

Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality

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Many experiments have shown that loss of biodiversity reduces the capacity of ecosystems to provide the multiple services on which humans depend^{1,2}. However, experiments necessarily simplify the complexity of natural ecosystems and will normally control for other important drivers of ecosystem functioning, such as the environment or land use. In addition, existing studies typically focus on the diversity of single trophic groups, neglecting the fact that biodiversity loss occurs across many taxa^{3,4} and that the functional effects of any trophic group may depend on the abundance and diversity of others^{5,6}. Here we report analysis of the relationships between the species richness and abundance of nine trophic groups, including 4,600 above- and below-ground taxa, and 14 ecosystem services and functions and with their simultaneous provision (or multifunctionality) in 150 grasslands. We show that high species richness in multiple trophic groups (multitrophic richness) had stronger positive effects on ecosystem services than richness in any individual trophic group; this includes plant species richness, the most widely used measure of biodiversity. On average, three trophic groups influenced each ecosystem service, with each trophic group influencing at least one service. Multitrophic richness was particularly beneficial for 'regulating' and 'cultural' services, and for multifunctionality, whereas a change in the total abundance of species or biomass in multiple trophic groups (the multitrophic abundance) positively affected supporting services. Multitrophic richness and abundance drove ecosystem

functioning as strongly as abiotic conditions and land-use intensity, extending previous experimental results^{7,8} to real-world ecosystems. Primary producers, herbivorous insects and microbial decomposers seem to be particularly important drivers of ecosystem functioning, as shown by the strong and frequent positive associations of their richness or abundance with multiple ecosystem services. Our results show that multitrophic richness and abundance support ecosystem functioning, and demonstrate that a focus on single groups has led to researchers to greatly underestimate the functional importance of biodiversity.

Global change is causing species loss across many trophic groups^{3,4}, with potential effects on the services that ecosystems provide to humans^{1,2}. The functional consequences of a decline in biodiversity across multiple trophic groups are hard to predict from studies focusing on single taxa, as the functional effects of different groups may complement or oppose each other^{5,6,9,10}. The effects of the diversity of plants and microbes are complementary, maximizing rates of nutrient cycling¹¹; plant and herbivore diversity, on the other hand, have opposing effects on biomass stocks^{10,12,13}. Consequently, we know very little about the relative effect of changes in the diversity of different trophic groups on the provision of individual^{2,5,6,9,13,14} or multiple (multifunctionality)^{11,15} ecosystem services.

In addition to decreasing species richness, global change is altering the total abundance (total number of individuals or amount of biomass within communities) of multiple trophic groups⁴. Changes in

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abundance could mitigate or exacerbate the functional consequences of species loss^{16,17} by influencing the ability of each trophic group to capture resources. However, studies normally focus on the effects of community evenness or of dominant species^{18–20}, whereas the simultaneous effects of changes in richness and total abundance on the functioning of ecosystems have been largely unexplored^{6,16}. The relative importance of richness and abundance may depend on the function or service of interest. Total abundance could be a main driver of biogeochemical process rates (for example, biomass production¹⁸, nutrient capture and cycling). By contrast, ecosystem services related to biotic interactions, such as pollination or pest control, could be predominantly driven by species richness¹⁶. Ecosystem services also depend on abiotic factors and, although experiments show that the effects of biodiversity loss on ecosystem functioning are as large as those of abiotic drivers^{7,8}, it is unclear whether species richness and abundance are similarly important in real-world ecosystems^{6,14,21,22}.

We adopted a multitrophic approach to evaluate relationships between biodiversity and multifunctionality in 150 real-world grasslands. We measured the richness and abundance of species in nine trophic groups: primary producers, above- and below-ground herbivores and predators, detritivores, soil microbial decomposers, plant symbionts, and bacterivores. These trophic groups comprised 4,600 plant, animal and microbial taxa, and were measured alongside 14 ecosystem variables (proxies for both functions and services, hereafter referred to as services). These are related to the four main types of ecosystem services²³: provisioning (fodder production and quality), supporting (potential nitrification, phosphorus retention, root biomass and decomposition rate, mycorrhizal colonization and soil aggregate stability), regulating (soil carbon levels, pollinator abundance, pest control, resistance to pathogens) and cultural services (recreation benefits of flower cover and bird diversity). We fitted linear models to our data to test for both positive and negative relationships between the richness and abundance of species within the nine trophic groups and each ecosystem service, the four types of services (provisioning, supporting, regulating and cultural), and ecosystem multifunctionality²² (see Methods). We accounted for potential confounding factors by performing our analyses on residuals, after controlling for variability in land-use intensity, soils and climate. We compared our results with models that included only plant-species richness, the most commonly used measure of biodiversity^{21,24,25}, and with models that included the richness and abundance of each individual trophic group. Additional analyses compared the amount of variance explained by, and the effect size (standardized slope) of, multitrophic richness and abundance with those of land-use intensity and environmental variables.

