Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland

M. C. Caldeira, A. Hector, M. Loreau and J. S. Pereira

We studied the temporal variability and resistance to perturbation of the biomass production of grassland communities from an experimental diversity gradient (the Portuguese BIODEPTH project site). With increasing species richness relative temporal variability (CV) of plant populations increased but that of communities decreased, supporting the insurance hypothesis and related theory. Species-rich communities were more productive than species-poor communities in all three years although a natural climatic perturbation in the third year (frequent frost and low precipitation) caused an overall decrease in biomass production. Resistance to this perturbation was constant across the experimental species richness gradient in relative terms, supporting a similar response from the Swiss BIODEPTH experiment. The positive biomass response was generated by different combinations of the complementarity and selection effects in different years. Complementarity effects were positive across mixtures on average in all three years and positively related to diversity in one season. The complementarity effect declined following perturbation in line with total biomass but, counter to predictions, in relative terms overyielding was maintained in all years. Selection effects were positively related to diversity in one year and negative overall in the other two years. The response to perturbation varied among species and for the same species growing in monoculture and mixture, but following the frost communities were more strongly dominated by species with lower monoculture biomass and the selection effect was more negative. In total, our results support previous findings of a positive relationship between diversity and productivity and between diversity and the temporal stability of production, but of no effect of diversity on the resistance to perturbation. We demonstrate for the first time that the relative strength of overyielding remained constant during an exceptional natural environmental perturbation.

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The continuing loss of biodiversity has generated concern over the consequences for the functioning of ecosystems and renewed interest in the relationship between diversity and stability (McCann 2000, Cottingham et al. 2001, Loreau et al. 2002). Stability can be viewed in two main ways: in terms of long term temporal variability and in terms of short term resistance and resilience to environmental perturbations (Pfisterer and Schmid 2002). Considering long term temporal variability, the insurance hypothesis (Yachi and Loreau 1999) and related ideas of portfolio effects (Tilman et al. 1998, Lehman and Tilman 2000) and

statistical averaging (Doak et al. 1998) predict that asynchronous responses of different species to environmental fluctuations could lead to more stable aggregate ecosystem properties in diverse systems (Cottingham et al. 2001, Loreau et al. 2002). More diverse systems could also be more resistant to perturbation if they have a greater chance of containing a species with resistance to that perturbation.

Several empirical studies have shown some evidence that the temporal stability of various ecosystem properties increases with increasing diversity (McNaughton 1985, Tilman and Downing 1994, Tilman 1996, McGrady-Steed et al. 1997, Morin and McGrady-Steed 2004, Pfisterer et al. 2004). For example, Tilman and Downing (1994) and Tilman (1996) showed that increased species richness increased community temporal stability but decreased population stability. In this work, however, species richness was not directly controlled but varied in response to nitrogen addition. While most results were robust to the incorporation of potential confounding factors into the analyses (e.g. root:shoot ratios, Tilman 1996), these other factors complicate the interpretation of this study. There have been fewer studies on the relationship between diversity and stability with direct manipulation of species richness. McGrady-Steed et al. (1997) manipulated protist diversity directly and showed that the variation in CO_2 flux declined with increasing diversity in aquatic microcosms. This effect, however, was due to decreased variation among communities, rather than decreased temporal variation within communities (Fukami et al. 2001, Morin and McGrady-Steed 2004). More recently, Pfisterer et al. (2004) showed greater relative temporal stability of species-rich communities from an experimental diversity gradient (the Swiss site of the BIODEPTH project) in terms of their coefficient of variation.

There have been few studies on the relationship between diversity and resistance and resilience that have directly experimentally manipulated species richness. In a recent study from the Swiss BIODEPTH site, Pfisterer and Schmid (2002) demonstrated that after a simulated drought imposed on artificial grassland communities the species-rich systems showed a greater decline in (absolute) biomass than the species-poor systems, although the relationship between diversity and biomass production remained positive. The more diverse communities were therefore less resistant to perturbation, counter to predictions. However, resistance was measured as the difference of the slope of the relationship between species richness and biomass production (absolute scale) before and after perturbation. This deviates from the more traditional definition of resistance (Pimm 1991), i.e. the ratio of biomass under the perturbation and biomass before the perturbation (relative scale). In the latter, the null hypothesis predicts

that there is no diversity effect. By this view, in our grassland experiments each plant individual would be expected to suffer equally from the perturbation in relative terms and this ratio should not change with diversity. An equivalent way of testing this null hypothesis is to use log-transformed productivity data and test whether the difference between the productivity–diversity relationships remains constant with diversity, i.e. whether the slopes are identical during and before perturbation.

