect at high levels of species richness. This suggests that the more species there are in a community the lower the probability that they will all mutually differ to a large enough degree to allow complementary resource use.

Acknowledgements

As part of “The Jena Experiment” this study was funded by the Deutsche Forschungsgemeinschaft (DFG-grant FOR 456), and supported by the Friedrich Schiller University of Jena, the Max Planck Society and the Institute of Environmental Sciences at the University of Zurich (BS). We are grateful to the many people who helped with set-up and maintenance of the plots, particularly the gardeners S. Eismann, S. Junghans, B. Lenk, H. Scheffler and U. Wehmeier. We also thank the many student helpers who worked during the weeding campaigns, assisted the biomass harvest and data collection, especially the TP 10 team: M. Rzanny, A. Gminder, A. Fröhlich, J. Trettin, A. Dassler, J. Dittmann, M. Geuther, L. Merbold and V. Höntsch. This manuscript benefited greatly from suggestions by R. F. Doren.
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O'Donovan, G., Otway, S. J., Pereira, J. S., Prinz, A., Read, D. J., Scherer-Lorenzen, M.,
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107*, 50–63.


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Table 1. Species and functional groups that were made numerically dominant in the uneven treatment of the experiment (see text for further explanation).

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<tr>
<th>Number of species</th>
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<table>
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<th>Legumes</th>
<th>Small herbs</th>
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<tr>
<td>Poa pratensis</td>
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Table 2. Repeated-measures ANOVA of aboveground community biomass production 2002–2004 (low sowing density treatment; the high-sowing density treatment was only followed from 2002–2003).

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Table 3, Repeated-measures ANOVA of aboveground community biomass production 2003–2004, with realized density as covariate (low sowing density treatment; in the high sowing density treatment realized density was only assessed in 2003).

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Figure legends

Fig. 1. Aboveground community biomass production as a function of species richness in uneven (□) and even subplots (+) started from low (a, c, e, g, h) or high sowing density (b, d, f) at five different harvest dates. Monocultures are considered uneven (see “Materials and Methods”). Lines represent regression slopes from the statistical model. Solid lines illustrate even subplots and dotted lines uneven subplots.

Fig. 2. Realized community density (number of surviving individuals per m²) as a function of species richness in uneven (□) and even subplots (+) started from low (a, c) or high sowing density (b) at two different harvest dates. Monocultures are considered uneven (see “Materials and Methods”). Lines represent regression slopes from the statistical model. Solid lines illustrate even subplots and dotted lines uneven subplots.

Fig. 3. Realized evenness (E₁/D-values based on number of individuals, see “Materials and Methods”) as a function of species richness in uneven (□) and even subplots (+) started from low (a, c) or high sowing density (b) at two different harvest dates. Dash-dot lines represent evenness at the time of sowing for uneven subplots (lower line) and even subplots (upper line). Monocultures are omitted (see “Materials and Methods”). Lines represent regression slopes from the statistical model. Solid lines illustrate even subplots and dotted lines uneven subplots.

Fig. 4. Relationship between realized evenness (index E₁/D) and aboveground community biomass production in low sowing density subplots of both evenness treatments for plant communities of 2, 4, 8 and 16 species in late spring 2003 and late spring 2004. Lines represent regression slopes from the statistical model. Solid line = regression slope for 16-
species mixtures (16), long dashed line = 8-species mixtures (8), medium dashed line = 4-species mixtures (4), short dashed line = 2-species mixtures (2). Small numbers indicate one subplot of the species richness treatments at the time of harvest.
Species richness (log scale)

Aboveground biomass production (g m⁻²)

Low-density subplots

High-density subplots

Late summer 2002

Late spring 2003

Late summer 2003

Fig 1
Aboveground biomass production (g m⁻²)

Late spring 2004

Species richness (log scale)

Late summer 2004

Fig 1 (continued)
Late spring 2003

Species richness (log scale)

Late spring 2004

Number of individuals per m²

Low-density subplots

High-density subplots

Fig 2
Fig 3
Aboveground biomass production (g m⁻²)

Index $E_{1/D}$

Fig 4
Chapter 4

Removing less-abundant plant species across a randomly assembled biodiversity gradient increases productivity

with
Michael Rzanny, Michael Scherer-Lorenzen, Peter N. Mwangi, Wolfgang W. Weisser, Andrew Hector and Bernhard Schmid
Abstract

Experiments on the effect of plant species loss on ecosystem functioning that assemble communities at random have been criticized because all species are assumed to have the same probability of extinction. We removed the less abundant half of the species from randomly assembled experimental grassland communities that formed a diversity gradient. As found in previous experiments, aboveground biomass production in the randomly assembled communities increased linearly with the logarithm of species richness. Species relative abundances and their probability of being removed were highly species-specific. Removing the less abundant species slightly increased community biomass production by 12.5 % due to increased evenness and over-compensating increases in the per-species yields of the remaining dominants. Communities from which the less abundant species had been removed produced on average 30.8 % more biomass than did randomly-assembled communities with the same number of species as that obtained after removal. The diversity gradient formed from randomly assembled communities and from communities with the less abundant species removed had the same slope for productivity regressed against logarithm of species richness. We conclude that, in the short term, non-random extinction of less-abundant plant species has no negative effects on community productivity but that in communities formed from only the more abundant species productivity is still positively related to increasing diversity.
Introduction

The consequences of the dramatic species loss caused by human activities (Pimm et al. 1995) are still poorly understood. Most experimental studies have focused on the influence of random species loss on ecosystem functioning (Schmid et al. 2002a, b, Hooper et al. 2005). They have found that plant productivity declines with reduced plant species richness (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). The question remains if non-random species loss has the same effect. If rare or subordinate species go extinct first, the effect of species loss on ecosystem functioning may be small (Lepš 2004, Raffaelli 2004, Schläpfer et al. 2005).

More realistic non-random extinction scenarios can be simulated by using rarity as a proxy for extinction probability (MacArthur and Wilson 1967, Davies et al. 2000, Wilsey and Polley 2004; but see Tilman et al. 1997, Henle et al. 2004). On plots of a biodiversity experiment with simulated random species loss, which had been running for 2 years (Roscher et al. 2004), we superimposed a removal experiment with non-random species loss. In plots with species originally sown at equal proportions, the less abundant half of the species in each community was removed. In a matched control subplot the same plant biomass was removed randomly. If rare species, which at the local scale of plots are equivalent with subordinate species (Grime 2002), do not contribute to ecosystem functioning, than removal and control subplots should subsequently have the same productivity.

Because the original randomly assembled species richness gradient and the gradient formed by removing the less abundant species both used a log2 series we could compare the productivity of removal subplots with 1, 2, 4 or 8 species with the productivity of the randomly assembled communities of 2, 4, 8 or 16 species from which they were derived.

Within the above framework of general questions, we tested the following specific hypotheses:
1) Plant species richness–biomass production relationships are positive and log-linear if 
extinction scenarios are random and when only dominant species are used.

2) Relative abundance in the randomly assembled species communities (and therefore 
probability of removal) is not random with regard to species identities, i.e. extinction 
probabilities are species-specific.

3) Removing the less-abundant species reduces community biomass production.

4) For a given diversity, removal-treatment communities formed from only dominant species 
produce more biomass than communities of randomly selected species.

5) Communities of dominant species show steeper species richness–biomass production 
relationships than communities of randomly selected species.

We will show that our data support hypotheses 1), 2) and 4) but not hypotheses 3) and 5). We 
conclude that, at least in the short term, non-random extinction of the less-abundant species 
has little effect on aboveground biomass production but that in communities formed only 
from species of high dominance productivity is positively related to increasing diversity.

Material and methods

Experimental design

Our factorial biodiversity x removal-treatment experiment was carried out in 60 plots of the 
grassland communities established for the “Jena Experiment” (see Roscher et al. 2004 for 
details). The experimental site is located on a former agricultural field in the floodplain of the 
Saale river near the city of Jena, Germany (50°55’ N, 11°35’ E, 135 m above sea level, mean 
anual temperature 9.3°C, mean annual precipitation, 587 mm; Kluge & Müller-Westermeier 
2000). The plant communities were established from seeds in May 2002 by constrained 
random selection from a pool of 60 grassland species typically occurring in mesophilic
grasslands of Central Europe (Roscher et al. 2004). A gradient of plant diversity was created with mixtures of 1, 2, 4, 8, and 16 species. The species were divided into four functional groups, defined by relevant functional traits: grasses, legumes small herbs and tall herbs. At each level of species richness, we established 16 replicates with different species composition, except at the highest richness level where we had only 14 replicates. In addition, species were distributed equally among the four functional groups and all possible combinations of functional group mixtures were represented. The experimental site was partitioned into four blocks to account for gradual differences in soil characteristics caused by former fluvial dynamics.

We used plots of 1.75 x 1.75 m (3.0625 m²), which were part of 12.25 m² plots with the same species composition. The quadrants used as plots for this study were sown with a density of 2000 seeds per m², divided equally among the component species. The species number of these plots varied on a logarithmic (log₂) scale from 2, 4, 8 to 16. In fall 2003, the plots were divided into two triangles, each with an area of 1.531 m². In one of those triangles the 50 % species from the tail of the rank–abundance curve obtained in the previous biomass harvest at peak vegetation development were removed by pulling out individuals with roots (removal triangle), whereas in the other triangle a similar amount of aboveground biomass was randomly clipped without reducing species richness (control triangle). This was done to avoid confounding species loss with loss of biomass (Diaz et al. 2004). Furthermore, removal disturbance was simulated in each control triangle by hoeing as often into the ground as numbers of plants were removed in the treatment triangle of the same plot. Removal and control treatment were randomly assigned to the two triangles within a plot. The treatments were repeated at the beginning of the growing season 2004. All triangles were weeded twice in April and July and mown in June and September 2004.
Control triangles can be regarded as communities whose species composition is based on random species loss. In contrast, the removal-treatment communities were created by selecting the more abundant half of the species in each species mixture from the randomly selected communities.