Effects on individual ecosystem services, service types, and multifunctionality were better predicted by changes in multitrophic richness and abundance than by those in the richness or abundance of any individual trophic group (Fig. 1 and Extended Data Fig. 1). The most parsimonious models included the richness and/or abundance of 3.14 ± 0.36 trophic groups (average ± s.e.m. across all 14 services) to predict the variation in each ecosystem service. These results remained when using raw data instead of environment-corrected residuals (Extended Data Fig. 2), different combinations of ecosystem services (Extended Data Fig. 3), and even when we accounted for well-established links between a predictor and service in our models (for example, plant cover versus biomass). Multitrophic richness had stronger and more positive relationships with the provisioning, regulating and cultural services than plant richness alone (Fig. 1 and Extended Data Fig. 1). For example, both plant and predator richness were related to high levels of pest control, suggesting that combined top-down and bottom-up effects of diversity²⁶ maximize the provision of this regulating service. Multitrophic richness also had a more positive effect than even the strongest positive-richness effect found across all individual trophic groups on the regulating and cultural services. The findings of our observational study were supported by a quantitative review of the few studies that manipulated the richness of more than one group. Our

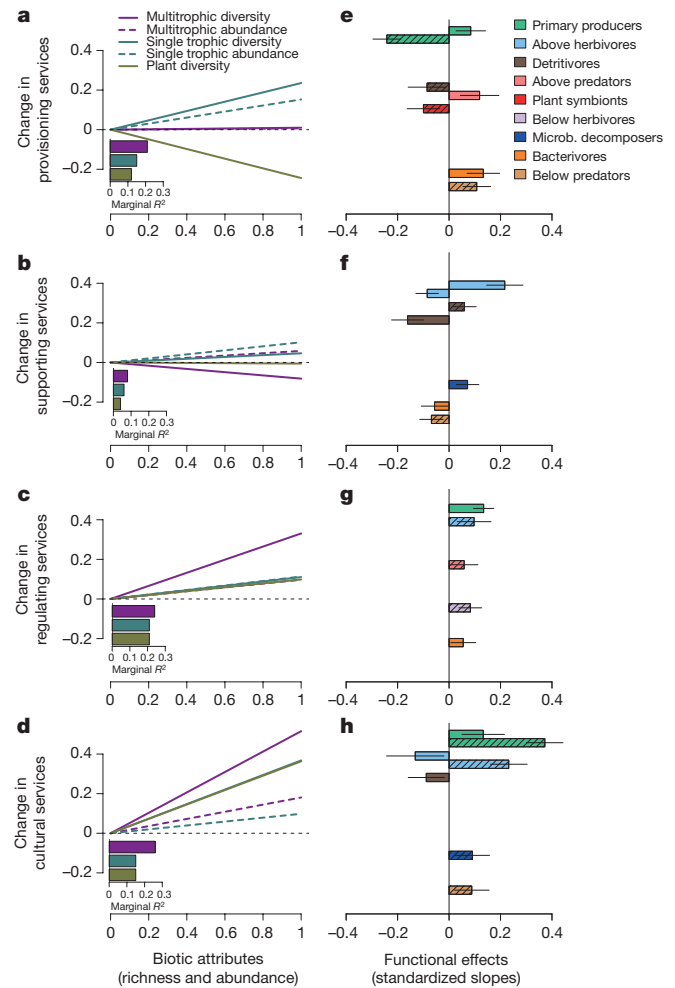


Figure 1 | Effects of multitrophic richness and abundance on grassland functioning. **a–d**, Variance explained after accounting for the influence of ‘site’ as random factor (marginal R^2 , the equivalent of R^2 for mixed models) and standardized effects for each ecosystem service when models included abundance and richness of multiple or individual trophic groups. **e–h**, Standardized effects (mean ± s.e.m.) of richness and abundance (full and hatched bars, respectively) of individual trophic groups on each ecosystem service type. Ecosystem services types are plant biomass and forage quality (provisioning); potential nitrification, phosphorus retention, mycorrhizal colonization, soil aggregate stability, root biomass and decomposition (supporting); soil carbon, pollinator abundance, pest control and resistance to pathogens (regulating); flower cover and bird diversity (cultural).

review showed that including the richness of a second trophic group increased the variance in ecosystem functioning by 14–96% for litter decomposition¹⁴, biomass production^{2,12,26}, or the number of carbon sources used⁵ (Extended Data Table 1). Collectively, our results show that high species richness in multiple trophic groups is necessary to maintain high levels of ecosystem functioning, particularly for regulating and cultural services.

