

Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment

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Biodiversity is rapidly declining¹, and this may negatively affect ecosystem processes², including economically important ecosystem services³. Previous studies have shown that biodiversity has positive effects on organisms and processes⁴ across trophic levels⁵. However, only a few studies have so far incorporated an explicit food-web perspective⁶. In an eight-year biodiversity experiment, we studied an unprecedented range of above- and below-ground organisms and multitrophic interactions. A multitrophic data set originating from a single long-term experiment allows mechanistic insights that would not be gained from meta-analysis of different experiments. Here we show that plant diversity effects dampen with increasing trophic level and degree of omnivory. This was true both for abundance and species richness of organisms. Furthermore, we present comprehensive above-ground/below-ground biodiversity food webs. Both above ground and below ground, herbivores responded more strongly to changes in plant diversity than did carnivores or omnivores. Density and richness of carnivorous taxa was independent of vegetation structure. Below-ground responses to plant diversity were consistently weaker than above-ground responses. Responses to increasing plant diversity were generally positive, but were negative for biological invasion, pathogen infestation and hyperparasitism. Our results suggest that plant diversity has strong bottom-up effects on multitrophic interaction networks, with particularly strong effects on lower trophic levels. Effects on higher trophic levels are indirectly mediated through bottom-up trophic cascades.

The loss of biodiversity from terrestrial ecosystems has been shown to affect ecosystem properties, such as primary productivity⁷, nutrient cycling⁸ and trophic interactions². In recent biodiversity experiments, focal organism groups (usually plants⁷) were used to establish gradients in species richness, and biodiversity effects were then measured at one or a few trophic levels^{5,9}. Traditionally, studies have focused on the effects of horizontal biodiversity loss, that is, loss of species within a single trophic level¹⁰. Biodiversity loss at a given trophic level has been predicted to affect the abundance, biomass and resource use of that trophic level⁵. However, horizontal species loss may also affect other

trophic levels, organism groups and processes, and, hence, vertical species loss and the associated multitrophic structure of ecosystems¹⁰. For example, declines in plant species richness may cause losses to herbivores, true predators, parasitoids, hyperparasitoids and omnivores, and may also alter mutualistic interactions such as pollination¹¹ or mycorrhizal association⁴. Overall, there is an increasing awareness that the network nature of ecological systems needs to be incorporated into studies of biodiversity–ecosystem functioning¹².

Recent meta-analyses^{4,5} and experiments at individual study sites^{13,14} have shown plant diversity effects on a wide range of different groups of organisms, including primary producers, first- and second-order consumers, detritivores, fungal diseases and mycorrhizae. Additional studies have addressed components of the below-ground subsystem and their linkages with above-ground biota¹⁵. However, interpretation and progress has been clouded by differences in study systems and by a general lack of an overarching theory incorporating both trophic and non-trophic interactions as well as direct and indirect interactions^{16,17}. So far, subcomponents of food webs have often been studied in isolation, for example primary producers, the decomposer subsystem¹⁸, soil nematodes¹⁹, soil microbes, plant pathogenic fungi²⁰, above-ground invertebrates¹³, pollinators²¹ and so on. Here we present data from one of the most comprehensive biodiversity experiments so far, and show that diversity effects on higher trophic levels are mostly indirect and mediated through bottom-up trophic cascades. We use structural equation modelling approaches to develop comprehensive above-ground/below-ground biodiversity food webs. Finally, we link our results to recent interaction web models and provide explicit parameter estimates that can be used in future modelling exercises.

We experimentally manipulated plant species and functional group richness in 82 sown grassland plots (Methods), and recorded abundances and species richness of all relevant organism groups and biotic interactions between 2002 and 2009 (Supplementary Table 1). All data were analysed on a standardized scale²² from zero to one and the relationship between plant species richness and the different response variables was modelled using a power function¹⁸ to allow comparisons and extrapolation to other systems (see Supplementary Table 1 and

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Supplementary Fig. 3 for untransformed data). Analyses consisted of three steps. First, every response variable was analysed separately using a common set of linear, saturating and exponential models with untransformed plant species richness as the main explanatory variable. The presence of legumes and grasses and the number of plant functional groups were fitted as additional covariates. Variance heterogeneity was modelled using variance functions. Model selection was based on the Akaike information criterion for small sample sizes (AICc). Then, for parsimony, models were refitted using a power function. This allowed comparisons between the abundance and species richness of herbivores, carnivores and all other functional groups. Finally, multivariate techniques (multivariate linear models and structural equation models) were used to account for non-independence of variables measured on the same field plots.

