

# Diversity-dependent production can decrease the stability of ecosystem functioning

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There is concern that species loss may adversely affect ecosystem functioning and stability. But although there is evidence that biodiversity loss can lead to reductions in biomass production<sup>1–4</sup>, there is no direct evidence that biodiversity loss affects ecosystem resistance (ability to withstand perturbation) or resilience (recovery from perturbation). Yet theory<sup>5,6</sup>, laboratory experiments<sup>7–11</sup> and indirect experimental evidence<sup>12–14</sup> strongly suggest that diversity and stability are related. Here we report results from a field experiment with factorially crossed perturbation and diversity manipulations. We simulated drought perturbation on constructed grassland ecosystems containing 1, 2, 4, 8 or 32 plant species. Under unperturbed conditions, the species-poor systems achieved lower biomass production than the species-rich systems. However, the species-poor systems were more resistant to perturbation than the species-rich systems. The species-poor systems also showed a larger initial resilience following perturbation, although the original relationship between diversity and productivity was fully restored after 1 year. Our results confirm that biodiversity increases biomass production, but they also point to the fact that such diversity–production associations may lead to an inverse relationship between biodiversity and the stability of ecosystem functioning.

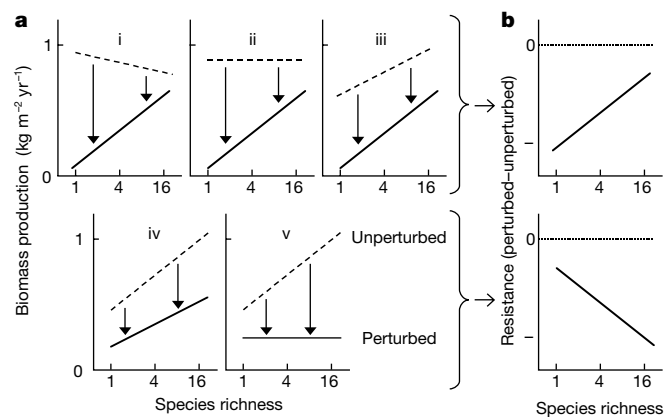
Ecosystems may resist change in functioning in the face of perturbation or, if change occurs, exhibit resilience by returning to their original state after perturbation<sup>15</sup>. According to the insurance hypothesis of biodiversity, resistance and resilience should increase with species richness, because a greater number of species can express a greater range of responses to environmental perturbation<sup>6,16</sup>. This increases the likelihood that some species with previously low performance will increase their performance and compensate for others. However, responses of an ecosystem to perturbation may depend on the form of the relationship between the response variable and biodiversity. Autotrophic biomass production (which we will refer to as ‘biomass production’) is an important response variable that has been shown to be associated with plant species richness in experimental grassland communities<sup>1,3</sup>. Given this diversity-dependence in production, there are five possible outcomes of perturbation experiments (see Fig. 1). Increasing resistance with increasing diversity (upper panel in Fig. 1b), as predicted by the insurance hypothesis, implies that the relationship between diversity and production has a larger slope under perturbed conditions than under unperturbed conditions (upper panels in Fig. 1a). This is more likely if the slope under unperturbed conditions is flat<sup>11</sup> or even negative<sup>10,13</sup>. If the slope is positive, which corresponds to the situation observed in grassland experiments, the post-perturbation slope is likely to be less positive or flat because species-poor systems already have reduced biomass production under unperturbed conditions and may therefore be less affected by perturbation than species-rich systems (lower panels in Fig. 1a). In this case, resistance decreases with increasing diversity (lower panel in Fig. 1b). Analogous arguments apply to resilience. In this experiment, we test the diversity-dependence of ecosystem resistance and resilience by exposing experimental grassland communities to drought perturbation.