**Measurements**

Between end of May and beginning of June 2004 the aboveground plant biomass in both triangles was harvested. A 20 x 50 cm frame was placed in the middle of a triangle and the plants were cut at 3 cm height and separated into species. The harvested biomass was dried 48 h at 70 °C and weighted thereafter. Subsequently, we analyzed community biomass, functional group biomass and species biomass. We excluded one 16-species plot from analysis because less than half of the eight species were established in the removal triangle.

We calculated the evenness index $E_{1/D}$ (Smith & Wilson 1996) based on Simpson’s D (Simpson 1949) to quantify the evenness in the plots:

$$E_{1/D} = \frac{1/D}{S} = \frac{1}{S} \cdot \frac{1}{\sum_{i=1}^{S} P_i^2},$$

where $P_i$ is the proportion of biomass of species $i$, and $S$ is the number of species sown in the plot. Monocultures (obtained by removing the less abundant species from 2-species mixtures) were excluded from evenness calculations, because their evenness is not defined. We chose this index because it is independent of species richness (Smith & Wilson 1996).

**Statistical analysis**

The data were analyzed using general linear models, taking care of the separation into treatment and error models when testing effects (Schmid et al. 2002a). The error model consisted of block, plot and subplot (triangle) effects and accounted for spatial variation. The
treatment model consisted of the two factors species richness and removal treatment (removal vs. control) and their interaction; in the analysis of functional group biomasses and species biomasses the factors functional group identity and species identity and their interactions with the previous factors were additionally included in the treatment model.

All hypotheses were tested using pre- and post-removal species richness as given by the design (sown species richness, divided by half in removal triangles for post-removal species richness) and as established at the end of the experiment (realized species richness). Because sown and realized species richness gave the same results we mainly present the analyses with sown species richness.

In addition to the above measurements, we also analyzed the probability of each species to be removed as less-abundant from an experimental community by logistic regression. This can be taken as an estimate of extinction probability. The data values were zero for each species in a removal triangle that was not removed and one for each species that was removed.

We tested if extinction probability differed in the four functional groups and between species within functional groups. To see if the non-removed functional groups or species responded differentially to the removal of rare species their biomass proportion in the total harvest was arcsin-square-root transformed and analyzed with a general linear model.

All statistical calculations were done with the GenStat 6.1 statistical programming language (Payne et al. 1993).

**Results**

Aboveground biomass production in spring 2003, the year before the start of the removal experiment, ranged from 52.6–2046.8 g m⁻² (mean: 833.6 g m⁻²). In spring 2004, after
removing the rare species, the community biomass varied between 37.1–1319.7 g m$^{-2}$ in the control triangles and between 84.6–1326.3 g m$^{-2}$ in the removal triangles.

Removal probabilities did not differ between functional groups (ratio of mean deviance changes functional groups / species within functional groups: $F_{3,52} = 0.62, p = 0.608$) but between species within functional groups (ratio of mean deviance change species within functional groups / mean residual deviance: $F_{52,351} = 8.35, p < 0.001$), supporting hypothesis (2) that “extinction” probabilities in our model communities were species-specific. The ranked observed removal probabilities are presented in Table 1.

Statistical analysis of community aboveground biomass revealed a log-linear relationship between pre-removal species richness and productivity in 2003, before the removal treatment (Table 2), as well as after the removal treatment in 2004 (Fig. 1a; Table 3). This is strong evidence for the corresponding hypothesis (1) stating a positive log-linear relationship between plant species richness and biomass production for random extinction scenarios. Comparing the community biomass production between removal and control triangles within a plot after the removal treatment showed a slightly but significantly increased rather than decreased biomass production in the removal triangles (Fig. 1a; Table): the mean community biomass in the control triangles was 440.6 g m$^{-2}$ ($\pm 28.4$ g m$^{-2}$ SEM) and increased in the removal triangles by about 12.5% to 495.9 g m$^{-2}$ ($\pm 30.4$ g m$^{-2}$ SEM). This is strong evidence against hypothesis (3) that removal of rare species reduces community biomass production. There was no difference between removing less abundant species from species-poor and from species-rich communities (Fig. 1a; non-significant interaction log species richness x treatment in Table 3). Thus, our results do not support the corresponding hypothesis (5) that communities of dominant species show steeper species–richness biomass production relationships than communities of randomly selected species. The same result was
obtained if realized instead of sown species richness was used in the analysis ($F_{1,55} = 41.64$, $p < 0.001$ for log realized species richness and $F_{1,55} = 4.65$, $p = 0.036$ for removal treatment).

To test hypothesis (4), we replaced pre-removal with post-removal species richness in the statistical analysis. In this case, the treatment effect refers to a comparison between removal-treatment communities containing $k$ dominant species and control communities containing $k$ species (including both dominants and subordinates). Removal-treatment communities formed from dominant species had on average 135.7 g m$^{-2}$ ($\pm 27.2$ g m$^{-2}$ SED) or 30.8 % higher biomass production than control communities of randomly selected species of the same species richness (Fig. 1b; $F_{1,55} = 18.48$, $p < 0.001$).

Evenness was significantly increased in the removal-treatment communities and decreased with increasing species richness in both the removal-treatment and control communities, i.e. the richness x treatment interaction was not significant (Table 4; Fig. 2). This suggests that the higher productivity of removal-treatment communities as compared with control communities was partly caused by increased evenness among selected dominants with potentially increased complementarity.

The biomass of dominant species was larger in removal-treatment than in control communities ($F_{1,58} = 121.80$, $p < 0.001$), suggesting that the rare species did compete with them in control communities. Apparently, the increase in dominant species biomass more than compensated for the removal of less-abundant species in our experiment, thus the negative result for hypothesis (3), which had assumed a reduction of community biomass due to the removal of the less-abundant species.
Discussion

Effects of removing rare species from randomly-assembled plant communities

There are many experimental approaches to study the effects of plant species loss on community aboveground biomass production, ranging from assembling synthetic communities (e.g. Naeem et al. 1996, Tilman et al. 1996, Hector et al. 1999) to creating diversity gradients indirectly via extinction drivers such as fertilizer addition (Tilman 1994, Schläpfer et al. 2005) to removal of species from natural communities (Symstad and Tilman 2001, Smith and Knapp 2003, Wardle & Zackrisson 2005). These experiments have generally found a positive relationship between plant species richness and community productivity. However, effects seemed to be less strong in cases where more productive species were preferentially included at low-species richness levels and rare species preferentially occurred at high richness levels (Lyons and Schwartz 2001, Schläpfer et al. 2005).

Here we report the results from a study in which we combined the synthetic with the removal approach. Randomly-assembled synthetic plant communities ranging from 2, 4, 8, to 16 species showed the expected log-linear increase in aboveground biomass production (according to hypothesis 1). However, removing the less abundant half of the species in each community did not further reduce biomass production (hypothesis 3) but rather increased it. The removal treatment led to a higher performance of the resulting communities of dominant species as opposed to control communities of the same species richness (according to hypothesis 4). Thus, the removal treatment can be compared with an experimental demonstration of the selection effect (Loreau and Hector 2001): communities of k species derived from a pool of 2k species on average had a 35 % higher biomass production than communities of k species derived from a pool of k species.
One possible explanation for the positive rather than negative effect of species removal could be that removal experiments are fundamentally different from experiments that assemble synthetic communities. Some removal experiments with random species loss carried out in natural communities also observed that biomass production was unaffected or increased with reduced species richness (Wardle et al. 1999, Symstad and Tilman 2001, Smith and Knapp 2003). We conclude that those species in our randomly-assembled experimental communities that constituted the second half of the rank–abundance distribution actually slightly decreased community productivity by competing with the dominants and reducing the biomass contribution of these dominants more than the amount of biomass the rare ones produced themselves. Weeding the rare species out allowed the dominants to invade the freed patches and convert the resources into biomass with greater efficiency than the less-abundant species did. Since we removed similar amounts of biomass from control and removal subplots and even simulated the same degree of soil disturbance, we believe that our result is not simply an effect of removal but rather one of changed species richness and composition. Indeed, the removal increased the evenness among the remaining dominant species, perhaps increasing complementarity between the remaining dominant species (Schmid et al. 2002a). Similarly, Fargione et al. (2003) and Roscher et al. (2005) found a greater degree of niche complementarity among dominant species compared to subdominant ones.

It has been suggested that non-random species loss could be less damaging to ecosystem functioning than random species loss, especially if non-random loss affects those species that contribute little to a particular ecosystem property such as productivity. This may be the case for rare species which are prone to extinction because of small population sizes (MacArthur & Wilson 1967). It may also be the case for species likely to go extinct due to human-caused alterations of the environment such as nitrogen deposition or climate change (Harte and Shaw 1995, Tilman and Lehman 2001, Reich et al. 2004). Some recent
experiments and simulations based on more realistic non-random extinction scenarios provide mixed support for a weaker effect on ecosystem functioning than with random extinction scenarios (Lyons and Schwartz 2001, Zavaleta and Hulvey 2004, Solan et al. 2004, Schläpfer et al. 2005). In our experiment, the identity of the species removed was determined by their relative abundance in the randomly assembled communities after two years. This coupling of extinction driver and system performance was not so close in the previous biodiversity experiments.