We tested the diversity–stability hypothesis in experimental communities of Mediterranean grassland plants using this approach. Our study is novel in that it combines a direct experimental manipulation of plant diversity with a natural climatic perturbation: the transition between the second and third year of the experiment was marked by a season, which was drier than usual and showed exceptional levels of winter frost. Overall biomass production declined only slightly from year 1 to 2 but dramatically in year 3 (by 83% compared to the average of the first two years). At the same time, the maximum number of species in biomass sub-samples decreased from an average of 8 species for the richest plots in the first two years to 4 species in the third year (note that species present in the biomass sub-samples can underestimate whole-plot diversity). We use this combination of experimental communities and natural perturbation to examine several aspects of stability. First, we used the coefficient of variation to study the relationship between diversity and temporal variability of biomass production during the three years of the experiment. We distinguish temporal variability of aggregate community and ecosystem properties from population properties following theory that predicts that community variability should decline with increasing species richness while population variability should increase. Second, we used the difference of the slope of the relationship between species richness and biomass production before (year 2 harvest) and under the perturbation (year 3; Pfisterer and Schmid 2002) but with log-transformed data. Pfisterer and Schmid (2002) suggest that the most likely explanation for their results is a decrease in complementarity due to drought, although they were not able to test this hypothesis. The third part of our study uses the additive partitioning equation (Loreau and Hector 2001) and related relative measures to examine how the stability of biomass production to the weather perturbation was determined by changes in the mechanisms driving the positive diversity-productivity relationships. These methods assesses whether increases in some species in mixtures are balanced by declines in others or whether there is evidence for complementarity (resource partitioning), positive (facilitation) or negative (physical or chemical interference) interactions that shift the total yield away

from the null prediction which assumes none of these additional interactions (Hector et al. 2002).

Material and methods

Study site and Experimental design

Our study was part of the BIODEPTH project (Hector et al. 1999, 2005, Spehn et al. 2005) and details of design are given in Caldeira et al. (2001). In 1996, an experimental gradient of species richness (1, 2, 4, 8 and 14 herbaceous species) was established and responses of ecosystem processes were monitored for three years (year 1: 1996/1997; year 2: 1997/1998; year 3: 1998/1999). All species were established in monoculture. We used a complete randomised design to establish 56 plots of 2×2 m. To separate the effects of species composition from those of diversity, each level of species richness had different assemblages of species (mixtures) chosen randomly from the local pool of grassland species constrained to produce certain functional group combinations (e.g. all the polycultures contained at least one grass). Species used for plot establishment were: *Avena sativa*, *Phalaris brachystachys*, *Holcus lanatus*, *Dactylis glomerata*, *Lolium multiflorum* (grasses); *Ornithopus compressus*, *Trifolium subterraneum*, *Vicia sativa* (nitrogen-fixing legumes); *Plantago lanceolata*, *Rumex pulcher*, *Conyza albida*, *Silene gallica*, *Misopates orontium*, *Torilis arvensis* (herbs).

The climate at this site is of the Mediterranean type. Average rainfall is 623.7 mm (29 years average, from 1951 to 1980). The vegetation growing period begins with the first rains, generally from October until May/June. The third year of the experiment was drier and had a higher number of days with frost than the two first years of the experiment (Fig. 1). During the growing period, the precipitation from January to May of year 3 was 33% lower and the number of days with frost was 49% greater than for the 29 years average in the same period. Low air temperatures were also more extreme in year 3. The minimum air temperatures (measured at 1.5 m height) reached values lower than $-5°C$ in year 3, while minimum temperatures were $-1.6°C$ and $-0.8°C$ for years 1 and 2 respectively.