We used experimental communities of characteristic grassland

species where we had observed a positive relationship between biodiversity and biomass production under unperturbed conditions (the Swiss site of the BIODDEPTH experiment<sup>3,17,18</sup>). After 4 years, we divided each plot, imposed an experimental drought perturbation on subplots of 1 m<sup>2</sup> and compared the above-ground biomass production in perturbed subplots with that of unperturbed control subplots. At the time of the drought treatment, the actual species richness had reached average levels of 1, 2, 4, 7 and 22 species per square metre. Replicate communities with different species combinations permitted additional contrasts to be made between plots with and without particular functional groups or species<sup>17,18</sup>. The drought perturbation consisted of a transparent, height-adjustable polycarbonate roof raised above the vegetation, with a tube attached to drain the collected rainwater outside the plots. The roofs remained in place for 8 weeks, from 20 July to 18 September 1998. Climatic variables other than the amount of precipitation varied little between perturbation and control plots, but light intensity was reduced by 15% in the perturbed subplots.

The species-rich systems produced more above-ground biomass than the species-poor systems, both under unperturbed and perturbed conditions ( $P < 0.001$  and  $P < 0.01$ , respectively, for log species richness effect tested separately for unperturbed and perturbed subplots) but the relationship was less steep in the perturbed plots (Fig. 2a, Table 1 ‘Biomass production during drought period’). Compared with pre-drought levels, diverse systems showed a greater reduction in biomass production under perturbation than did species-poor systems (Fig. 2b, Table 1 ‘Resistance’). This result contrasts with the prediction of the insurance hypothesis. Rather, it supports our predicted outcome that resistance should decrease with increasing diversity in cases where diversity–production relationships are positive under unperturbed conditions (outcome iv in Fig. 1a).

Of the alternative mechanisms that can explain these results, our



**Figure 1** Possible effects of perturbation on relationships between diversity and ecosystem functioning. (Diversity here is the number of plant species on a logarithmic scale and ecosystem functioning is biomass production). **a**, Five possible outcomes in which perturbation leads to diversity-dependent reductions between unperturbed (dashed lines) and perturbed (solid lines) ecosystems. **b**, Resistance, measured as the difference between perturbed and unperturbed ecosystems (solid line; dotted reference line refers to zero difference, that is, full resistance), increases (upper panel) or decreases (lower panel) with increasing diversity, depending on the outcomes shown in **a**. Evidence that diversity increases ecosystem resistance so far comes from observations of outcomes i (refs 10, 13) and ii (ref. 11), cases in which diversity did not increase ecosystem functioning under unperturbed conditions. If diversity already has a positive effect on ecosystem functioning under unperturbed conditions, outcomes leading to positive diversity–resistance relationships (iii) may be less likely than outcomes leading to negative diversity–resistance relationships (iv, v). Our experiments demonstrate this (outcome iv), but at the same time refute the most extreme outcome (v), in which the perturbation is so severe that it reduces ecosystem functioning to a constant, diversity-independent level.

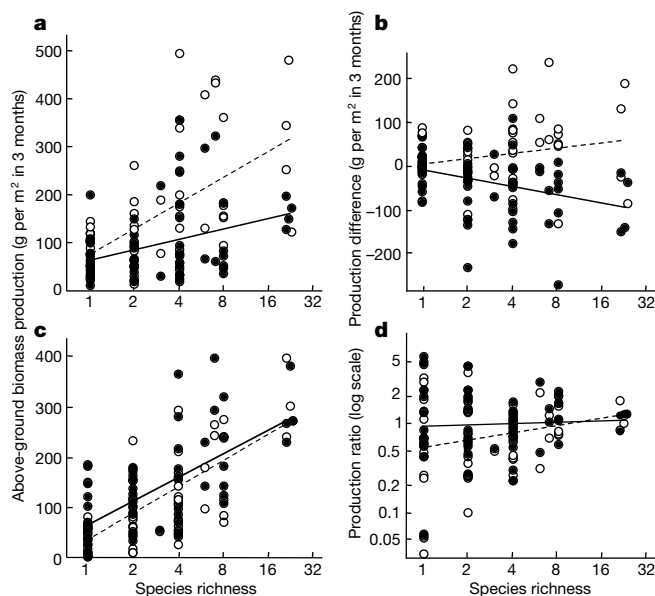
findings best support a perturbation-induced reduction in niche complementarity among plant species that probably accounts for diversity-dependent production in this system<sup>4</sup>. The occurrence or response of particular species in the experimental ecosystems also affected resistance, but these effects were independent of diversity. The presence of a particular functional group or species may render a community as a whole more or less resistant. When species richness was replaced by a variable coding for the presence or absence of legumes, it became apparent that plots containing legumes suffered greater reductions in biomass production under perturbed conditions than did plots without legumes ( $P < 0.05$  for legume  $\times$  drought interaction). A similar analysis revealed that plots containing *Poa pratensis* suffered less than plots without it ( $P < 0.05$  for *P. pratensis*  $\times$  drought interaction). A particular species may be more or less sensitive to perturbation independently of the community context. Thus, whereas drought reduced biomass production of the grasses *Arrhenatherum elatius*, *Dactylis glomerata* and *Trisetum flavescens* more than threefold ( $P < 0.05$  for main effect of drought), the biomass production of the legumes *Lotus corniculatus* and *Trifolium pratense* and the non-leguminous forbs *Knautia arvensis* and *Plantago lanceolata* was reduced less than twofold ( $P > 0.1$  for main effect of drought). These varying responses of individual species to perturbation led to decreased species evenness in perturbed subplots when compared with unperturbed subplots ( $P < 0.05$  for main effect of drought). However, because species with different responses occurred at all diversity levels, the decrease in evenness due to perturbation was not affected by diversity.