Alongside multitrophic richness, the combined effect of a high multitrophic abundance strongly affected ecosystem functioning (according to the amount of variance explained and its effect size). Multitrophic abundance had positive effects on the provisioning and supporting services, but these were generally weaker than those found for the individual trophic group that had the strongest positive effect. This suggests that an abundance of some trophic groups can dampen the effect on ecosystem functioning induced by others. Figure 1, for instance, shows that a higher abundance of predators partially counteracted the positive effects of abundant herbivores on supporting services. Conversely, a high level of richness in a given trophic

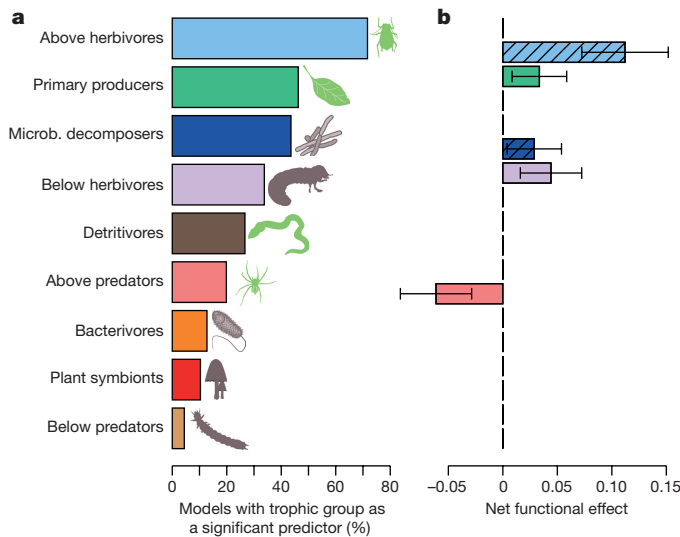


Figure 2 | Functional importance of multiple trophic groups.

a, Proportion of the multifunctionality metrics (calculated using every possible combination of 1–9 services; $N = 501$; see Methods) in which the biotic attributes (richness and/or abundance) of each trophic group was included in the most parsimonious model. **b**, Functional effects (standardized slopes (mean \pm s.e.m.)) in the model fitted to all 14 services of the richness (open bars) and abundance (hatched bars) of each group. Bars are shown only for the predictors included in the most parsimonious models. Green and brown cartoons indicate above- and below-ground trophic groups, respectively.

group generally complements the positive effects of other trophic groups on ecosystem services (see a comparison of multitrophic and unitrophic richness in Fig. 1). These contrasting effects caused multitrophic abundance to increase ecosystem multifunctionality only at low-to-moderate levels (Extended Data Fig. 1). Overall, our results underline the important role of species richness in driving the functioning of ecosystems^{1,2,14–17,24,25}, while also highlighting the often-overlooked effect of total biomass abundance on the supporting and provisioning services.

To test how generally applicable the trends in relationships between multitrophic richness and abundance were, we calculated multifunctionality metrics using all possible combinations of services. High multitrophic richness or abundance had increasingly positive effects as more services were considered and this effect was consistent across a wide range of levels of multifunctionality (Extended Data Fig. 3). To further explore this result, we calculated the similarities in the identities of the trophic groups driving a given pair of ecosystem services (the functional overlap, \bar{o} (ref. 25)). On average, we found functional overlaps lower than 30% ($\bar{o} = 0.27 \pm 0.03$, mean \pm s.e.m.), similar to results found for plant species in grassland experiments ($\bar{o} = 0.19–0.49$)²⁵. This demonstrates low multitrophic redundancy and means that different services are supported by different trophic groups (Fig. 1 and Extended Data Fig. 1). We also found that different groups positively affected multifunctionality when it was calculated according to scenarios representing different land-use objectives (Extended Data Fig. 4). Finally, five of the nine trophic groups had the strongest net-positive effects on at least one ecosystem service (for example, primary producers on pest control, soil microbial decomposers on aggregate stability; Extended Data Fig. 1), with each group affecting at least one service. Collectively, these results show the low functional redundancy found between the multiple trophic groups studied, explaining why high multitrophic richness is needed to support high levels of ecological multifunctionality or to promote a larger number of ecosystem services.