Measurements

Aboveground biomass was measured in each plot at the end of the growing season in years 1 to 3. A sample quadrat of 20×50 cm was used. Biomass was cut at 5 cm and separated by species, dried at $80°C$ for 48 h and weighed. Observed species richness was measured as the actual number of species found in biomass samples. Percent plant cover was estimated visually. Evenness (E)
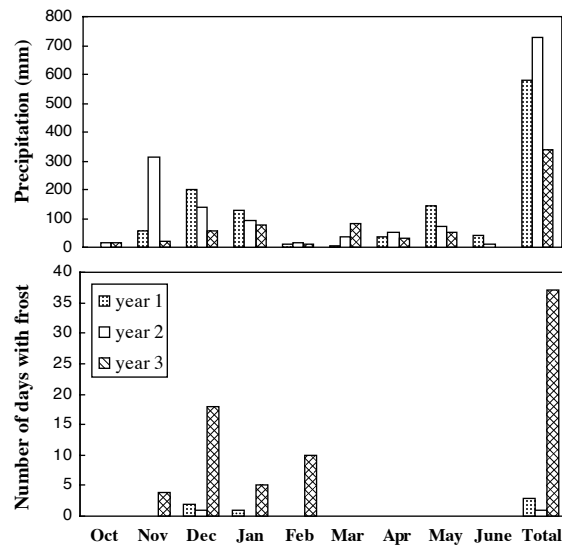

Fig. 1. Monthly precipitation (mm) and number of days with frost from October to June (the growing season) and totals for the same period for each of the three years of the experiment (year 1: 96/97, year 2: 97/98 and year 3: 98/99). Data for October of year 1 is missing.

was determined as the complement of Berger-Parker dominance index (Berger and Parker 1970) using percentage cover instead of number of individuals (E $= 1 -$ Cmax/C, Cmax- percentage cover of the most abundant species in each plot; C- total percentage cover of the plot).

Two measures of stability were used: temporal variability in biomass production (inversely related to temporal stability) and resistance of biomass production to perturbation. Temporal variability in biomass production was measured as the coefficient of variation (Tilman 1996). The coefficient of variation (CV, CV $= 100 \times$ standard deviation/mean) has the advantage of being scale-free, allowing relative amounts of variation in statistical populations having different means to be compared (Zar 1999). Community biomass variability was measured as the CV of aboveground biomass per plot, measured over the three years. The CV of population was determined for species present in each plot for at least two years.

The CV of community biomass can also be expressed as (Lehman and Tilman 2000, Petchey et al. 2002):

$$\text{CV} = \frac{\sqrt{\sum \text{Variance} + \sum \text{Covariance}}}{\sum \text{Biomass}}$$

where the denominator is the average community biomass of the three years. Total variance (ΣVariance) is the sum of the variances of community biomass during the three years of the experiment; total covariance (ΣCovariance) is the sum of covariances between all pair of species during the three years of the experiment. This equation provides a tool to understand how these

three components (total variance, total covariance and total biomass) affect the temporal variability (Petchey et al. 2002) of biomass production of the communities and how temporal variability varies with species richness. For example, increased total variance and covariance should contribute to increase temporal variability (Tilman 1999, Petchey et al. 2002).

Resistance of communities to perturbation was assessed with analysis of covariance by determining if the slopes of the relationship between diversity and biomass production (on a log scale) changed before and during the year of the perturbation. We used proportional deviations from expected values (Loreau 1998b) and the additive partitioning method (Loreau and Hector 2001, Hector et al. 2002, 2005, Spehn et al. 2005) to look into the mechanisms generating the relationship between above ground biomass and diversity and how these changed with perturbation. The proportional deviation method defines the expected proportion of species i in a mixture, E_i, as its expected yield based on its yield in monoculture (M_i):

$$E_i = p_i M_i$$

where p_i is the initial (e.g. sown) proportion of species i in the mixture. Species i's deviation from the expected value, D_i, is defined as:

$$D_i = \frac{O_i - E_i}{E_i}$$

where O_i is the observed yield in mixture. The average proportional deviation from the expected yield in a mixture follows as:

$$\overline{D} = \sum_i p_i D_i$$

$\overline{D}$ is related to the complementarity effect (CE) as:

$$\overline{D}\overline{M} = CE$$

where $\overline{M}$ is the average monoculture yield of the species in a mixture. $\overline{D}$ is also equivalent to the related relative yield total (RYT) but scaled to zero rather than one: $RYT = \overline{D} + 1$ (Loreau 1998b). One advantage of this is that the null hypothesis of $\overline{D} = 0$ is automatically tested by standard statistical methods (e.g. ANOVA and regression).