Plant species richness had highly significant overall effects on the abundances of other organisms ($T_{PB} = 0.56$ (Pillai–Bartlett trace), approximately F-distributed with $F_{10,37} = 4.741$, $P < 0.001$; Fig. 1a, c), the species richness of other organism groups ($T_{PB} = 0.788$, approx. $F_{9,38} = 15.69$, $P < 0.001$; Fig. 1b, d) and on trophic interactions ($T_{PB} = 0.733$, approx. $F_{10,22} = 6.04$, $P < 0.001$; Supplementary Fig. 1; see Supplementary Methods for definitions of interactions). The abundance and species richness of organisms and biotic interactions were affected in broadly similar ways by changes in plant species richness (Fig. 1 and Supplementary Fig. 1).

Model selection using the complete range of linear, saturating and exponential models (Supplementary Tables 2 and 3) showed that 90% of all relationships could be approximated by a power model of the form $y = a + bS^z$ (ref. 18), where the exponent z can take any real value (in particular zero and one as special cases). Only five out of 38 organism groups declined with plant species richness (abundances of hyperparasitoids, fungivorous nematodes and mites, and abundance and

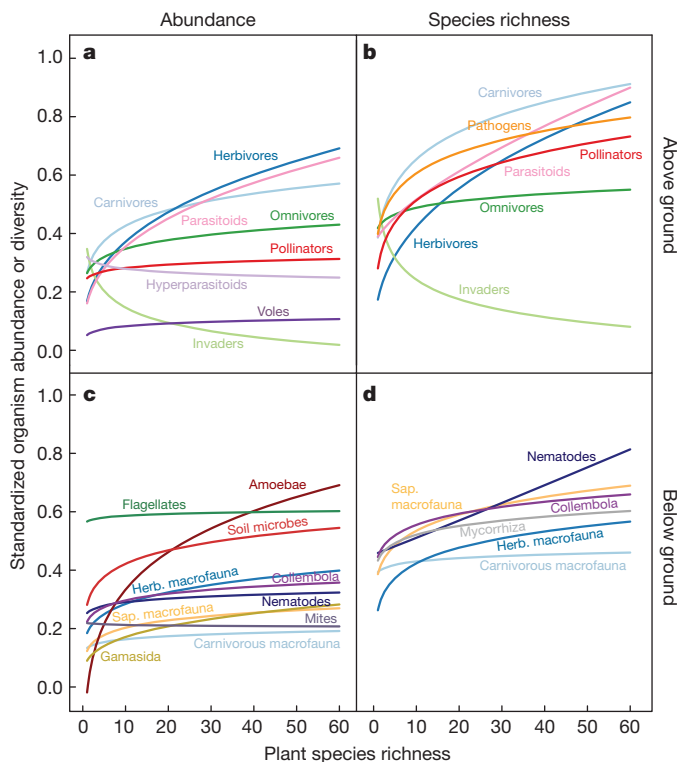


Figure 1 | Effects of plant species richness on above- and below-ground organisms in temperate grassland. **a, b**, Abundance (**a**) and species richness (**b**) of above-ground organisms. **c, d**, Abundance (**c**) and species richness (**d**) of below-ground organisms. All response variables scaled to [0, 1]. Every curve is fitted using a power function with covariates (Methods). Identical colours in each pair of panels indicate identical groups of organisms. For sample sizes, see Supplementary Table 1. Herb., herbivorous; Sap., saprophagous.

species richness of plant invaders; Supplementary Table 4). Responses of the below-ground subsystem were consistently smaller (average power model exponent of 0.11) than above-ground responses (exponent of 0.14).

Although most responses were saturating, closer inspection (Supplementary Table 5a–c) revealed consistent differences between the responses of herbivores, carnivores, omnivores and other trophic groups that are likely to reflect a general pattern (Fig. 2): with increasing trophic distance and for omnivores, species richness effects dampened—as indicated by the magnitude of the exponent of the common power function (Supplementary Table 4). This effect was found both for organism abundances and organism species richness, both above and below ground, and it was further supported by structural equation models (Fig. 3 and Supplementary Tables 6–10). Together, these findings indicate that species richness effects are generally dampened along trophic cascades.