Our results are relevant for the short term over which the experiment was carried out (it had to be discontinued at the end of the 2004 vegetation season). Despite the negative impact of the rare species on community productivity in the short term, it is conceivable that the removed rare species might have become more important again with regard to ecosystem functioning in the longer term under varying environmental conditions or if the remaining dominant species would have decreased in performance due to intrinsic population dynamics or external influences. Thus, in the longer term, effects such as invasion resistance (Lyons & Schwartz 2001, Fargione et al. 2003) or further less conspicuous consequences such as filter or founder effects (Grime 1998, Schmid et al. 2002b, Diaz et al. 2003, Lepš 2004) may still impact ecosystem responses to rare species loss in nature. Furthermore, rarity may not be a good predictor of extinction probability in all cases and with all drivers. Indeed, Lambers et al. (2004) have shown that low-yielding species in experimental grassland communities can be buffered from extinction by diversity-promoting interactions.

Comparing removal communities with randomly-assembled control communities

Removing the less-abundant half of the original species number, we created a new species richness gradient in the removal communities. We had expected that biodiversity effects on community productivity would be stronger for this gradient than for the original richness
gradient formed by the randomly assembled control communities (hypothesis 5). However, the positive log richness–productivity relationship had the same slope for both gradients. In fact, the positive effect of removal treatment could have suggested the opposite, i.e. that removal communities should show a flatter richness–productivity relationship. However this was also not the case, that is, species-poor removal-treatment communities did still produce less aboveground biomass than species-rich removal communities. This is consistent with Roscher et al. (2005) who also found more or less parallel relationships in communities assembled from only dominant species and in communities assembled from both dominant and subordinate species, based on abundances in semi-natural grasslands. Indeed, our experiment built on the second type of communities from Roscher et al. (2005). The dominant species selected by our removal treatment included most of the dominant species from the previous experiment (see Table 3).
Conclusions

In conclusion, we reconfirm the positive biodiversity–ecosystem functioning relationship as found in many experiments investigating randomly assembled grassland communities (hypothesis 1). Low species abundance in the randomly-assembled communities was species-specific (hypothesis 2). In contrast to hypothesis (3), removing these less abundant species led to a slightly increased biomass and an increased evenness at all species richness levels in the following growing season. Communities from which the less abundant species were removed produced much more biomass than randomly-assembled communities of the same species richness (hypothesis 4). Nevertheless, and in contrast to hypothesis (5), the relationship between species richness and productivity had the same positive slope in communities consisting of dominant species only and in randomly-assembled communities.

Acknowledgements

As part of “The Jena Experiment” this study was funded by the Deutsche Forschungsgemeinschaft (DFG-grant FOR 456), and supported by the Friedrich Schiller University of Jena, the Max Planck Society and the Institute of Environmental Sciences at the University of Zurich. We are grateful to the many people who helped with set-up and maintenance of the plots, particularly the gardeners S. Eismann, S. Junghans, B. Lenk, H. Scheffler and U. Wehmeier. We also thank the many student helpers who worked during the weeding campaigns, assisted in the biomass harvest and data collection, especially the TP-10 team: A. Gminder, A. Fröhlich, J. Trettin, A. Dassler, J. Dittmann, M. Geuther, L. Merbold and V. Höntsch.
References


Table 1 Ranking of plant species according to their removal probability in the treatment triangles. The species in bold type were used as “a-priori” dominants in another biodiversity experiment at the same site (Roscher et al. 2005). For nomenclature see Rothmaler (2002).

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Table 2 Summary of statistical analysis for aboveground community biomass production in 2003 (before the removal treatment). Model terms were added sequentially and tested against the residual. Significant P-values (P < 0.05) are in bold.

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Table 3 Summary of statistical analysis for aboveground community biomass production in 2004, after the removal treatment, but still using pre-removal species richness as explanatory variable. Treatment refers to species removal vs. control. Model terms were added sequentially, the first three tested against plot and the following ones against the residual as error term. Significant P-values (P < 0.05) are in bold.

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**Table 4** Summary of statistical analysis of evenness quantified by the index $E_{1/D}$ in 2004.

Treatment refers to species removal vs. control, species richness refers to the post-removal richness level. Model terms were added sequentially and tested against the residual as error term. Significant P-values ($P < 0.05$) are in bold.

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<td>0.25</td>
<td>0.863</td>
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<td>2.796</td>
<td>147.99</td>
<td>&lt; 0.001</td>
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<td>Species richness (deviation)</td>
<td>2</td>
<td>0.041</td>
<td>2.16</td>
<td>0.126</td>
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<td>Treatment</td>
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<td>19.88</td>
<td>&lt; 0.001</td>
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<td>Species richness log x Treatment</td>
<td>1</td>
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<td>0.19</td>
<td>0.666</td>
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<td>0.011</td>
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<td>2.19</td>
<td>0.005</td>
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<tr>
<td>Residual</td>
<td>42</td>
<td>0.009</td>
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<td></td>
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<td>Total</td>
<td>103</td>
<td>0.043</td>
<td></td>
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</tbody>
</table>
**Figure legends**

**Figure 1a** Aboveground biomass production as a function of pre-removal species richness (post-removal species richness for removal-treatment communities indicated on upper x-axis). Symbols are aboveground biomasses for each community: ● control; ○ removal treatment. Lines represent the mean aboveground biomass predicted from the regression model: solid line = control communities; dashed line = removal-treatment communities.

**Figure 1b** Aboveground biomass production as a function of post-removal species richness (species richness of the removal-treatment communities refers to the new halved richness level). Symbols are aboveground biomasses for each community: ● control; ○ removal treatment. Lines represent the mean aboveground biomass predicted from the regression model: solid line = control communities; dashed line = removal-treatment communities.

**Figure 2** Evenness index (E1/D) as a function of post-removal species richness (species richness of the removal-treatment communities refers to the new halved richness level). Monocultures (resulting from removal treatment of 2-species mixtures) are excluded, because of undefined evenness. Symbols are index values for each community: ● control; ○ removal treatment. Lines represent the mean index values predicted from the regression model: solid line = control communities; dashed line = removal-treatment communities.
Figures

**Figure 1a**

**Figure 1b**
Figure 2
Chapter 5

Evidence for Niche Pre-emption as Plant Diversity Increases in Grassland Experiment

with
Peter N. Mwangi, Christoph Scherber, Christiane Roscher, Jens Schumacher, Michael Scherer-Lorenzen, Wolfgang W. Weisser and Bernhard Schmid
**Abstract**
Experimental studies support the theoretical prediction that establishment of new species (e.g. invaders) decreases with increasing diversity. Using native species as transplant phytometers, we tested the proposed mechanism that diverse communities are less vulnerable to ‘invasions’ because they offer less empty niche space. We transplanted a grass (*Festuca pratensis*), a small herb (*Plantago lanceolata*), a tall herb (*Knautia arvensis*) and a legume (*Trifolium pratense*) into plots of a plant diversity experiment (The Jena Experiment). Diversity treatments varied species richness, and presence and number of functional groups. Phytometer density was low and thus the effect of the phytometers on the resident community was considered negligible.

The overall performance of the transplants decreased with increasing species richness. Grasses showed a strong negative effect on the performance of the transplants whereas small and tall herbs had neutral and legumes positive effects. These results are echoed in the levels of belowground resources and to some extent in the community’s leaf area index indicating that niche pre-emption inhibits establishments of new species. Assemblages containing one functional type were more inhibitive to transplants of their functional group, supporting that high niche overlap among residents and new species enhances inhibition of the latter.

*Key words:* transplant phytometers; ecosystem functioning; species richness; functional group richness; resource use; The Jena Experiment
**Introduction**

Understanding the mechanisms behind the relationship between biodiversity and the establishment of new species (e.g. invaders) in natural communities is a major goal in ecology. This relationship has a potential for application in conservation, restoration and prediction of communities’ susceptibility to invasions. Theoretical studies predict a negative relationship between species diversity of a community and the likelihood that an intruder will be able to establish itself in this community (Elton 1958, Levine and D’Antonio 1999). While such relationships are found in an increasing number of experimental studies, using mainly plant communities (Tilman 1997, Knops et al. 1999, Naeem et al. 2000, Joshi et al. 2000, Prieur-Richard et al. 2000, Diemer and Schmid 2001, Kennedy et al. 2002, Pfisterer et al. 2004), comparative observational studies so far have yielded mixed results. Most field studies find an increase in exotic species richness with increasing native species richness (Stohlgren et al. 1999, Stadler et al. 2000, Stohlgren et al. 2002, Pysek et al. 2002) though Stohlgren and others (1999) found the opposite at one site of their study. The discrepancy in observational studies is often attributed to uncontrolled extrinsic factors, whose effect on native and exotic species is the same (Stohlgren et al. 1999, Levine 2000, Shea and Chesson 2002). Additionally, observational studies mostly use number of introduced species (e.g. Stohlgren et al. 1999, Meiners et al. 2004) while many experimental studies use biomass of the unsown species to measure invasion success or resistance (see e.g. Prieur-Richard et al. 2000, Diemer and Schmid 2001).