The relationships between multitrophic richness, multitrophic abundance and ecosystem services were not always positive (Figs 1, 2 and Extended Data Fig. 1), consistent with previous studies^{27,28}. Negative relationships might be explained by interference between species

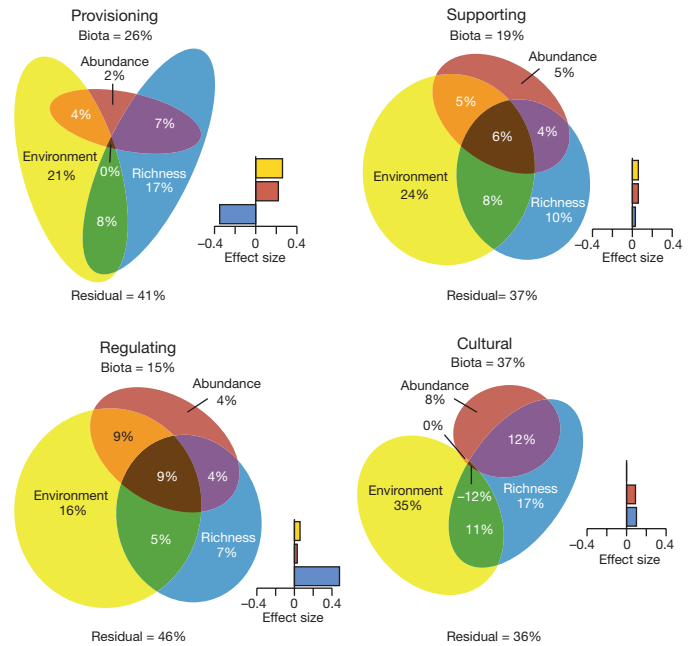


Figure 3 | Biotic versus abiotic drivers of ecosystem functioning.

Variation partitioning for three predictor categories in our statistical models: environment, species richness and total abundance (details in Methods). Diagrams show the average across services within each ecosystem service type (detailed results are in Extended Data Figs 2 and 5). Shown are the unique variance explained by each predictor category, the shared variance between these categories (intersections of circles), and the variance not explained by the models (the residual). Biota refers to the total variance explained by species abundance and richness combined. Standardized effect sizes are shown as bar plots.

within a given trophic group¹⁰ or by compositional shifts leading to declines in ecosystem functioning^{17,20,29}. Despite these negative associations or harm to services, our results suggest that the most important trophic groups for maintenance of the services considered are above-ground herbivorous insects, primary producers and soil microbial decomposers. The richness or abundance of these trophic groups were most often correlated to ecosystem multifunctionality (43–72% of the 501 possible combinations between the services we measured), and had net-positive effects across all services (Fig. 2). These three groups also showed strong and frequent positive associations with the four main ecosystem service types (Fig. 1). These results agree with other studies that have identified plants and soil microorganisms as key drivers of ecosystem functioning^{11,14,15,29}, extending these findings to the richness and abundance of different trophic groups, including primary producers and consumers both above and below ground. The species richness of some of these functionally important trophic groups relate to whole-ecosystem diversity^{3,30} and, thus, management strategies focused on them may foster synergies between biodiversity conservation and high multifunctionality levels.

The relative importance of both multitrophic richness and abundance compared to the environmental drivers of ecosystem functioning has been rarely studied outside of experiments or individual functions^{7,8,11,15,21,24}. We therefore calculated the proportion of variance in ecosystem functioning that was explained by multitrophic richness, abundance and environmental (soil, topography and land-use) factors. Our models accounted for a large proportion (54–64%) of the variance in the provisioning, supporting, regulating and cultural ecosystem service types (Fig. 3 and Extended Data Fig. 5). Multitrophic richness and abundance explained at least as much of the variance in ecosystem functioning as abiotic conditions or land-use intensity did, and generally had stronger effects (Fig. 3; Extended Data Fig. 5). These results provide evidence that biodiversity is of comparative importance to environmental factors in driving ecosystem functioning. This is true

not only for individual functions in small-scale experiments^{7,8}, but also for multiple ecosystem services in realistic landscapes (see refs 15, 24).