If plant species richness acts on other organisms along trophic cascades, and plant species richness is the only experimentally manipulated variable, then the simplest conceptual model in our case is a bottom-up model of plant species richness effects; that is, plant species richness effects are passed from one trophic level to the next. Several authors have suggested such a ‘bottom-up template’ perspective for terrestrial food webs²³. Both decomposers and predators have long

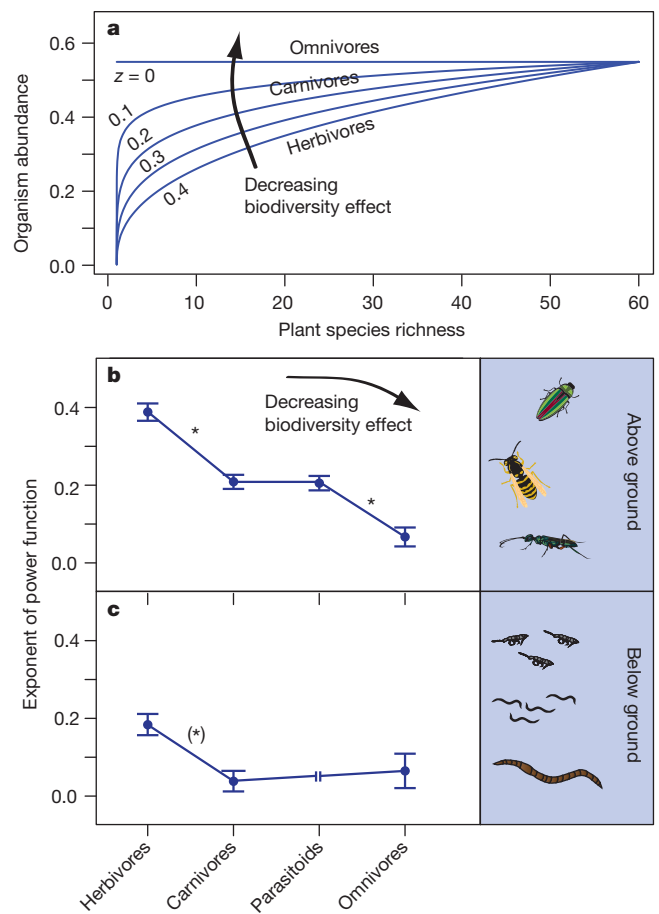


Figure 2 | Dampening of plant species richness effects with increasing trophic level. **a**, Conceptual figure showing how different values of z may influence biodiversity effects (x axis shows example range of 1–60 plant species). **b**, Estimates of z for above-ground herbivores, carnivores, parasitoids and omnivores. **c**, As in **b**, but for below-ground organisms. The y axes in **b** and **c** show estimated exponents of power functions fitted to data scaled to [0, 1]. Significant differences in z values are indicated by asterisks ($*P < 0.05$, $N = 50$ for above-ground organisms; $(*)P = 0.06$, $N = 82$ for below-ground organisms). Estimates are model predictions \pm s.e.