The $\overline{D}$ method can detect deviations from expected values that are consistent with positive and complementary interactions but cannot quantify the effect on total yield of changes in the relative abundance of species in mixtures. For that we use the additive partitioning method (Loreau and Hector 2001) by which the effect of biodiversity on aboveground biomass production can be partitioned into a 'selection effect' and a 'complementarity effect' (which sum to the 'net biodiversity effect'). The selection effect is measured by the covariance between the monoculture yield of species and their

change in relative yield in the mixture. The complementarity effect measures the net change in the average relative yield of species, that is increases in some species that are not compensated by decreases in others (and vice versa for negative effects) which can indicate facilitation, resource-partitioning and related niche-differentiation processes (as above). As the approach requires a comparison between performance of species in mixture and in monoculture, it can only be applied to the subset of experimental mixtures that contained species for which monoculture yields were available. The additive partitioning calculations follow Loreau and Hector (2001) and Hector et al. (2002) modified to better incorporate missing species in Portugal. Species with zero sampled biomass became more common in biomass harvest later in the experiment. Species sometimes had zero harvested biomass in monoculture, polyculture or both. Where a species was missing in monoculture, expected values cannot be calculated. We therefore ignore these species entirely (species richness was taken as the original richness minus the number of missing species). Where a species was present in monoculture but missing from a mixture it contributed the negative value of its expected contribution (i.e. a species that is expected to contribute 10 g when present contributes -10 g when missing). The details of the calculations and individual species biomass data used therefore match Spehn et al. (2005) and Hector et al. (2005) but differ somewhat from the older Loreau and Hector (2001, discussed by Spehn et al. 2005). The additive partitioning values and $\overline{D}$ were square-root transformed (preserving original signs) to meet the assumptions of the analyses.

Statistical analyses

We used the regression with replication procedure (Zar 1999) to test the effect of species richness. The linear effect of species number ($\log_2$ transformed) was tested against the effect of species composition ("mixture effect": a nominal variable identifying different species compositions). Biomass data were transformed using natural logs and biodiversity effects by square-roots (preserving original positive and negative signs) to meet the underlying statistical assumptions of normal linear models. We favoured analysing the biomass data after log transformation for two reasons. First, from a statistical perspective transformation was necessary to meet the linear model assumptions: log transformation improved the normality and constancy of variance of the residuals. Second, working with log-transformed data also better matched the null hypothesis about the relationship between diversity and stability on the relative scale (ratio of biomass before and during perturbation – Introduction). Spearman correlation

was used for data that could not be successfully transformed to a normal distribution. We present analyses using the number of species originally sown into the plots for several reasons. Using the observed number of species introduces the complexity of a given plot changing its diversity across years and makes interpreting the analyses and graphs difficult. We have also found that the number of sown species has greater explanatory power in analyses when compared to observed numbers (Hector 2002, Hector et al. 2002) as well as matching our a priori hypotheses more closely. However, Portugal was the site that suffered the greatest reductions of diversity. Therefore we also did the analyses presented here using the observed number of species and found that they produce qualitatively similar results to using the number of sown species.

Results

Temporal variability

Temporal variability in community biomass, measured as the CV of plot biomass for the three years, was negatively correlated (Spearman, $r = -0.373$; $n = 52$, $P = 0.006$) with the increase in species richness (Fig. 2a). The CV of biomass was also tested by multiple regression analysis against: species richness (log_2), mixture of species, aboveground biomass in year 2 (before
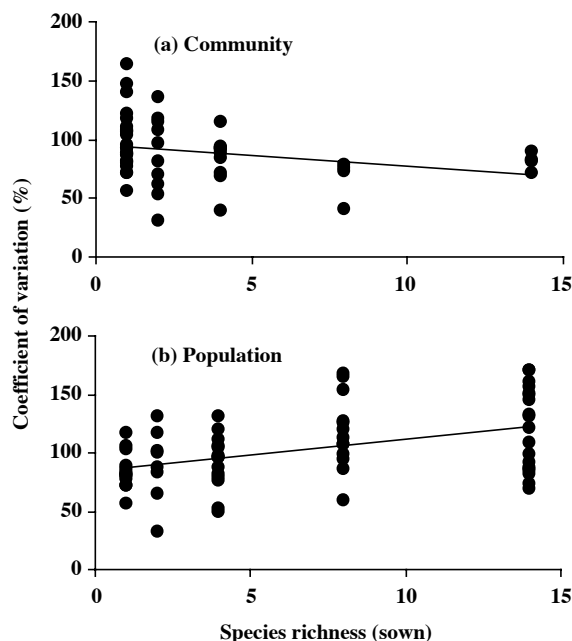