We evaluated the resilience of the experimental grassland ecosystems 9 and 12 months after the drought perturbation by calculating post- to pre-drought biomass production ratios (September–June

and June–September time intervals, respectively). The recovery from perturbation was fast. At 9 months, the species-poor systems had already produced more above-ground biomass in the previously perturbed subplots than in the unperturbed subplots (Table 1 ‘Biomass production early after drought’). In the later evaluation, this was the case also for species-rich systems (Fig. 2c, Table 1 ‘Biomass production late after drought’). Thus, the initial resilience response was faster for low than for high diversity (Table 1 ‘Early resilience’), in contrast, once again, to the prediction of the insurance hypothesis and in line with our observations for the resistance response. However, species richness did not significantly influence the later resilience response (Fig. 2d, Table 1 ‘Late resilience’).

The diversity-dependent early resilience was not related to the occurrence of particular species at low diversity levels. However, the generally high resilience of our experimental systems measured after the drought perturbation was in part caused by strong increases in the biomass production of the grasses *P. pratensis*, *D. glomerata* ( $P < 0.05$  for main effect of drought at both post-drought harvests) and *A. elatius* ( $P < 0.05$  for main effect of drought only at the later post-drought harvest). The marked increase in *D. glomerata* and *A. elatius*, which were also among the least resistant species, was still not enough to restore the evenness of species abundances in perturbed plots to the high level measured in unperturbed plots ( $P < 0.05$  for main effect of drought). This indicates that despite the full recovery made in biomass production, the responses we were recording were still transient, and even longer periods of observation would be required to show further compensatory changes.

The pre-perturbation effects of diversity have not usually been considered in theoretical work on diversity–stability relationships. Our results show that incorporating these effects can alter predictions. As we suggest in Fig. 1, the immediate effect of a drought perturbation is less pronounced in species-poor systems than in species-rich systems if biodiversity loss already reduces ecosystem functioning under unperturbed conditions. Although the insurance hypothesis did not work in the expected way, explaining increased resistance and resilience with increasing diversity, it is still con-



**Figure 2** Effects of drought perturbation on the relationship between species richness and production. (Species richness is plotted on a logarithmic scale.) Solid lines and filled circles refer to subplots with experimental drought, and dashed lines and open circles refer to control subplots ( $n = 120$ ). **a**, Drought perturbation reduced the slope of the diversity–production relationship (September 1998 harvest). **b**, Consequently, the difference between drought and pre-drought biomass production (September 1998–September 1997 harvests) is more negative at high than at low species richness, indicating decreasing resistance with increasing diversity. **c**, One year after the drought perturbation, the positive relationship between diversity and biomass production is fully restored (September 1999 harvest). **d**, Consequently, the ratio between pre-drought and post-drought biomass production (September 1997 / September 1999 harvests) is the same for high and low species richness, indicating that late resilience is no longer diversity-dependent (for early resilience, see the appropriate entries in Table 1).