Our study shows that the functional importance of biodiversity in real-world ecosystems has been greatly underestimated, as a result of focussing on individual trophic groups. We demonstrate here that the functional effects of multitrophic richness and abundance are as strong as, or even stronger than, those of the environment or land-use intensity. We identified primary producers, above-ground herbivores and soil decomposers as particularly important trophic groups for maintaining a functioning ecosystem. Our results suggest that it is important to preserve high levels of species richness, abundance or both within a wide range of taxa. This must include taxa often ignored by conservation efforts such as soil microbial decomposers¹⁵, or those considered pests in agricultural systems such as herbivorous insects, if we are to promote high levels of the multiple ecosystem services upon which human well-being depends.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Author Contributions S.S. and E.A. conceived the idea of this study. M.F. initiated the Biodiversity Exploratories project aimed at measuring multiple diversities and functions in the field sites. All authors but S.S., E.A. and F.V.D.P. contributed data. S.S. and F.V.D.P. performed the analyses. S.S. and S.C.R. performed the literature search. S.S. wrote the first draft of the manuscript and all the authors (especially E.A., P.M., F.V.D.P., M.M.G. and D.P.) contributed substantially to the revisions.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to S.S. (santiago.soliveres@ips.unibe.ch).

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METHODS

No statistical methods were used to predetermine sample size. The experiments were not randomized. The investigators were not blinded to allocation during experiments and outcome assessment.

Study sites. We selected a total of 150 grassland sites (50 m × 50 m) in three regions of Germany (50 sites per region) to cover a gradient of land-use intensities, characterized by contrasting grazing, fertilization and mowing levels (www.biodiversity-exploratories.de, ref. 31). The regions in the south-west (Schwäbische Alb) and the north-east (Schorfheide-Chorin) are UNESCO Biosphere Reserves, whereas the central region is in and around the Hainich National Park. The three regions differ substantially in geology, climate and topography³¹, covering a range of ~3 °C in mean annual temperature and 500 mm in annual precipitation. Plots in each region cover the range of land-use intensities typical for Central European grasslands. We obtained information on land use via questionnaires sent to land owners, asking about the number and type of livestock (converted to livestock units) and the duration of grazing in each plot, the fertilization (from which we calculated the amount of nitrogen added), and the mowing (number of cuts per year^{31,32}). We used this information to calculate three standardized indices summarizing grazing, fertilization and mowing intensity (see ref. 32 for full methodological details).

Diversity measures. At each site, we measured the species richness and abundance of nine functional groups using standard methodologies (Extended Data Table 2). In total we observed about 4,600 taxa on the 150 grasslands studied. The nine trophic groups were: primary producers (vascular plants and bryophytes), below-ground herbivores (herbivorous insect larvae sampled in the soil), below-ground predators (carnivorous insect larvae sampled in the soil), detritivores (insects and Diplopoda feeding on leaf litter and other detritus), soil microbial decomposers (soil bacteria), above-ground herbivores (insects feeding solely on above-ground plant material), above-ground predators (carnivorous insects, spiders and Chilopoda), plant symbionts (arbuscular mycorrhizal fungi), and bacteria-feeding protists (heterotrophic flagellates and ciliates). Lichens and omnivores were not considered in our analyses as they were too rare. We directly measured species richness for most groups, but richness was quantified as family richness for below-ground insects and soil bacteria and as the number of operational taxonomic units (OTUs) for the mycorrhizae and protists. The abundance of each trophic group was also measured using different methods: number of individuals for arthropods, amount of cover for vascular plants and bryophytes, and relative proportion of sequence reads assigned to each family or OTU for protists, soil bacteria and mycorrhiza. To avoid multicollinearity, we did not include the abundances of protists or detritivores as they were highly correlated (Spearman's $\rho > 0.6$) with richness (for more details see Extended Data Table 3).

We also measured the abundance and richness of foliar fungal pathogens, pollinators and birds; however, to include a broader range of ecosystem services in our analyses, we treated these groups as proxies of ecosystem services. Total pollinator abundance and the inverse of pathogen abundance were treated as proxies of regulating services (pollination and disease regulation), and we used bird-species richness as a measure of a cultural ecosystem service. Lepidoptera behave as herbivores during juvenile stages and as pollinators when adults. To avoid accounting for them twice, we assigned them to only one trophic group (pollinators), as the data were counts of the adult butterflies, not the caterpillars.