In most cases species richness is the only component of diversity manipulated in experimental studies (e.g. Prieur-Richard 2000, Troumbis et al. 2002), though a few studies have attempted to assess the importance of functional diversity in competitive suppression of new-arrivals (see the review in Hector 2001, Prieur-Richard et al. 2002, Xu et al. 2004). Functional groups are sets of species (not necessarily taxonomic) that show close similarities in traits that affect ecosystem functioning, e.g. traits related to resource uptake and biomass production. With respect to ecosystem processes other than invasibility, increasing evidence suggests that the influence of functional diversity in a community might be more important than pure species richness (Diaz and Cabido 2001, Garnier et al. 2004, Petchey et al. 2004, Heemsbergen et al. 2004).
Species packing (MacArthur 1970) is thought to be the main mechanism underlying invasion resistance in diverse communities. This is viewed as an extension of the vacant niche concept (Hutchinson 1957) because diverse species assemblages may extract available resources more completely from the environment than species-poor assemblages (Scherer-Lorenzen et al. 2003, Dimitrakopoulos and Schmid 2004), thereby pre-empting resources for new arrivals (Tilman 1999, Hector et al. 2001). A correlate of this theory is that, at a given species richness, functionally rich assemblages should be more resistant to new arrivals than assemblages with few functional groups. In this case, each functional group makes a unique contribution to suppression of new arrivals outside its region of niche overlap with other functional groups. Additionally, new arrivals should find it particularly difficult to ‘invade’ communities in which similar species are already abundant, i.e. communities that already contain the functional group to which the invader belongs (but see Symstad 2000). Such effects of functional similarity between new arrivals and resident species have not been explicitly tested so far (Levine and D’Antonio 1999).

So far, suppression of new arrivals (invasion resistance) has mostly been studied by monitoring the spontaneous occurrence or the success of sown or transplanted species external to the species pool from which experimental communities had been randomly assembled (Tilman 1997, Knops et al. 1999, Hector et al. 2001, Prieur-Richard et al. 2002, Pfisterer et al. 2004). One problem with this approach is that it is hard to deduce the underlying mechanisms if there is an interaction between the exotic species response and the resident community effect (see e.g. Joshi et al. 2001). Using native species that are part of the species pool (and therefore occur themselves as residents in some of the experimental communities) as introduced species will allow for control of the potential confounding factors that have been shown to influence establishment of new arrivals in invasion studies. For example, average competitive ability of invaders being greater than that of residents (Vilá and Weiner 2004, but see Colautti et al. 2004).

As early as in the 1920ies, Clements and Goldsmith (1924) used phytometers mainly for measuring abiotic factors but development of instruments overtook this approach. Phytometers are still important in quantifying some ecological factors such as invasion resistance or competitive suppression, which cannot be measured by instruments.
In this study, we tested the effect of both species richness and functional group composition on suppression of introduced phytometer species in experimental grassland communities. The experimental communities and choice of the phytometer species allowed us to control for the extrinsic factors that may confound the effect of plant diversity. Our experimental design also allowed us to explore the potential mechanisms that lie behind invasion resistance phenomenon. Specifically, we wanted to find out: a) if the higher the species richness or number of functional groups, the more the suppression of introduced species, b) whether presence of a particular functional group in a community enhances suppression of introduced species, c) whether the success of an introduced species is reduced if the resident community already contains residents belonging to the same functional group (success of the introduced, in contrast to suppression in a, b).

Material and methods
Our study was part of a large biodiversity experiment, The Jena Experiment in Germany (50°55' N, 11°35' E, and 130 m above sea level). This experiment was established in May 2002 on a former agricultural field in the flood plain of the Saale river (Roscher et al. 2004). Plant communities were assembled by constrained random selection from a pool of 60 species typical to Central European mesophilic grasslands. The species were categorized into the four functional groups, grasses (16 species), small herbs (12 species), tall herbs (20 species), and legumes (12 species), based on multivariate analysis of their traits (Roscher et al. 2004). Seventy-eight plots, each measuring 20 x 20 m plots were sown with 1, 2, 4, 8, or 16 species. A near orthogonal design was formed with all possible species richness by functional group richness mixtures. There were 16 replicates in each species richness level except the highest, which had 14 replicates. Four additional large plots contained mixtures of all species in the pool. The field was partitioned into four blocks following a gradient in soil characteristics perpendicular to the river (Roscher et. al 2004). The plots were mown twice a year (June, September) to mimic the typical management of meadows in the region and weeded twice a year to maintain the original species composition. Mowing and weeding was done block-wise such that this management effects are accounted for in block term in statistical analysis.
As introduced species, we selected four species that occurred in a large number of experimental communities also as resident species, one species from each of the four functional groups. The selected species, *Festuca pratensis* Huds. (grass), *Plantago lanceolata* L. (small herb), *Knautia arvensis* L. (tall herb) and *Trifolium pratense* L. (legume) are perennial, form clearly defined compact individuals and are relatively easy to transplant.

In mid March 2003, we germinated the phytometer species on moist filter paper in a greenhouse. Individual seedlings were planted in 132-cm³ cells of potting trays filled with a soil-compost-perlite mixture (3:2:1 in terms of volumes). We used a 14h light regime with 22°C day and 15°C night temperatures. In mid April 2003, we hardened the plants by placing them outside the greenhouse for one week before transplanting them into the experimental communities at an average size of 4 to 7 leaves. Five plants of each phytometer species were randomly allocated to positions at 28-cm intervals in a 2 x 2-m subplot within each large plot and the initial size determined by counting number of leaves and the number of ramets (only *F. pratensis* and *T. pratense*). Transplanted phytometer individuals were marked by fixing numbered plastic labels next to the plant to distinguish them from resident individuals and from possibly spontaneously ‘invading’ individuals.

In mid August, in addition to counting the number of leaves, we measured the maximum height of the phytometers. For *T. pratense* and *F. pratensis*, we also counted the number of ramets as before. We calculated the mean growth rate of the transplants using the formula

\[ RGR = \frac{\ln l_{t2} - \ln l_{t1}}{d}, \]

where \( l_{t2} \) is the mean number of leaves in August, \( l_{t1} \) is the mean number of leaves in April and \( d \) is the length of time interval in days (Harper 1977). As a measure of plant fitness, we counted the number of inflorescences in *P. lanceolata* and *T. pratense* transplants. *F. pratensis* requires vernalization to induced flowering and *K. arvensis* transplants were still at rosette stage at this time. In the last week of August 2003, all transplants were harvested at 5 cm above ground. The harvested parts of the five plants of each species per plot were pooled together and dried at 70°C to constant weight to determine mean aboveground biomass. In early June 2004, we once again measured the
height of the transplants and harvested them for aboveground biomass. We also counted the number of
inflorescences in *P. lanceolata* and *T. pratense*.

In August 2003, we determined the resident community leaf area index (LAI) in undisturbed
area next to the phytometers using LAI-2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln,
Nebraska, USA).

**Statistical analysis**
We used general linear models with sequential sum of squares (Type I) for data analysis using Genstat
6th Edition, Release 6.2. (GenStat Committee 2002). Response variables were mean aboveground
plant biomass, plant height, number of leaves and relative growth rate of the phytometers. The data
were transformed if residuals showed deviation from the normal distribution. The full model included
block, sown species richness, functional richness, presence/absence of grasses, small-herbs, tall-herbs
or legumes and their interactions with species richness, plot (= composition), phytometer species and
its interactions with the previous diversity terms. Functional richness was often not significant and
therefore removed from the final model. We partitioned species richness into a log-linear contrast and
devation and phytometer species into contrasts for each against the others. The phytometer species
contrasts were fitted one at a time but the results of the four alternative ways of forming contrasts were
summarized in one table to save space (see lower part of Table 2). We tested the effects of community
diversity, i.e. species richness, functional richness and presence of particular functional groups, the
latter again as four alternative contrasts summarized in the same table to save space (see upper part of
Table 2), at the between-plot level (each plot had a unique species composition). Differences between
phytometer species and their interaction with community diversity - as well as phytometer species
contrast x functional group presence contrast interactions (only matching combinations, e.g. *F. pratensis*
phytometer x presence of grasses in resident communities) within this larger interaction term
- were tested at the within-plot level (Schmid et al. 2002). We also analyzed the data of each
phytometer species separately (results reported in the text without reference to a table). Finally, we
used a reduced data set of communities with only one functional group (*n* = 34 plots) to test if a
transplant species was more affected by its own functional group than by others (question c in the
Introduction). To do this the resident x transplant functional group interaction was decomposed into a “home versus away” contrast (and no contrasts among particular functional groups were made; see Table 3). Lastly, we illustrate the home versus away contrast with an equivalent of the relative-neighbour-effect of Markham and Chanway (1996), using the formula \((P_h - P_a) / \max(P_h, P_a)\), where \(P_h\) is performance (e.g. biomass) of phytometers in assemblies of their own functional group (home) and \(P_a\) is performance in assemblies of other functional groups (away) and \(\max(P_h, P_a)\) is the bigger of the two.
Results
Effect of species richness and functional richness

Four months after transplanting, on 25 August 2003, phytometers of *P. lanceolata* and *T. pratense* had matured and produced inflorescences in 78% and 85% of the plots, respectively, while *F. pratensis* and *K. arvensis* phytometers were still in their vegetative stage. The latter two species and *P. lanceolata* reached maturity in spring 2004, when *T. pratense* phytometers were mainly in the vegetative stage (and reached a second flowering peak in summer 2004). Except for plant height in *P. lanceolata* and *K. arvensis*, the measured morphological variables of phytometers were highly correlated with their aboveground biomass (Table 1), indicating that the latter is a good measure of overall phytometer performance.