**Table 1** Perturbation effects on the diversity–production relationship

Mean in 8-species mixtures			Slope		
Control subplot	Drought subplot	Significance of drought effect	Control subplot	Drought subplot	Significance of slope difference
Biomass production during drought period*					
236.0 $\pm$ 19.9	128.2 $\pm$ 15.1	$P < 0.001$	53.6 $\pm$ 10.2	21.6 $\pm$ 7.7	$P < 0.001$
Resistance†					
40.6 $\pm$ 14.4	–67.2 $\pm$ 13.8	$P < 0.001$	12.7 $\pm$ 7.4	–19.3 $\pm$ 7.1	$P < 0.001$
Biomass production early after drought‡					
461.6 $\pm$ 31.5	462.4 $\pm$ 34.5	$P < 0.05$	96.4 $\pm$ 16.2	58.3 $\pm$ 17.7	$P < 0.05$
Early resilience§					
0.16 $\pm$ 0.14	0.20 $\pm$ 0.16	$P < 0.01$	–0.04 $\pm$ 0.07	–0.15 $\pm$ 0.08	$P < 0.05$
Biomass production late after drought					
189.1 $\pm$ 12.5	204.0 $\pm$ 15.0	$P < 0.01$	52.0 $\pm$ 6.4	46.8 $\pm$ 7.7	n.s.
Late resilience¶					
–0.04 $\pm$ 0.18	0.19 $\pm$ 0.09	$P < 0.05$	0.19 $\pm$ 0.09	0.04 $\pm$ 0.10	n.s.

Effects of drought in experimental grassland systems on the relationship between species richness (log<sub>2</sub> scale) and above-ground biomass production (g m<sup>–2</sup>), resistance, and resilience. Estimates  $\pm$  s.d. at the richness level of 8 species and slopes  $\pm$  s.d. in the first, second, fifth and sixth rows refer to the regression lines in Fig. 2a–d. We calculated significance levels from multiple regression analyses (main effect of drought evaluated at mean actual species richness).

\*18 June to 18 September 1998.

†Production difference drought minus pre-drought period ((18 June to 18 September 1998) – (20 June to 19 September 1997)).

‡18 September 1998 to 21 June 1999.

§Natural logarithm of production ratio early post-drought divided by pre-drought ((18 September 1998 to 21 June 1999)/(19 September 1997 to 18 June 1998)).

||21 June to 17 September 1999.

¶Natural logarithm of production ratio late post-drought divided by pre-drought ((21 June to 17 September 1999) / (20 June to 19 September 1997)).

ceivable that it worked in the opposite way: if species-rich systems have a greater chance of including species growing well under unperturbed conditions, they may also have a greater chance of losing this growth potential under perturbation if the two are negatively correlated. This offers an explanation of why more productive systems could suffer more from perturbation than those that are less productive<sup>19</sup>. Indeed, the biomass production of our perturbed systems was a more or less constant proportion of that of the unperturbed systems. When we calculated these proportions with the data presented in Fig. 2a or as ratios of drought/pre-drought biomass production (instead of the differences represented in Fig. 2b), they did not decrease significantly with increasing species richness ( $P > 0.05$ ).

Although ecosystem resistance and resilience decreased with increasing diversity in our experiments, the relationship between diversity and biomass production was still positive, even under perturbed conditions. This shows that the perturbation was not strong enough to remove the positive diversity-dependence of ecosystem functioning altogether, and it is an argument for protecting diversity where maintaining high levels of production is desirable, even if systems with fewer species are more resistant or resilient. It is also possible that systems in which niche complementarity is not the mechanism for diversity dependence (for example, sampling or facilitation are more important<sup>4</sup>), in systems where multiple perturbations may exist (for example, drought, fire, insect outbreaks), and where higher trophic levels rather than diversity may govern production, different relationships between stability and diversity might be obtained. Independent of these possibilities, however, our study points to a potential trade-off between production and stability in systems where production is diversity-dependent. This trade-off may be important in understanding the ecosystem consequences of changing biodiversity. □