Ecosystem functioning measures. At each site, we measured 14 different ecosystem variables (both functions and service proxies; Extended Data Table 2) and classified them into four types of services following the Millennium Ecosystem Assessment²³. These 14 ecosystem services were: i) supporting services related to nutrient capture and cycling (root biomass, root decomposition rates, potential nitrification (based on urease activity in soil samples), phosphorus retention (calculated as a ratio between shoot and microbial phosphorus stock and soil extractable phosphorus), arbuscular mycorrhizal fungal root colonization (measured as hyphal length), soil aggregate stability (proportion of water-stable soil aggregates)); ii) provisioning services related to agricultural value (forage production (above-ground plant biomass) and forage quality (based on crude protein and relative forage value)); iii) regulating services for neighbouring crop production or climate regulation (that is, regulating services: resistance to plant pathogens, pest control, pollinator abundance and soil organic carbon); or iv) cultural services linked to recreation (bird diversity and flower cover). Because the values for trophic groups and ecosystem functions varied widely, we standardized all variables to a common scale ranging from 0 to 1 according to the following formula: $STD = (X - X_{min}) / (X_{max} - X_{min})$; where STD is the standardized variable and X , X_{min} and X_{max} are the target variable, and its minimum and maximum value across all sites, respectively. This made slope estimates for different predictors comparable.

We calculated ecosystem multifunctionality metrics from the 14 services as the percentage of measured services (measured services only to correct for the

fact that some services that had not been measured in all sites) that exceeded a given threshold of their maximum observed level across all study sites. To reduce the influence of outliers we calculated the maximum observed level as the average of the top five sites^{22,33}. Given that any threshold is likely to be arbitrary, the use of multiple thresholds is recommended to better understand the role that biodiversity plays in affecting ecosystem multifunctionality and to understand trade-offs between functions of interest²². Therefore, we used four different thresholds (25%, 50%, 75% and 90%) to represent a wide spectrum in the analyses performed (Extended Data Figs 1–3). As an alternative approach we also calculated multifunctionality scenarios, weighting the services differently according to the different potential views of stakeholders (that is, stakeholders willing only to promote provisioning services versus those trying to maximize cultural and recreation services or the sustainability of soils and crops; Extended Data Fig. 4)³⁴.

Effects of multitrophic richness and abundance on grassland ecosystem services and multifunctionality. We used linear models to evaluate the relationships between species richness and abundance in the nine trophic groups and each of the 14 individual ecosystem services, along with the different multifunctionality metrics (four thresholds and the metrics were obtained by weighting each ecosystem service according to different potential stakeholders' needs; for example, only provision, sustainable soils and crops, or cultural scenarios, see ref. 34). In all cases, we used a Gaussian error distribution as the errors of our response variables were normally distributed. We report the effects of the different trophic groups on the different functions as slopes from the multiple regression model; these are corrected for the effects of all other variables in the model. Since our main focus was on calculating the independent effects of the richness and abundance of the different trophic groups, we corrected them for co-varying factors. Thus, we calculated residuals for all our variables (both biotic predictors and functioning measures) from linear models including region, land-use intensity (standardized measures of mowing, grazing and fertilization intensity) and other important environmental factors (soil type and depth, pH, a topographic wetness index based on position within the slope and orientation, and elevation). As an alternative to using residuals, we also fitted models with all the environmental and land-use predictors (standardized to give comparable coefficients) alongside the diversity and abundance measures. These approaches gave very similar results (Extended Data Fig. 2). Standardized coefficients of the functional effects of richness were very similar, whether or not abundance was included ($\rho = 0.80$, $P < 0.0001$, $N = 162$; data not shown). We also fitted models with the abundance and richness of only one individual trophic group to compare the results of the best individual trophic group with the multitrophic analyses (Extended Data Fig. 1). Finally, we fitted models with only richness of vascular plant species as a predictor. The latter is the most common measure of biodiversity^{7,8,21,24,25,35–38} and we used it to compare our results with those found in previous studies on biodiversity–ecosystem functioning relationships.

We performed model simplification using the stepAIC function in R, and further simplified the minimal models produced using AIC by removing all terms that were not significant according to F -ratio tests (Extended Data Table 4). Results using alternative approaches for model selection are presented in Extended Data Fig. 6. We did not fit interactions between the richness and abundance of different trophic groups, or between those and environmental factors, as this would require a large number of coefficients, would be difficult to interpret and would require an even larger data set than ours (see ref. 20 for a study evaluating the interaction between land-use and diversity). We did not find evidence of nonlinear relationships between our predictors and the ecosystem services measured when checking all bivariate relationships; thus we did not include nonlinear terms in the models to keep them simple.