<table>
<thead>
<tr>
<th>Plant Trait</th>
<th><em>F. pratense</em> (N=71)</th>
<th><em>P. lanceolata</em> (N=78)</th>
<th><em>K. arvensis</em> (N=76)</th>
<th><em>T. pratense</em> (N=68)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of leaves</td>
<td>0.919***</td>
<td>0.887***</td>
<td>0.855***</td>
<td>0.776***</td>
</tr>
<tr>
<td>Number of ramets</td>
<td>0.904***</td>
<td>-</td>
<td>-</td>
<td>0.866***</td>
</tr>
<tr>
<td>Height</td>
<td>0.467***</td>
<td>0.128**</td>
<td>0.228*</td>
<td>0.415***</td>
</tr>
<tr>
<td>Number of flowers</td>
<td>-</td>
<td>0.974***</td>
<td>-</td>
<td>0.938***</td>
</tr>
<tr>
<td>Relative growth rate</td>
<td>0.804***</td>
<td>0.610**</td>
<td>0.720***</td>
<td>0.680***</td>
</tr>
</tbody>
</table>

* P<0.05; ** P<0.01; *** P<0.001

At the first harvest in summer 2003, i.e. 4 months after transplanting, the performance of phytometer individuals was negatively affected by increasing species richness (reduced number of leaves or number of ramets, reduced biomass and reduced growth rate, Fig. 1a, c, d and Table 2). However, phytometer height was not affected and even increased with species richness in one of the phytometer species (*F. pratensis*; F1,70=9.30, p<0.01 in separate analysis), indicating that reduced light penetration in diverse communities may force transplants to grow tall in relation to their size especially *F. pratensis* (Fig. 1b, Table 2; see also lower correlations of plant height than of other variables with biomass in Table 1). The length of the leaves in *F. pratensis* also increased with
increasing species richness ($F_{1,73}=15.64$, $p<0.001$ in separate analysis). The influence of community species richness on phytometer performance varied among phytometer species, the herbs (*P. lanceolata* and *K. arvensis*) being more affected than the grass (*F. pratensis*) and the legume (*T. pratense*) (see species richness x phytometer species (TFG) interaction in Table 2). The negative effect of species richness on phytometer aboveground biomass was still significant in spring 2004, when the re-grown plants were harvested ($F_{1,73}=27.80$, $p<0.001$, Fig. 2b) but again plant height was not affected by species richness ($F_{1,73}=1.19$, $p<0.172$, Fig. 2a).

Functional richness had no effect on the performance of the phytometers after controlling for species richness in both seasons ($p>0.05$). However, if fitted before species richness, functional richness also had significant negative effects on all phytometer variables except height (aboveground plant biomass: $F_{1,67}=4.74$, $p=0.03$; plant height: $F_{1,67}=1.38$, $p=0.24$; number of leaves: $F_{1,67}=7.13$, $p=0.01$; growth rate: $F_{1,67}=6.12$, $p=0.01$; Fig. 1e-h); and in addition the species richness effects remained significant ($p<0.05$) except for plant height, as before. The pattern was the same in spring 2004 (Fig. 2c and d). This highlights the importance of species richness even if functional richness in statistical terms is “held constant”, i.e. the species richness effect remains negative within a particular level of functional richness.
FIG. 1 Effect of plant species richness (a-d) and functional group richness (e-h) on performance of four transplant phytometer species in the first season (summer 2003). Points and vertical bars are means and ± standard errors respectively. All panels use the legend in panel (a).
TABLE 2 Summary of analyses of variance of the performance of the four phytometer species in summer 2003. Residual d.f. are $a=225, b=219,$ and total $=308$ for number of leaves and plant height and $a=240, b=234$ and total $=327$ for growth rate. 1TFG (transplant functional group) is the phytometer species. Note that we used four alternative ways of forming contrasts for each, the composition term (GR = grasses, SH = small herbs, TH = tall herbs, LG = legumes), the TFG term (FP = *Festuca pratensis*, PL = *Plantago lanceolata*, KA = *Knautia arvensis*, TP = *Trifolium pratense*), the SR x TFG interaction (SR x FP, SR x PL, SR x KA, SR x TP), the composition x TFG interaction (GR x FP, SH x PL, TH x KA, LG x TP) and the SR x composition x TFG interaction (SR x GR x FP, SR x SH x PL, SR x TH x KA, SR x LG x TP). These contrasts are assembled in this table although only one at the time was fitted in a single model sequence.

<table>
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<tr>
<th>Source</th>
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<th>MS</th>
<th>F</th>
<th>Source</th>
<th>df</th>
<th>MS</th>
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<td>2.63</td>
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<td>GROWTH RATE</td>
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<tr>
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<td><strong>9.39</strong></td>
<td>14.84</td>
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<td>13.59***</td>
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<td><strong>4.28</strong>*</td>
<td>0.49</td>
<td><strong>4.30</strong>*</td>
<td>&lt;0.01</td>
<td><strong>3.07</strong>*</td>
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<td>13.59***</td>
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<td><strong>4.36</strong>*</td>
<td>0.48</td>
<td><strong>4.13</strong>*</td>
<td>&lt;0.01</td>
<td><strong>3.07</strong>*</td>
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<td>0.17</td>
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<td>&lt;0.01</td>
<td>0.46</td>
<td></td>
<td></td>
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<tr>
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<tr>
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<td>Composition</td>
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<tr>
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<td><strong>3.29</strong>*</td>
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</tbody>
</table>

**P < 0.05; **P < 0.01; ***P < 0.001.
Separate analyses showed that increasing species richness led to a significant reduction in number of inflorescences per plant in \textit{P. lanceolata} (F$_{1,70}=25.58$, \(p<0.001\)) and \textit{T. pratense} (F$_{1,69}=6.07$, \(p=0.01\)), the two phytometer species which flowered before the first harvest in August 2003 (Fig. 3a). The same negative effect of species richness on number of inflorescences per plant was observed in \textit{P. lanceolata} (F$_{1,69}=18.31$, \(p<0.001\)) and \textit{K. arvensis} (F$_{1,68}=18.88$, \(p<0.001\)) in spring 2004 (Fig. 3a). Again the effect of functional richness on the number of inflorescences was not significant after controlling for species richness but was highly significant if fitted first (summer 2003: \textit{P. lanceolata}; F$_{1,70}=11.15$, \(p<0.001\), \textit{T. pratense}; F$_{1,69}=6.13$, \(p=0.016\); spring 2004: \textit{P. lanceolata}; F$_{1,69}=12.04$, \(p<0.001\), \textit{K. arvensis}; F$_{1,68}=14.71$, \(p<0.001\); Fig. 3b), with the effect of species richness fitted afterwards again remaining significant (\(p<0.01\)).

FIG. 2 Effect of plant species richness (a-b) and functional group richness (c-d) on performance of four transplant phytometer species in second season (spring 2004). Points and vertical bars are means and ± standard errors respectively. All panels use the legend in panel (a).
FIG. 3 Effect of plant species richness (a) and functional groups richness (b) on number of inflorescences on introduced phytometer species in summer 2003 (solid lines) and spring 2004 (broken lines). Points and vertical bars are means and ± standard errors respectively.

Effects of the presence of particular functional groups

While the presence of grasses or of legumes in the communities had significant overall effects on phytometers, this was not the case for the presence of the other two functional groups (Table 2). Grasses significantly reduced number of modules (number of leaves or number of ramets), aboveground biomass, and growth rate of all the phytometer species as well as number of inflorescences in *P. lanceolata* in summer 2003 ($F_{1,68}=5.66$, $p=0.02$) and spring 2004 ($F_{1,67}=7.56$, $p=0.008$). The presence of legumes had an overall significant positive effect on the performance of the phytometer species (Table 2). However, the separate analysis for each phytometer showed that the presence of legumes actually reduced aboveground biomass of the legume phytometer, *T. pratense*, at least in the spring 2004 ($F_{1,61}=8.97$, $p=0.004$), which confirms observations made in a legume seeding experiment carried out with a similar species pool (Turnbull et al., submitted). The negative effect of legume presence on the legume phytometer as opposed to a positive effect on the other phytometers can also be seen by the significant LG x TP interaction in Table 2 and by comparing the positions of lines with open and closed symbols in the last row of panels in Figure 4 and 5.
FIG. 4 Effect of plant species richness and presence/absence of different functional groups on plant mass in four transplants phytometer species in the first season (summer 2003). Columns represent phytometers species *F. pratensis*, *P. lanceolata*, *K. arvensis* and *T. pratense* from left to right and rows represent presence/absence of grasses, small-herbs, tall-herbs and legumes from top to bottom. Closed and open symbols for presence and absence of functional groups in the resident communities, respectively. For example, the second panel in the first row shows the response of *P. lanceolata* to species richness in the plots containing grasses (closed symbols) and in plots without grasses (open symbols). Vertical bars are means ±SE.