Fig. 2. Coefficient of variation (CV) of (a) community biomass and (b) population biomass across the three years of the experiment. Dots are plot values and lines show the significant correlations.

the onset of the frost) and evenness. The only variable selected by stepwise procedure in this model was species richness ($R^2 = 0.101$, $n = 50$; species richness (log_2), $\beta = -0.318$, $t = -2.34$, $P = 0.023$). These results confirmed the significant negative relationship between the CV of community biomass and species richness. Although evenness was not selected in a stepwise multiple regression analysis it was significantly correlated with species richness (Spearman, $n = 51$, $r = 0.931$, $P < 0.001$) and with the CV (Spearman, $n = 51$, $r = -0.308$, $P = 0.028$). With the increase in evenness (dominance decreases) species can make a more equal contribution which can dampen temporal variability.

The three components of the CV were positively correlated with species richness: the summed variance (Spearman, $n = 52$, $r = 0.428$, $P = 0.002$), summed covariance (Spearman, $n = 52$, $r = 0.267$, $P = 0.056$) and average biomass (Spearman, $n = 52$, $r = 0.580$, $P < 0.001$). The increase in average community biomass with the increase in species richness was expected from the positive slopes of diversity with biomass production found for the three years of the experiment.

The results for the CV of species biomass (population) differed from those of community biomass. The CV of all species populations together had a significant positive correlation (Spearman, $n = 67$, $r = 0.431$, $P < 0.001$) with the increase in species richness (Fig. 2b). From these species, two had a positive correlation with the increase in species richness (Spearman; *Lolium multiflorum*: $n = 8$, $r = 0.976$, $P < 0.001$; *Avena sativa*: $n = 15$, $r = 0.538$, $P = 0.038$; data not shown) while four other species had a positive but not significant correlation (*Dactylis glomerata*: $n = 8$; $r = 0.655$, *Plantago lanceolata*: $n = 8$ $r = 0.215$, *Holcus lanatus*: $n = 14$, $r = 0.460$, *Ornithopus compressus*: $n = 10$, $r = 0.120$, $P > 0.05$ for all species) with the increase in species richness.

Resistance

The analysis of the log-transformed data confirmed that biomass production was significantly related to increasing diversity in all three years (Fig. 3; Year 1: $F_{1,24} = 8.913$, $P = 0.006$; Year 2: $F_{1,24} = 7.731$, $P = 0.010$; Year 3: $F_{1,21} = 10.277$, $P = 0.004$). The slopes remained positive during the three years despite the large decrease in biomass production from the first to the third year. The slope of the relationship was parallel in the later two years (Fig. 3b and 3c; ANCOVA test of the year × log(species richness) interaction versus the year × mixture interaction: $F_{1,17} = 1.018$, $P = 0.673$) indicating effects which are additive on the log scale (with unlogged biomass data the effect resembles that found by Pfisterer and Schmid 2002).
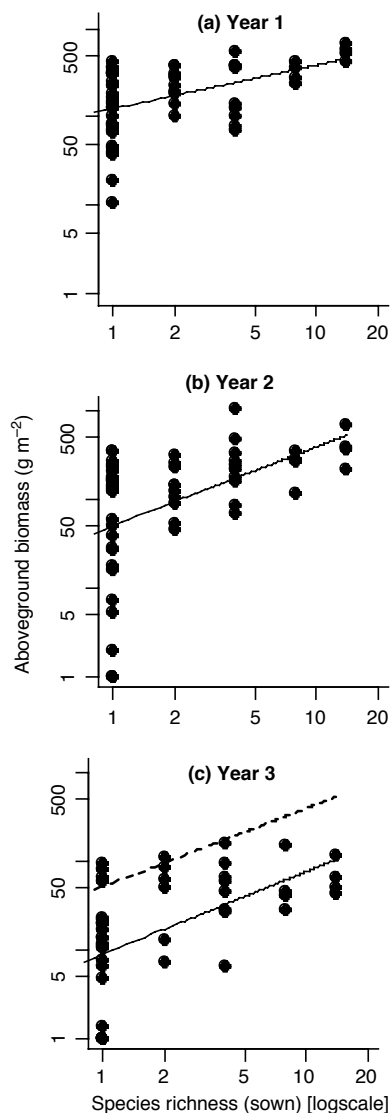
Fig. 3. Aboveground biomass as function of species richness for years 1–3 (a–c). Solid circles are values per plot and solid lines are regression slopes. The dashed line in panel c repeats the slope for year 2 for easy comparison with the year 3 slope (solid line).