Not all trophic groups or ecosystem services were measured on all sites; thus different services were analysed using different sized data sets (N ranged between 111 and 54, depending on the service). The different sampling sizes used were not related to the number of trophic groups included in the most parsimonious model (Spearman's rank correlation coefficient $\rho = 0.32$), the increase in variance explained by vascular plant species richness ($\rho = -0.21$) or the net effect of richness or abundance ($\rho = -0.01$ or 0.05 , respectively; $N = 14$ and $P > 0.25$ in all cases). Thus, fitting models differing in sample size for different services did not affect our results.

The inclusion of many predictors in statistical models increases the chance of type I error (false positives). To account for this we used a Bernoulli process to detect false discovery rates, where the probability (P) of finding a given number of significant predictors (K) just by chance is a proportion of the total number of predictors tested ($N = 16$ in our case: the abundance and richness of 7 and 9 trophic groups, respectively) and the P value considered significant ($\alpha = 0.05$ in our case)^{39,40}. The probability of finding three significant predictors on average, as we did, is therefore, $P = [16! / (16 - 3)!] \times 0.053(1 - 0.05)^{(16 - 3)} = 0.0359$, indicating

that the effects we found are very unlikely to be spurious. The probability of false discovery rates when considering all models and predictors fit (14 ecosystem services \times 16 richness and abundance metrics) and the ones that were significant amongst them (52: 25 significant abundance predictors and 27 significant richness predictors) was even lower ($P < 0.0001$). All analyses were performed using R version 3.0.2 (ref. 41).

Net functional effects of the different trophic groups across ecosystem service types. We calculated the net effect of each trophic group on each ecosystem service type (provisioning, supporting, regulating and cultural) by fitting all services belonging to these types into a single model. To do so, we added two extra predictors to our models: 'service identity' as a fixed factor, to account for differences between individual services, and 'site' as a random factor, to account for correlations between services, abundance and richness values measured on the same site. Since we were interested in the net effects of each group across all services, we did not fit interactions between our multitrophic predictors and service identity. The net effect across all services was analysed using the same approach, while fitting a single model for the 14 ecosystem services at the same time. This approach corrects for the fact that the individual service models vary in their explanatory power and in the predictor variables included. Fitting all services into a single model allows us to obtain a robust estimate of the net functional effect (the standardized coefficient from the model) of the abundance and richness of each trophic group on the service type of each ecosystem and on ecosystem multifunctionality, together with an estimate of its error. If the standardized coefficient was positive, we interpreted it as a net overall positive effect of either richness or abundance across all services, or on a given service type (Figs 1 and 2). In all cases, we used standardized coefficients of the most parsimonious models after model reduction. However, our results remained when using other approaches that account for differences in model fit, such as multi-model averaging coefficients (coefficients were weighted according to the AIC weight of the models in which each predictor is included) or when weighting the standardized coefficient for each ecosystem service by the adjusted R^2 of each model (which should also be comparable across models with different response variables; Extended Data Fig. 6).

Variance partitioning analyses. Variance partitioning analyses (also known as commonality analyses) were performed with standard techniques^{42,43} based on the comparison of variance explained by models including every possible combination of variables. Variables were organized by environment (study region, soil type, pH, topographic wetness index, grazing and fertilization, with the remaining environmental predictors removed to prevent multicollinearity; shown in Extended Data Table 3), species richness (standardized species richness of the nine trophic groups) and abundance (standardized abundance of those trophic groups in which abundance and richness were not strongly correlated ($\rho < 0.6$; shown in Extended Data Table 3)). Thus, we fitted a series of seven models for each service and multifunctionality metric (at the 25%, 50%, 75% and 90% thresholds) to extract the unique and shared variance for each combination of variables (environment only, richness only, abundance only, environment + abundance, environment + richness, richness + abundance, and all predictors together). Variance-partitioning analyses were performed with the full models (without model simplification) to allow us to compare between different services. As a consequence, we used R^2 rather than the adjusted R^2 because, owing to the large number of predictors, some adjusted R^2 values were negative, complicating the extraction of unique variance explained by each predictor. Venn diagrams were drawn using Euler APE for Windows⁴⁴.