There were no significant interactions between species richness and the presence of particular functional groups in the communities on phytometer performance and thus competitive suppression. We mention this explicitly because such interactions could be expected if not only the presence but also the sowing proportion of a functional group would be important for invasion resistance for
example (the proportion of the functional group on average increases with decreasing species richness in the plots where it is present).
FIG. 5 Effect of plant species richness and presence/absence of different functional groups on plant mass in four transplants phytometer species in the second season (spring 2004). Columns represent phytometers species *F. pratensis*, *P. lanceolata*, *K. arvensis* and *T. pratense* from left to right and rows represent presence/absence of grasses, small-herbs, tall-herbs and legumes from top to bottom. Closed and open symbols for presence and absence of functional groups in the resident communities respectively. Vertical bars are means ±SE.

In August 2003, community leaf area index (LAI) increased with increasing species richness ($F_{1,68}=6.42$, $p=0.014$). Functional richness had no effect on LAI; neither did the presence of any of the functional groups, suggesting that other resource use such as belowground may be an important factor in the observed high competitive suppression of phytometers in communities with grasses. As a covariate, LAI had a significant negative effect on number of leaves, height, and growth rate of the
phytometers (p<0.05) but not on aboveground biomass. A significant species richness effect could not be accounted for by LAI, as it (species richness) remained significant in all response variables.

**Effects of the functional group of the phytometer species**

As suggested by hypothesis (c) in the Introduction, comparing the competitive suppression of introduced species between communities with different functional groups is not the same as looking at the success of the introduced functional groups. In the first case (hypotheses a, b in the Introduction), the panels in Fig. 4 and 5 are compared row-wise, in the second case they are compared column-wise. If the two views are combined, we can look at performance of introduced species in assemblages containing only species of its functional group versus performance in assemblages without of its functional groups, i.e. “home-vs.-away” (see e.g. Joshi et al. 2001), for which our hypothesis (c) predicts a particularly strong negative effect (i.e. the left to right downward diagonal in Fig. 4 and 5 but only with single-functional-group assemblages).

The single-functional-group assemblages did not differ in their effect on overall performance of the phytometers (number of modules (leaves or ramets), aboveground biomass, growth rate, Table 3). However, the height of the phytometers significantly differed among these communities: it increased from grass < small-herb < tall-herb < legume communities, indicating that with regard to light competition the order was just reversed in comparison with competition for soil resources. Overall, the two herb phytometer species showed the smallest response to differences between mono-functional communities of the four different types, whereas the grass (*F. pratensis*) and the legume (*T. pratense*) phytometer were more affected by these differences (Fig. 5). A contrast between monocultures versus multi-species assemblages containing one functional group showed that the number of modules (leaves or ramets), aboveground biomass and growth rate of the phytometers was significantly lower in the latter (Table 3). This reinforces the statistical observation made above that competitive suppression increases with species richness of a community even if functional richness is held constant, in this case at the lowest level.
TABLE 3 Summary of analyses of variance of summer 2003 data for home-vs.-away effect on the four phytometer species using plots with resident communities consisting of species from only one functional group.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Biomass</th>
<th>F</th>
<th>Leaves</th>
<th>F</th>
<th>Height</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>3</td>
<td>11.63</td>
<td>4.09*</td>
<td>2.33</td>
<td>2.08</td>
<td>553.61</td>
<td>8.43</td>
</tr>
<tr>
<td>Resident Functional Group (RFG)</td>
<td>3</td>
<td>3.11</td>
<td>1.09</td>
<td>0.26</td>
<td>0.23</td>
<td>962.34</td>
<td>14.66***</td>
</tr>
<tr>
<td>Monoculture vs. Mixture (Mono)</td>
<td>1</td>
<td>22.02</td>
<td>7.75*</td>
<td>9.16</td>
<td>8.19**</td>
<td>49.64</td>
<td>0.76</td>
</tr>
<tr>
<td>RFG x Mono</td>
<td>3</td>
<td>0.53</td>
<td>0.19</td>
<td>0.06</td>
<td>0.06</td>
<td>6.44</td>
<td>0.10</td>
</tr>
<tr>
<td>Composition</td>
<td>23</td>
<td>2.84</td>
<td>4.19***</td>
<td>1.12</td>
<td>5.61***</td>
<td>65.66</td>
<td>1.68*</td>
</tr>
<tr>
<td>Phytometer species (TFG)</td>
<td>3</td>
<td>3.36</td>
<td>4.95**</td>
<td>5.99</td>
<td>30.08***</td>
<td>1818.79</td>
<td>46.65***</td>
</tr>
<tr>
<td>Home vs. Away (RFG x TFG main diag.)</td>
<td>1</td>
<td>4.25</td>
<td>6.26*</td>
<td>1.59</td>
<td>7.98**</td>
<td>169.93</td>
<td>4.36*</td>
</tr>
<tr>
<td>RFG x TFG (residual interact.)</td>
<td>8</td>
<td>0.84</td>
<td>1.24</td>
<td>0.22</td>
<td>1.13</td>
<td>191.49</td>
<td>4.91***</td>
</tr>
<tr>
<td>Phytometer species x Mono</td>
<td>3</td>
<td>2.47</td>
<td>3.64*</td>
<td>0.28</td>
<td>1.40</td>
<td>42.37</td>
<td>1.09</td>
</tr>
<tr>
<td>Home vs. Away x Mono</td>
<td>1</td>
<td>0.19</td>
<td>0.28</td>
<td>0.38</td>
<td>1.89</td>
<td>8.51</td>
<td>0.22</td>
</tr>
<tr>
<td>Residual</td>
<td>79</td>
<td>0.68</td>
<td>0.20</td>
<td>0.20</td>
<td></td>
<td>38.99</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>128</td>
<td>1.68</td>
<td>0.63</td>
<td></td>
<td></td>
<td>128.91</td>
<td></td>
</tr>
</tbody>
</table>

* P < 0.05; ** P < 0.01; *** P < 0.001.
The analyses of interactions between the functional group of resident community and the functional group of the phytometers (RFG x TFG) showed that except for plant height, these interactions were almost entirely due to the main diagonal, i.e. home-vs.-away effects (Table 3). As predicted, the phytometers had significantly lower performance when transplanted into communities consisting of the same rather than a different functional group (neighbor effects of away-functional groups were weaker than of home-functional group, i.e. negative bars in Fig. 6). The significant residual RFG x TFG interaction for plant height indicates that here the home effect is not as clear-cut because *T. pratense* phytometers were shortest in grass and small herb mono-functional group communities (Fig. 6). The four phytometer species responded differentially to mono-specific versus multi-species single-functional-group assemblages (Table 3): the biomass of *P. lanceolata* declined from 5.3 g in mono-specific to 0.9 g in multi-species single-functional-group assemblages whereas the other three phytometer species showed little reduction in aboveground biomass. The home-disadvantage was similar in mono-specific and multi-species single-functional-group assemblages (interaction home x mono not significant in Table 3).
FIG. 6 Performance of the phytometers in single-functional-group assemblages of grasses (GR), small herbs (SH), tall herbs (TH) and legumes (LG) relative to performance in mono-functional group assemblages similar to the phytometer. Negative values indicate that resident species belonging to functional group different from phytometers were less inhibitive, while positive values indicate opposite.

**Discussion**

Our results demonstrate increasing niche pre-emption by high diversity, supporting that high diversity of plant communities enhances competitive suppression of newly arriving species in processes of invasion or colonisation. With perhaps the most balanced design in terms of species and functional diversity, we were able to demonstrate that species richness is a better indicator niche pre-emption than functional group richness, contrary to recent articles which supports the latter (e.g. Diaz and Cabido 2001). Two factors may explain our result. First, in our experiment species richness had a much wider spectrum (six levels from 60 species) than functional richness (four levels from four groups). Second, the effects of functional diversity on the different phytometer species were probably cancelling each other out to some extent because of the balanced design in which each functional group was represented equally among the four phytometer species and among the resident plant.
communities. Using microcosms that reflected the observed local non-random species loss in grassland, Zavaleta and Hulvey (2004) found that species richness enhanced resistance to invasive species contrary to the study by Dukes (2001) who assumed random species loss in his experiment. Our experiment shows that species richness increased competitive suppression of newly arriving species even within plant assemblages consisting of a single functional group despite random species loss.

In our experimental plots, soil nitrogen decreases with species richness (Oelmann et al. submitted) while aboveground biomass and leaf area index (Roscher et al. 2005) increases suggesting that niche pre-emption drives invasion resistance in diverse communities. Functional group richness, which had smaller effects on competitive suppression of phytometers, also had smaller effects on LAI ($F_{1,68}=3.37$, $p=0.071$). A further reason that the relationship between functional diversity and suppression of phytometers was weak in our study could be due to counteracting effects of different functional groups on resources. For example, our results indicate that legumes can enhance establishment of new arriving species by increasing soil nitrogen while grasses deplete this resource. This supports assertion in Crawley (1997) that many vascular plants colonialists are nitrogen fixing species help build up nitrogen in soil pool. Thus, the weak influence of functional group richness on suppression of phytometers appears to be correlated with a weak effect on resource pre-emption, indirectly supporting resource pre-emption as mechanism of invasion resistance in our experiment. Stronger effects of functional group richness on invasion resistance have been found in cases where effects on resource pre-emption were also more likely (Symstad 2000, Prieur-Richard 2000).