## Methods

### Biodiversity and drought experiment

The experiment was carried out at the Swiss site of the BIODEPTH project<sup>3,17</sup>, which was designed to study the influence of biodiversity loss in grassland on ecosystem processes. Two replicate blocks, each with 32 plots measuring 8 m × 2 m, were sown with different mixtures of 1, 2, 4, 8 or 32 plant species in spring 1995. The number of plant functional groups (grasses, legumes, non-leguminous forbs) ranged from one (in monocultures and in 2-, 4- and 8-species mixtures) to three (in 4-, 8- and 32-species mixtures)<sup>17</sup>. For every species and functional-group richness level, several different species compositions were used to reduce possible confusion between number and compositional effects. Similar total densities of about 500 seedlings per square metre were achieved by adjusting seed numbers in relation to germination rates and to proportions in mixtures<sup>17</sup>. The plots were mown twice during the vegetation period (June and September). To maintain the original diversity treatments, all plots were regularly weeded by hand. After 4 years, very few species had been lost from the mixtures, and four monoculture plots (*Trifolium repens* and *T. pratense*) had been destroyed by fungal infection.

After the June harvest in 1998, we applied a drought treatment within each plot and left it in position from 20 July–18 September 1998. The treatment consisted of height-adjustable, 1 m × 1 m polycarbonate roofs installed just above the vegetation (initial height 25 cm on one side, 30 cm on the other side). As the vegetation grew taller, the height of the roofs was increased twice by 10 cm in all plots. A 20-cm-deep vertical cut into the soil around the sheltered area prevented water uptake by plants with side roots. Hoses fixed to the lower end of the roofs directed the rainfall 1 m away from the plots. A 1 m × 1 m area adjacent to the roofed area was used as control. The roofs reduced light intensity by 15% and volumetric soil moisture by 13.5–27.5% with no difference between species richness levels ( $P > 0.2$ ). Over the 8-week drought interval, the control subplots received 232 mm of natural rain (automatic weather station WS01, Delta-T Devices, Burwell, UK).

We measured the above-ground plant biomass production between the following harvest dates: 20 June and 19 September 1997, 18 June and 18 September 1998, 21 June and 17 September 1999. At each harvest, we cut the vegetation 5 cm above the ground, sorted the biomass samples from a 0.1-m<sup>2</sup> area into species and dried and weighed these separately.

### Data analysis

We analysed the data resulting from the different harvests separately, because they reflected different growth intervals (3 months for the September harvests and 9 months for the June harvests) and different phases of drought response, that is, resistance (September 1998 harvest) and resilience reactions (1999 harvests). The dependent variables were (1) total above-ground biomass production and their differences (resistance) or ratios (resilience) over time, (2) evenness of partial biomass contributions of individual species to total

biomass (calculated from the Shannon diversity index  $H$  as  $H/H_{\max}$ ; ref. 18), and (3) biomass production of individual species. We corrected the production of individual species for the decreasing proportion with which they occurred in mixtures of increasing diversity to obtain biomass production 'per seed sown'. We analysed evenness only for mixture plots (because by definition evenness is 1 for monocultures) and biomass production of individual species only for sets of plots in which they occurred. We used the logarithmic transformation for the analysis of resilience ratios in order to obtain constant variances.

We calculated the regression parameters listed in Table 1 by linear regression with log species richness as continuous explanatory variable and drought perturbation as grouping variable. For the statistical tests reported in text and Table 1 ( $P$  level), we used the analysis of variance (ANOVA) approach to multiple linear regression as implemented in Genstat software<sup>20</sup>. This was necessary in order to test the number effect of species richness against the identity effect of species composition rather than against the plot variation. The full model included positional terms (block as grouping variable and distance from southern edge within blocks as continuous explanatory variable), diversity terms (log species richness as continuous explanatory variable and residual species richness and functional-group richness as grouping variables) and compositional terms (species composition as grouping variable, decomposed into contrasts for the presence/absence of particular functional groups or species) at the plot level<sup>17,18</sup>, and the drought term (as grouping variable) and interactions of the diversity and compositional terms with the drought term at the sub-plot level. From this full model, we selected reduced best models using AIC values<sup>21</sup>. On the basis of AIC values, original species richness was replaced by actual species richness in all models the results of which are presented here. Actual species richness was measured before the drought treatment in June 1998 in subplots of 1 m<sup>2</sup>.

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### Competing interests statement

The authors declare that they have no competing financial interests.

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