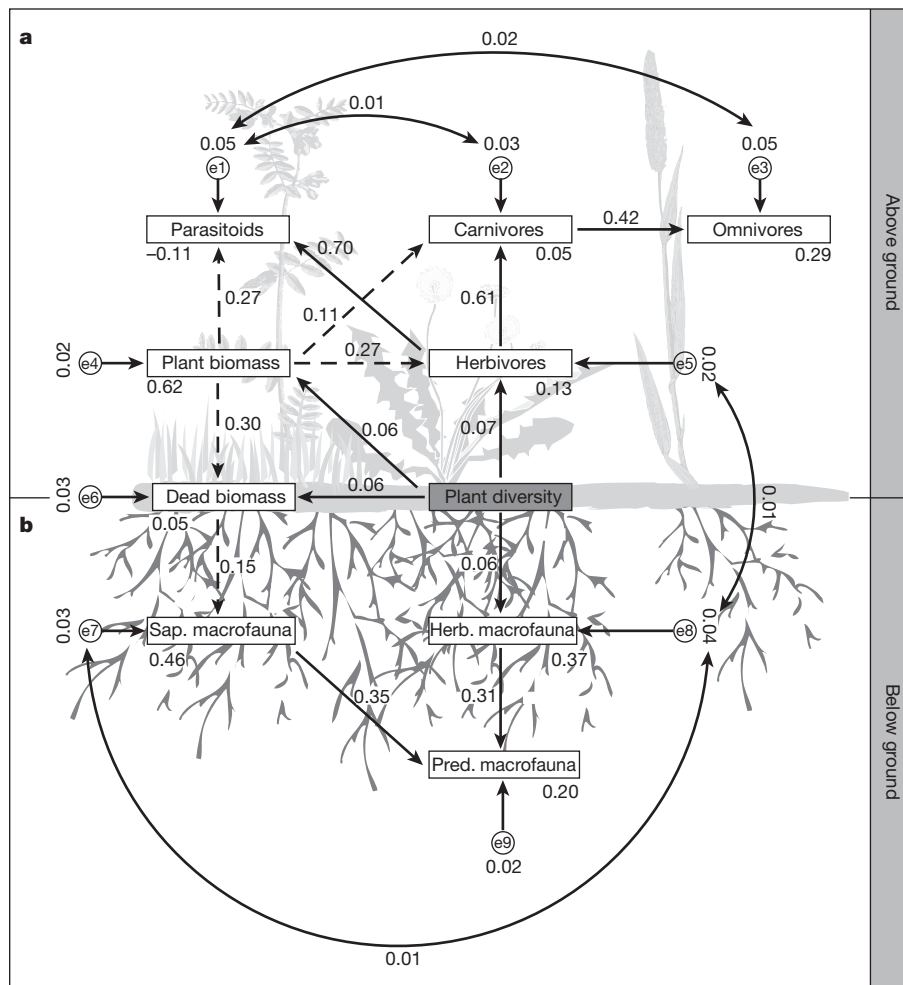


Figure 3 | Food web of above- and below-ground biodiversity. Results of a structural equation model with $N = 50$, $\chi^2 = 32.56$, $P = 0.212$, 27 degrees of freedom and a root mean squared error of approximation of 0.065 (90% confidence interval, [0, 0.135]). A model with top-down control of herbivores by carnivores had $\chi^2 = 32.07$, $P = 0.156$ and 25 degrees of freedom. **a**, Above-ground compartment; **b**, below-ground compartment. Unshaded rectangles represent observed variables (organism abundances). Circles indicate error

terms (e1–e9). Solid and dashed arrows connecting boxes show significant and non-significant effects, respectively. Numbers next to arrows and boxes are unstandardized slopes and intercepts, respectively. Double-headed arrows indicate correlations between error terms. Plant species richness was experimentally manipulated and has no error term. For details, see Supplementary Tables 6–10. Herb., herbivorous; Pred., predatory; Sap., saprophagous.

been proposed to be controlled essentially from the bottom up²⁴. However, top-down effects may also be expected, in particular if herbivores are not food limited²⁴.

Using structural equation models, we constructed a minimal adequate above-ground/below-ground biodiversity food web and found that plant species richness had almost exclusively bottom-up effects on higher trophic levels, both above and below ground (Fig. 3 and Supplementary Fig. 2). Three different theoretical constructs were used: a full model with bottom-up paths only; a full model with bottom-up and top-down paths; and all possible sets of reduced models, generated by single deletions of connections from full models (Supplementary Methods). These analyses showed that top-down control of herbivores by predators was not supported by the data. Other models (for example assuming direct effects of plant species richness on predators or omnivores) were rejected; that is, their implied covariance matrix differed significantly from the observed covariance matrix. In addition, we were able to reject hypotheses that assume positive responses only for specific trophic levels²⁵. Although plant biomass was indirectly linked to changes in predator or parasitoid abundance, these effects were not significant. This indicates that plant species richness effects are generally not mediated through vegetation density or biomass (Fig. 3a).

In a separate structural equation model for below-ground organisms, the amount of above-ground dead plant biomass entering the

below-ground system was generally less important than plant species richness per se (Supplementary Fig. 2). Hence, plant species richness had direct effects mainly on primary consumers, for example herbivorous macrofauna or herbivorous nematodes. In addition, there were strong direct effects of plant species richness on soil microbes and protozoans (Supplementary Fig. 2). It is likely that many of these below-ground responses are mediated either through changes in root production or through root exudates, but not through dead biomass or the amount of litter input (Supplementary Fig. 2). The direct plant species richness effects on microbes and protozoans could be mediated by changes in litter chemistry, litter diversity¹⁸ or root exudates²⁶.