Our results suggest that, with regard to functional rather than species richness, effects of compositional and identity of species may be more important than effects pure numbers (Schmid et al. 2002). Thus, competitive suppression of particular phytometer species was strongly affected by the presence or absence of particular functional groups in the plant assemblages. Competitive suppression of all phytometers was strongly enhanced by presence grasses, which probably most strongly reduced soil resources in the experimental plant communities. Due to their extensive root systems, grasses are efficient in taking up resources from the upper soil layers. Other studies have also reported grasses as a keystone functional group against invasion (Dukes 2002, Prieur-Richard et al. 2002). Crawley et al.
(1999) found that an assembly of 80 herbaceous species was more vulnerable to invasion than assemblies composed of 1, 2 or 4 grass species. In our experimental assemblies, it also appeared that non-legume herbs had no general effect on suppression of the phytometers and they did not affect resource levels (e.g. LAI: small herbs, F_{1,69}=1.68, p=0.20; tall herbs F_{1,69}=1.39, p=0.24) although they in fact rendered the assemblies more resistant to establishment of herbs. This indicates that high niche overlap between newly arriving species and local species can reduce chances of an invasion, rate of colonisation or even success of restoration. This goes in line with results from Fargione et al. (2003) who could show that resident species more strongly inhibit new invading species from their own functional group due to similar patterns of resource use. In the study by Xu et al. (2004), the presence of a functionally similar herb in the resident community increased resistance to invasion by Alligator weed (*Alternanthera philoxeroides*), which was also attributed to niche overlap.

In contrast to grasses, legumes seem to facilitate establishment of new species by increasing soil nitrogen. It is now well documented that legumes can promote invasion in low nitrogen ecosystems (Yelenik et al. 2004 and reference therein) and colonisation process by adding nitrogen to the soil. A related effect of legumes could be reducing competition for soil nitrogen. Data on possible uptake of nitrogen fixed by the legumes (δ^{15}N values and N concentrations in tissues of the phytometers) from our experiment indicate that, the transplants actually benefited from nitrogen added by legumes (Temperton et al submitted). However, we cannot rule out that the legumes also enhanced suppression of phytometer by facilitating the other resident species through soil enrichment. Additionally, observation that legume monocultures are more resistant to invasion by legumes (Turnbull et al., submitted) and our results that *T. pratense* was more inhibited in legumes-only assemblies indicate that resident legumes pre-empt other resources that limit legumes, most likely phosphorus, water and light (Vitousek and Howarth 1991). This is consistent with high niche overlap along other resource-use axis between resident legumes and newly arriving legume species, and further supports niche pre-emption as a mechanism of invasion resistance.
Acknowledgement
We thank Christina Fischer, Anne Froehlich and Anja Dassler for their assistance in the field and lab. We are also grateful to the gardeners and numerous students who assisted in weeding campaigns. Ernst-Detlef Schulze guided the development of the Jena Experiment and of this project. This research was supported by grants from the German Science Foundation (grant no. FOR 456 - WE 2618/6-1 to WWW and BS) and the Swiss National Science Foundation (grant no. 31–65224.01 to BS) and by the Friedrich-Schiller-University of Jena and the Max-Planck-Institute for Biogeochemistry, Jena.
References


Chapter 6

General Discussion
Introduction

So far, many biodiversity experiments have been measuring ecosystem properties in an aggregated way. In contrast, this study makes an attempt to gain more insight into the ecological phenomenon behind the effects of biodiversity on ecosystem functioning, by also focusing on the population level, the species level and the level of the individual plant.

The results from biodiversity studies using synthetic plant communities have been criticized to be biased by experimental factors (e.g. Schmid et al. 2002a, Lepš 2004, Raffaelli 2004). Thus, I tested some major experimental factors regarding their importance for the relationship between species richness and productivity.

Experimental factors

Previous biodiversity experiments varied in their range of plot sizes from less than 1 to more than 100 m². Thus, the experimental effects might have been confounded with scale effects (Schmid et al. 2002a). Scale effects have been often related to the increasing amount of edge vs. center parts with decreasing plot size (see e.g. Groppe et al. 2001; Fahring 2003). Therefore biodiversity effects in experimental plots might be influenced by the surrounding environment, increasing environmental heterogeneity with increasing plot size (Schmitz et al. 2002), biotic factors (e.g. population size), or other factors. In this study, the comparison of two experiments with the same species pool but different plot sizes (large plots of 20 x 20 m vs. small plots of 3.5 x 3.5 m) resulted in no significant difference of biomass production. Thus, results of small-scale experiments are not biased by the small plot size, at least not in short term of our experiment. This shows that scaling up findings from small-scale experiments is appropriate and thus should be taken seriously.

Another experimental factor in biodiversity studies which has been criticized is the simulation of random species loss (Lêps 2004, Raffaelli 2004). Most biodiversity experiments which found that plant productivity declines with reduced species richness examined the influence of random species loss on ecosystem functioning (Schmid et al. 2002b, Hooper 2005). Using plots of our biodiversity experiment with simulated random species loss, we removed the less abundant half of the original species number after 2 years. Thus, we superimposed a removal experiment with non-random species
loss. The resulting positive log richness–productivity relationship, however, had the same slope as in the control plots with random species loss. Therefore, I conclude that random species loss in biodiversity experiments is a good simulation of species loss in natural ecosystems.

Evenness is another factor which, contrary to natural plant communities, is usually maximized by sowing equal proportions of the species in biodiversity experiments. The manipulation of evenness in our study, however, did not affect the positive biodiversity–productivity relationship. Different species abundance distributions converged by the end of the experiment so that all resulting communities were not at maximum evenness. The experimental plant communities showed in fact rank-dominance patterns similar to semi-natural grasslands (Roscher et al. 2005). Thus plant communities in biodiversity experiments which are sown at maximum evenness have a more realistic species abundance distribution than previously thought (e.g. Houston 1997, Grime 1998, Mulder et al. 2004, Wilsey & Polley 2004). This suggests that varying species richness only is probably a sufficient manipulation to study general patterns of biodiversity–ecosystem functioning relationships in experiments and that other designs may not be anymore realistic.

**Community level**

All experiments described here indicated a positive biodiversity–ecosystem functioning relationship at the community level. The overall finding that increasing species richness increased biomass production independent of other experimental manipulations provides additional evidence for the assumption of better resource-use efficiency in species-rich communities. The manipulation of sowing density in one of our experiments indicated that increasing plant species richness had a positive effect on the realized density of individuals in the community. The individuals of different species in species-rich communities must have used local resources more efficiently. This suggests a mechanism for complementarity effects in biodiversity experiments (Naeem et al. 1994, Tilman, Lehmann & Thomson 1997, Loreau 2000, Silvertown 2004). The same result was obtained in a phytometer-experiment where higher plant diversity lowered the success of newly arriving individuals in the community. Thus, species-rich communities should have less empty niche space due to higher
resource-use efficiency, which again suggests the importance of complementarity effects. The positive effect of realized evenness on community biomass production within a species-richness level also suggests that complementarity effects have contributed to the positive species richness–biomass production relationship. This was analog to the removal experiment, where evenness was significantly increased in treated plots without the less abundant half of the species of the original plots. The resulting increase in biomass productivity of the treatment communities was at least partly caused by the increased evenness among selected dominants with potentially increased complementarity.

In contrast, realized evenness decreased while biomass production increased if the community contained more species. Thus, higher biomass production was reached at lower levels of realized evenness if species richness was increased. This might be explained with the finding that complementarity effects reach a maximum at lower diversity levels, whereas selection effects increase linearly with species richness.

**Population and species level**

Manipulating population densities showed a negative correlation between realized density and community biomass at low species richness levels. This indicates that some degree of community-level thinning may allow higher biomass production. This would be in accordance with the self-thinning rule in single-species stands (Harper 1977). Extrapolating the constant-yield and self-thinning rules form single- to multi-species stands (Bazzaz & Harper 1976, He et al. 2005) would also lead to the prediction that community-level thinning should remove populations of subordinate species first as found in the removal experiment. Thus, a higher sowing density should lead to faster gains of dominant species. Varying initial community density, however, did not affect realized evenness in our communities. Therefore, the self-thinning rule cannot be directly extrapolated to multispecies communities, because the effects of community-level thinning are influenced by species identities. This was also one result in the removal experiment, where the “extinction” probabilities were species-specific: some species were always removed, because of low performance, while other species were never removed if they were present in the plot.
Individual plant level

By using individual plants as native test invaders, we could show that plant diversity enhances competitive suppression of those new invaders. In addition, the overall performance of the test invaders decreased with increasing species richness. This suggests that species-rich communities contain less empty niches which can be occupied by further individuals. Thus, invasion resistance of experimental plant communities is related to the degree of niche overlap between resident species and invaders. Introducing a test plant into a community containing resident species of only one functional group had also shown that the test plant belonging to the same functional group as the resident species was mostly inhibited. This again supports the idea of high niche overlap between resident species and invaders of the same functional group.

In contrast, the better performance of test plants in communities with legumes corresponded with findings that invasive plants benefit form nitrogen fixed by those resident legumes (Temperton et al. 2006). Actively fixing atmospheric nitrogen makes legumes independent of soil-nitrogen pools. Thus, the competition for soil-nitrogen is reduced in communities containing legumes. Other studies are reporting that the presence of legumes increases invasion resistance. In those studies, the negative effect of legumes on invasive plants usually correlates with the effect of legumes on aboveground resources, such as light (Hector et al. 2001, Fargione et al. 2003). Consequently, legumes might reduce invasion in fertile soils, while they promote invasion in poor soils.
References


Summary

Biodiversity experiments worldwide provide increasing evidence that human-induced species loss affects ecosystem functioning negatively. This is supported by “The Jena Experiment” (The role of biodiversity for element cycling and trophic interactions – an experimental approach in a grassland community), a large integrated biodiversity project in Jena, Germany. In this project, several studies were conducted on grassland assemblages of different species and functional diversity established in 2002. Analyzing the effect of biodiversity on ecosystem functioning from the individual plant to the community level, the research focused on underlying plant population processes. The results confirm the assumed negative impact of species loss on ecosystem functioning and show that it is independent of spatial scale and planting density and evenness.