Overyielding

In the first year (Fig. 4a) the grand mean selection effect was significantly negative ($F_{1,27} = 5.77$, $P = 0.023$) and the complementarity effect positive with increasing diversity ($F_{1,10} = 7.58$, $P = 0.02$). In the second year (Fig. 4c), the complementarity effect remained positive overall ($F_{1,27} = 22.464$, $P < 0.001$) but the slope with diversity became non-significant. The selection effect was negative during the second year at low diversity but positive at high diversity generating a positive slope ($F_{1,10} = 5.42$, $P = 0.042$). The third year (Fig. 4e) saw the selection effect return to a condition similar to the first

year: negative overall with no diversity slope ($F_{1,21} = 11.5$, $P = 0.003$). The complementarity effect declined slightly relative to year 2 but remained positive overall ($F_{1,21} = 21.39$, $P = 0.0001$), although the slope with diversity was not significant.

Relative overyielding ($\overline{D}$) mirrored the results for the complementarity effect in having a positive relationship with diversity in only the first year ($F_{1,10} = 7.205$, $P = 0.023$; Fig. 4b) but significant overall mean values in years two and three (Year 2: $F_{1,27} = 24.862$, $P < 0.001$; Year 3: $F_{1,21} = 8.8503$, $P = 0.006$; Fig. 4d and f). There was no significant difference in overyielding values between years 2 and 3 (ANCOVA test of the year $\times$ log(species richness) interaction versus the year $\times$ mixture interaction: $F_{1,9} = 0.965$, $P = 0.648$).

The selection effect is the covariation between the performance of species in monoculture and mixture, so one easy way to visualise it is to look at the average performance of different species in mixtures in relation to their monoculture biomass (standardised as proportions of the maximum monoculture biomass to control for differences in absolute biomass, Hector et al. 2002). Plotting these data illustrates the shift from year two to three for a more negative selection effect and makes clear the stronger dominance on average of species with lower monoculture biomass after the climate perturbation (Fig. 5). The frost affected both the rank order of performance of the species in monoculture (change in sequence on the x axis) and their average dominance of mixtures (change in sequence on y axis). Species were impacted by frost to different degrees and also responded in different ways depending on whether they were growing in monocultures or mixtures. Dominance of mixtures by the most productive monoculture was stronger in year 2 (*Ornithopus*, 20%) than in year 3 (*Dactylis*, 5%). *Holcus* and *Plantago* both perform relatively well in mixtures in both years but their monoculture performances are lower relative to the maximum in year 3 than in year 2 indicating that frost affected their monoculture yields more strongly than their yield in mixtures. While the relative abundance of *Ornithopus* in mixtures is similar in both years its monoculture performance was much reduced after the frost.

Discussion

Temporal variability

Our results showed a decrease in temporal variability in community biomass with the increase in species richness which was also shown for grassland communities by Tilman (1996) and Pfisterer et al. (2004). Less biomass variability indicates that richer communities were more stable during the three years of the experiment than communities depauperate in species. Species richness