Although structural equation models can be used to infer causality²⁷, strong inference requires experimental manipulation of trophic levels in addition to manipulations of plant diversity. We therefore exposed experimental nesting sites for prey (wild bees) and measured parasitism rates (Supplementary Fig. 1) as proxies for top-down control (Supplementary Methods). Parasitism increased with plant species richness, resulting in enhanced potential for biological control in species-rich systems.

One of the most fascinating developments in the theory of biodiversity and ecosystem processes is the inclusion of trophic and non-trophic interactions into generalized Lotka–Volterra models¹⁶. These models have theoretically predicted a bottom-up control of carnivores by plants,

with carnivore biomass indirectly controlled by plant and herbivore biomass, and top-down control of herbivores by carnivores. Structural equation models are a powerful tool for detecting such mutual dependencies, greatly enhancing our understanding of biodiversity effects in multitrophic systems. Overall, our results from a wide variety of organism groups provide strong support for a prominent role of plant species richness (rather than productivity or other covariates) in shaping multitrophic interactions.

Our results present the intriguing possibility that the effects of the species richness of one trophic level on others decrease with trophic distance. This hypothesis merits exploration by means of experimental manipulations of species numbers on other trophic levels. Because even an experiment as large as ours (82 plots) limits how many variables can reasonably be included in a multiple regression or structural equation model, future studies should be designed explicitly with a particular network of trophic interactions in mind. These studies could also be combinations of observational and experimental approaches.

We scaled all response variables to allow us to seek generalizations across different types of organism and trophic levels, but note that unscaled analyses might offer other types of insight. We also note that detailed collection of data at the level of each individual species, although prohibitively time consuming in a broad survey such as ours, is also likely to offer added insight. Our study should therefore be seen as a starting point rather than as an end point for further analyses of other data sets.

We have shown that the consequences of biodiversity loss are consistently negative for most organism groups and interactions, with particularly far-reaching feedback effects on basal trophic levels. Below-ground organisms will be less affected by biodiversity change (or will respond more slowly) than above-ground ones. Changes in plant species richness will affect neighbouring trophic levels and cascade up to higher trophic levels. Exponents of power functions ($y = bS^c$) will decline with trophic level. Our results highlight the importance of a diverse resource base²⁸ for trophic interactions in terrestrial ecosystems.

METHODS SUMMARY

Experimental design. In a 10-ha former arable field near Jena (Germany), we controlled the number of plant species, functional groups and plant functional identity in 82 plots, each 20 m × 20 m, in a randomized block design²⁹. Plots were seeded in May 2002 with 1, 2, 4, 8, 16 or 60 perennial grassland plant species, with 16, 16, 16, 16, 14 and 4 replicates, respectively. Plot compositions were randomly chosen from 60 plant species typical for local *Arrhenatherum* grasslands. Plots were maintained by mowing, weeding and herbicide applications.

Ecosystem variables. Sown and realized plant species richness were highly correlated (2006: Spearman's rank correlation coefficient, 0.995; $t = 91.94$; 80 degrees of freedom; $P < 2.2 \times 10^{-16}$); hence, sown richness was used for analysis. Above-ground invertebrates were collected on $N = 50$ plots using pitfall traps and suction sampling. Below-ground macro- and mesofauna were extracted from Kempton soil cores. Special sampling protocols were used for microorganisms (fungi, bacteria). Decomposition was measured using litter bags. Flower visitation was a count of pollinator visits. Parasitism was measured using a trap-nest technique. Hyper-parasitism was measured from aphid mummy counts in 6.25-m² replicate plots. Pathogen damage above ground and herbivory were estimated visually. Plant invasion was a count of the numbers of an invader plant species per unit area. Microbial biomass was measured using glucose as an artificial substrate. A full description is available in the Supplementary Methods.

Statistics. Explanatory variables in linear models were block, plant species richness, plant functional group richness, and grass and legume presence. Nonlinear models contained plant species richness, with legume and grass presence and functional richness as covariates. Models were simplified and compared using AICc. To test for differences between slopes, multivariate linear models were constructed, and orthogonal contrasts were used to test linear hypotheses. Structural equation models were fitted to test specific hypotheses on causal relationships.

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