Chapter 2 compares experiments with different species pools at two different spatial scales. One study had a pool of 60 plant species that ranged from dominant to subordinate competitors on large 20 x 20 m and small 3.5 x 3.5 m plots (main experiment), and one had a pool of nine potentially dominant species on small 3.5 x 3.5 m plots (dominance experiment).

The same positive species richness–aboveground productivity relationships were found at both scales in the main experiment. This result suggests that scaling up, at least over the short term, is appropriate in interpreting the implications of such experiments for larger-scale patterns. However, the species richness–productivity relationship was more pronounced in the dominance experiment (46.7 % and 82.6 % yield increase compared to mean monoculture, respectively). Additionally, transgressive overyielding occurred more frequently in the dominance experiment (67.7 % of cases) than in the main experiment (23.4 % of cases). Additive-partitioning and relative-yield-total analyses showed that both complementarity and selection effects contributed to the positive net biodiversity effect. The complementarity effect, however, seems to operate most strongly between dominant species and at low species richness, where it is the prominent driver for the observed increase in ecosystem functioning with increasing plant diversity.
Chapter 3 is concerned with density and evenness in plant communities, which are usually not manipulated in biodiversity experiments. For this experiment I integrated density and evenness treatments in the existing random species loss design with five species richness levels as used in the main experiment. This was done by using high and low total planting densities (2000 or 1000 seeds/m$^2$) with both high (equal proportions of seed of each species were sown) and low (seed of species of one functional group dominated) evenness treatments. The analysis of the data form all three years of the experiment showed that aboveground plant biomass increased linearly with the logarithm of species richness in all density and evenness treatments. Furthermore, realized density was higher and realized evenness was lower for high species richness treatments in all density and evenness treatments. For given richness levels, the different density and evenness treatments converged over time to similar levels of biomass production, realized density, and realized evenness. The remaining variation in realized density and realized evenness showed a negative and positive correlation respectively with the remaining variation in biomass production. The results suggest that species richness had a much larger influence on biomass production and population dynamics than did initial density or initial evenness. The study also demonstrates that species abundance distributions rapidly equilibrate in experimental communities, independent of initial density and evenness conditions. Thus, it is sufficient to manipulate plant species richness if effects on aggregated ecosystem variables are addressed in biodiversity experiments.

Chapter 4. Biodiversity experiments such as “The Jena Experiment” which assemble communities at random have been criticized because all species are assumed to have the same probability of extinction. In a split-plot experiment, I removed the less abundant half of the species from the randomly assembled experimental grassland communities that formed the diversity gradient. Species relative abundances and their probability of being removed were highly species-specific.

Aboveground biomass production in the randomly assembled communities increased linearly with the logarithm of species richness, as in other experiments. Removing the less abundant species,
however, slightly increased community biomass production due to increased evenness and over-compensating increases in the per-species yields of the remaining dominants. Nevertheless, the diversity gradient formed from randomly assembled communities and from communities with the less abundant species removed had the same slope for productivity regressed against species richness. This suggests that, at least in the short term, non-random extinction of less-abundant plant species has no negative effects on community productivity. However, in accordance with the results of chapter 2, this study also showed that in communities formed from only dominant species productivity is positively related to increasing diversity.

Chapter 5 provides a test of the hypothesis that successful establishment of new species invading existing plant communities decreases with increasing diversity. This prediction, which has been supported by experimental studies, is based on the proposed mechanism that diverse plant communities are less vulnerable to species invasions because of less empty niche space. In this study, native species were used as transplant phytometers. That is, a grass (*Festuca pratensis*), a small herb (*Plantago lanceolata*), a tall herb (*Knautia arvensis*) and a legume (*Trifolium pratense*) were transplanted into plots within the five species richness levels of “The Jena Experiment”. Since phytometer density was low in treated plots, the effects of the phytometers on the resident community were considered negligible.

Consistent with the prediction, the overall performance of the transplants decreased with increasing species richness. In particular, grasses showed a strongly negative effect on the performance of the transplants, whereas small and tall herbs had neutral and legumes positive effects. These findings are reflected in the levels of belowground resources and to some extent in the communities’ leaf area index, indicating that niche pre-emption inhibits establishments of new species. Assemblages containing only one functional group were more inhibitive to transplants of their own functional group, supporting that high niche overlap among residents and newly transplanted species enhances inhibition of the latter.
Zusammenfassung


Kapitel 2 vergleicht Experimente mit unterschiedlichen Artenzusammensetzungen und verschiedenen Flächengrössen. Die eine Studie basiert auf einem Artenpool von 60 Pflanzenarten – dominante wie subdominante Arten – auf einer Fläche von 20 x 20 m, sowie 3.5 x 3.5 m (Hauptexperiment). Demgegenüber steht ein Artenpool von 9 potenziell dominanten Pflanzenarten auf 3.5 x 3.5 m Versuchsparzellen (Dominanzexperiment). Beide Experimente zeigen den gleichen positiven Zusammenhang zwischen Artenzahl und oberirdischer Produktivität. Die Ergebnisse bestätigen, dass eine Extrapolation von kleinen Flächen auf grössere Einheiten, zumindest kurzfristig, ein korrektes Mittel der Übertragung experimenteller Daten auf die Verhältnisse in einem grösseren räumlichen Zusammenhang darstellt. Im Dominanzexperiment war der Zusammenhang zwischen Artenzahl und Produktivität jedoch deutlicher ausgeprägt (46.7 % bzw. 82.6 % Erntezuwachs im Vergleich zu der Monokultur). Zusätzlich trat „Transgressive Overyielding“ (überdurchschnittlicher Erntezuwachs im Vergleich zu den Monokulturernnten) häufiger im Dominanzexperiment (67.7 % der Fälle), als im Hauptexperiment (23.4 % der Fälle) auf. „Additive-Partitioning-“ und „Relative-YieldTotal-“Analysen zeigten, dass Komplementaritäts- und Selektionseffekte zu dem positiven Netto-Biodiversitätseffekt beitragen. Der Komplementaritätsfekt scheint jedoch im Dominanzexperiment und bei geringen Artenzahlen deutlicher ausgeprägt zu sein, wo er den wesentlichen Antrieb für den
beobachteten Anstieg der Ökosystemfunktionen im Zusammenhang mit einem Anstieg der Artenzahlen darstellt.


*Kapitel 4.* Biodiversitätsexperimente wie das „Jena Experiment“ werden wegen der zufälligen Artenzusammensetzung auf den Versuchsflächen kritisiert, da man damit voraussetzt, dass jede Art die gleiche Chance hat, auszusterben. In dieser Studie wurde jedoch von den experimentell nach dem Zufallsprinzip zusammengesetzten Pflanzengemeinschaften, die weniger häufige Hälfte der Arten
entfernt. Dabei stellte sich heraus, dass die relative Häufigkeit und die Wahrscheinlichkeit entfernt zu werden, sehr artabhängig war.


In Übereinstimmung mit der oben genannten Hypothese, nimmt die Leistung der Phytometer in den Parzellen mit zunehmender Artenzahl ab. Insbesondere zeigen die Gräser einen sehr negativen Effekt auf die Leistung der Phytometer. Demgegenüber haben die kleinen und grossen Kräuter keinen
Literature


Acknowledgements

As part of “The Jena Experiment” this research was supported by grants from the German Science Foundation (grant no. FOR 456 - WE 2618/6-1 to WWW and BS) and the Swiss National Science Foundation (grant no. 31–65224.01 to BS), and by the Friedrich Schiller University of Jena, the Max Planck Society (Max-Planck-Institute for Biogeochemistry, Jena) and the Institute of Environmental Sciences at the University of Zurich. Special thanks to Ernst-Detlef Schulze who guided the development of the Jena Experiment and provided me an office at the Max-Planck-Institute for Biogeochemistry. I am grateful to the many people who helped with set-up and maintenance of the plots, particularly the gardeners S. Eismann, S. Junghans, B. Lenk, H. Scheffler and U. Wehmeier. I also thank the many student helpers who worked during the weeding campaigns, assisted in the biomass harvest and data collection, especially the TP-10 team: A. Gminder, A. Fröhlich, J. Trettin, A. Dassler, J. Dittmann, M. Geuther, L. Merbold, M. Bärwolff, C. Fischer, and V. Höntsch.

Very special thanks to Katja Corcoran, Jörg Zehnder, my colleagues Peter M. Mwangi and Luca Wacker for their support during the whole time of my dissertation. I also thank my friends in Jena and Zürich for their encouragement; especially Yvonne Kreutziger, Beat Stutzer and all the people of Suite55. For help with linguistic problems I want to thank Bob Doren, Julian Käser and Alexandra Bernoulli.

Finally I want to thank my advisers Bernhard Schmid, Wolfgang W. Weisser, Andy Hector and Michael Scherer-Lorenzen for their support and the great working atmosphere (special thanks to M. S.-L. for his good advice in the starting phase of the field-experiment).

Last but not least thank you to Bill Platt who encouraged me to participate in this great research project and for all I have learned during the time I worked with him.
### Curriculum vitae

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