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Fig. 4. Relationships between species richness and biodiversity effects in years 1–3 (a, c, e) and relative overyielding (b, d, f). Solid points and lines are the complementarity effect and open points and broken lines the selection effect. Grey lines show zero effect. Points have been staggered on the x-axis for clarity.
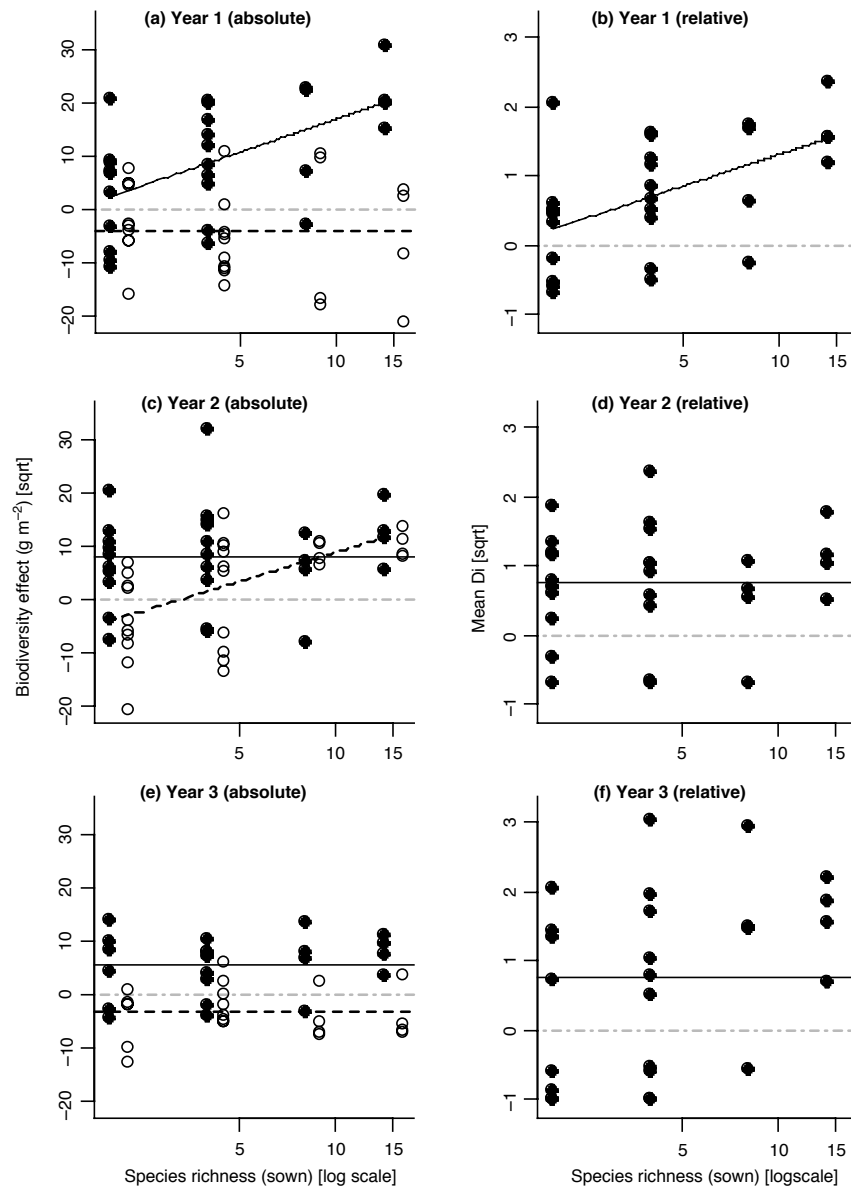
also affected the temporal variability of biomass at the population level. The CV of population, i.e. variability of biomass of individual species, was positively correlated with species richness or showed no effect. This positive correlation with diversity is consistent with the idea that populations were destabilised by increases in species richness as was described by Tilman (1996). Community properties, however, result from summation across these individual fluctuations, and the probability that these fluctuations average out increases with the number of species when they are not perfectly positively correlated with each other. This averaging reduces variation in the aggregate property relative to variation in the average individual species (Ives et al. 1999, 2000, Cottingham et al. 2001, Ives and Hughes 2002). Greater asynchrony

among species, resulting from biological differences in response to environmental change among species, leads to greater dampening of the variability of the aggregate community metric. However, greater asynchrony among species can also result from biological similarity in resource use requirements leading to stronger competition.

The various components of the CV of community biomass increased with species richness. Although increased summed variances contribute to increase temporal variability they can also lead to a stabilising effect if the slope between the log of the variance and the log of the mean is greater than 1 (Doak et al. 1998, Tilman et al. 1998) as we found with our data. Negative summed covariances may occur if some species increase in
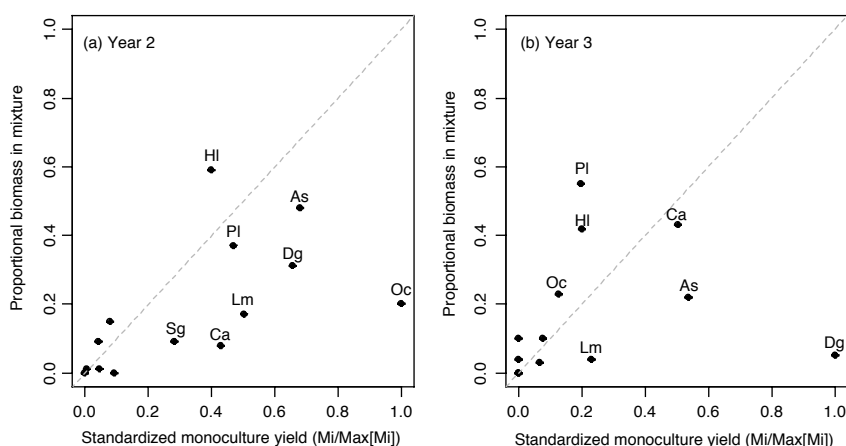
Fig. 5. Relationship between monoculture yield (proportion of the maximum) and relative abundance in mixture (proportion of mixture biomass) in (a) Year 2 and (b) Year 3. Eight abundant species are labelled: As = *Avena sativa*; Ca = *Conyza albida*; Dg = *Dactylis glomerata*; Hl = *Holcus lanatus*; Lm = *Lolium multiflorum*; Oc = *Ornithopus compressus*; Pl = *Plantago lanceolata*; Sg = *Silene gallica*.

abundance while others decrease as a result of competitive interactions (Tilman 1999, McCann 2000, Cottingham et al. 2001) or of different responses of species to environmental fluctuations (Doak et al. 1998, Ives et al. 1999, Yachi and Loreau 1999). Both the variance and covariance terms, however, contribute to stabilise community properties through the same basic mechanism, i.e. asynchronous species fluctuations (Yachi and Loreau 1999). Even positive covariances among species, as we found in richer communities, can make for increased stability as long as perfect synchrony does not occur (Yachi and Loreau 1999). Contrary to the possibility suggested by Lehman and Tilman (2000), negative summed covariances due to competitive interactions do not seem to be a major temporal stabilising force in our study. Lastly, increased average community biomass as species richness increases contributes to reduce temporal variability (Petchey et al. 2002). This factor also comes into play as shown by the positive slopes between biomass production and species richness found in the three years of our study.

Resistance

Our results mirror those of Pfisterer and Schmid (2002) in finding a decline in productivity in response to perturbation that was proportional to the pre-existing positive diversity–productivity relationship. In absolute terms higher diversity communities suffered a greater decline but in relative terms the effect is of similar magnitude across the diversity gradient. The apparent difference in results between our study and that of Pfisterer and Schmid (2002) is resolved once the different scale of measurement is noted: multiplicative effects become additive on logarithmic scales. Our results reveal that the relative resistance of aboveground biomass to frost was equal across the diversity gradient. Similarly Pfisterer and Schmid (2002) noted that when analysed after log transformation the biomass production of their

perturbed systems was a more or less constant proportion of that of the unperturbed systems. In contrast, when Pfisterer and Schmid (2002) analysed their data on the untransformed scale, there was an apparent mismatch between the apparent lower resistance of high-diversity communities and the fact that these mixtures remained the more productive on average following perturbation. This mis-match disappears when resistance is assessed on a relative (logarithmic) scale as constant resistance across a diversity gradient is consistent with the fact that plots that were more productive before perturbation remain more productive after perturbation. In summary, while it is informative to look at both absolute and relative scales the latter can provide a more consistent overall picture.

Overyielding

Our results confirm theoretical predictions that selection effects should be more variable and less predictable than complementarity (Loreau 1998a, 2000). The selection effect ranged from a positive slope with diversity in year 2 to negative grand means in years 1 and 3 while complementarity remained consistently positive over all polycultures. If we focus on the changes from year 2 to 3, then the reduction in biomass and of the net biodiversity effect can be seen to be due partly to a reduction in the complementarity effect but mostly due to a shift from positive to negative selection. Understanding the selection effect is quite complex since the response to perturbation differed depending on species identity, and species were also differently affected by the frost depending on whether they grew in monoculture or in mixture. However, the overall selection effect became negative because frost shifted dominance of communities to species with lower monoculture yields.

While the complementarity effect (absolute scale) declined together with the decrease in biomass, relative overyielding ($\overline{D}$) was maintained across all three years,

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counter to previous predictions. Our study reveals for the first time that, on a relative scale, overyielding was maintained during a major natural environmental perturbation despite changes in species relative abundances, diversity and total community production. In our experimental system, the complementary and positive species interactions that generate biodiversity effects and which may contribute to species coexistence were largely unaffected by the perturbation despite changes in the other community and ecosystem properties.

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Subject Editor: Ove Eriksson