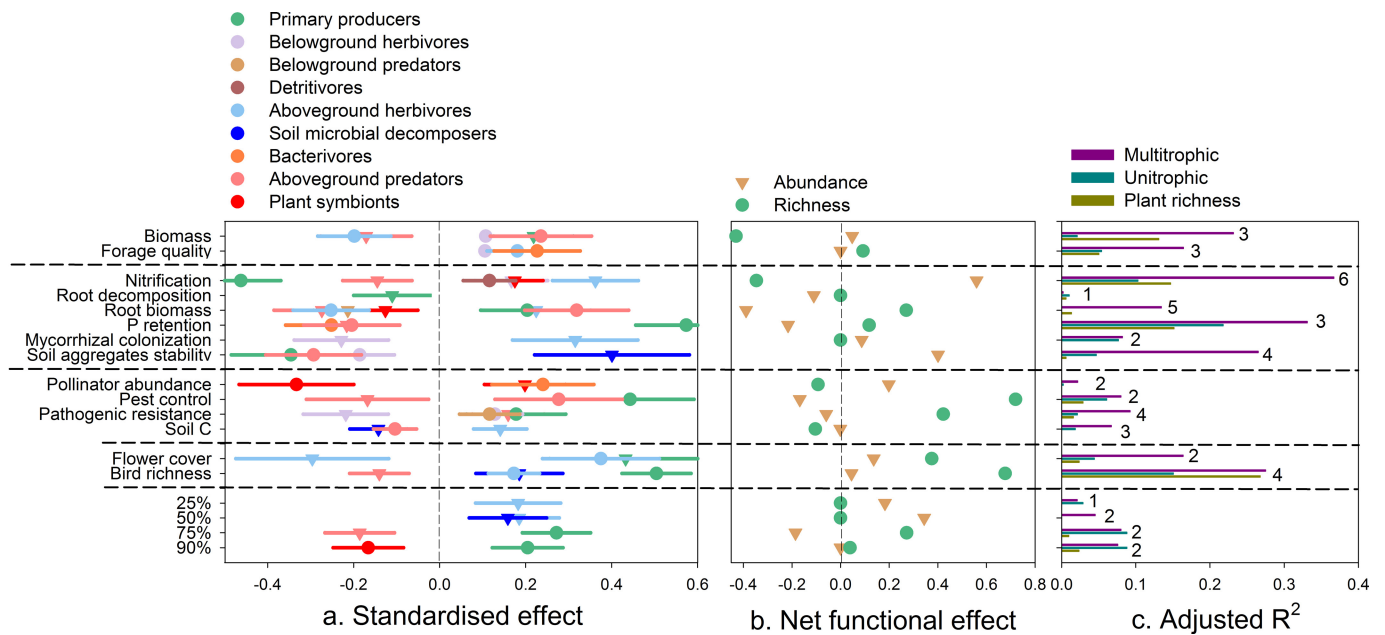
To compare the effect size among richness, abundance and environment on the different ecosystem services and multifunctionality metrics, we summed the standardized coefficients of all predictors from each component (the abundance of five trophic groups (abundance), the richness of nine trophic groups (richness), and pH, fertilization, grazing, and topographic wetness index (environment)). We excluded study region and soil type when summing effects, as these were categorical predictors and their coefficients were not straightforward to interpret. We performed these calculations for each of the 14 ecosystem services and 4 multifunctionality metrics in isolation (Extended Data Fig. 4), and for each ecosystem service type (Fig. 2) by using models containing all the ecosystem services belonging to each type into a single model (again, adding 'service identity' and 'site' as fixed and random predictors, respectively).

Analysing every possible combination of ecosystem services. Studies on multifunctionality are difficult to compare as they include different measures of ecosystem functioning. To allow us to generalize our results and to test whether multitrophic richness and abundance are more important in supporting higher numbers of services simultaneously, we also calculated multifunctionality

indices using every possible combination of the services we measured. We did this after removing those services with more than 20 missing sites, leaving a total of 9 services (501 combinations) as response variables. We calculated multifunctionality at the 25%, 50%, 75% and 90% thresholds for all these combinations (Extended Data Fig. 3). We also tested the sensitivity of our analyses to missing data by repeating our analyses for every possible combination of 1–13 of the 14 measured services (16,368 combinations; results for multifunctionality calculated with all 14 ecosystem services are presented in Extended Data Figs 1, 2). To allow the comparison of models with different services, data gaps were filled with the average value of a given service in a given region, which is a conservative approach. In both cases (combinations of 1–13 or 1–9 functions), the most parsimonious models possible were selected on the basis of their AIC. This avoids inflated type I error, caused by fitting a large number of models, as model selection was not based on P values. Results using 9 or 14 functions were qualitatively the same and therefore only the former are shown here.

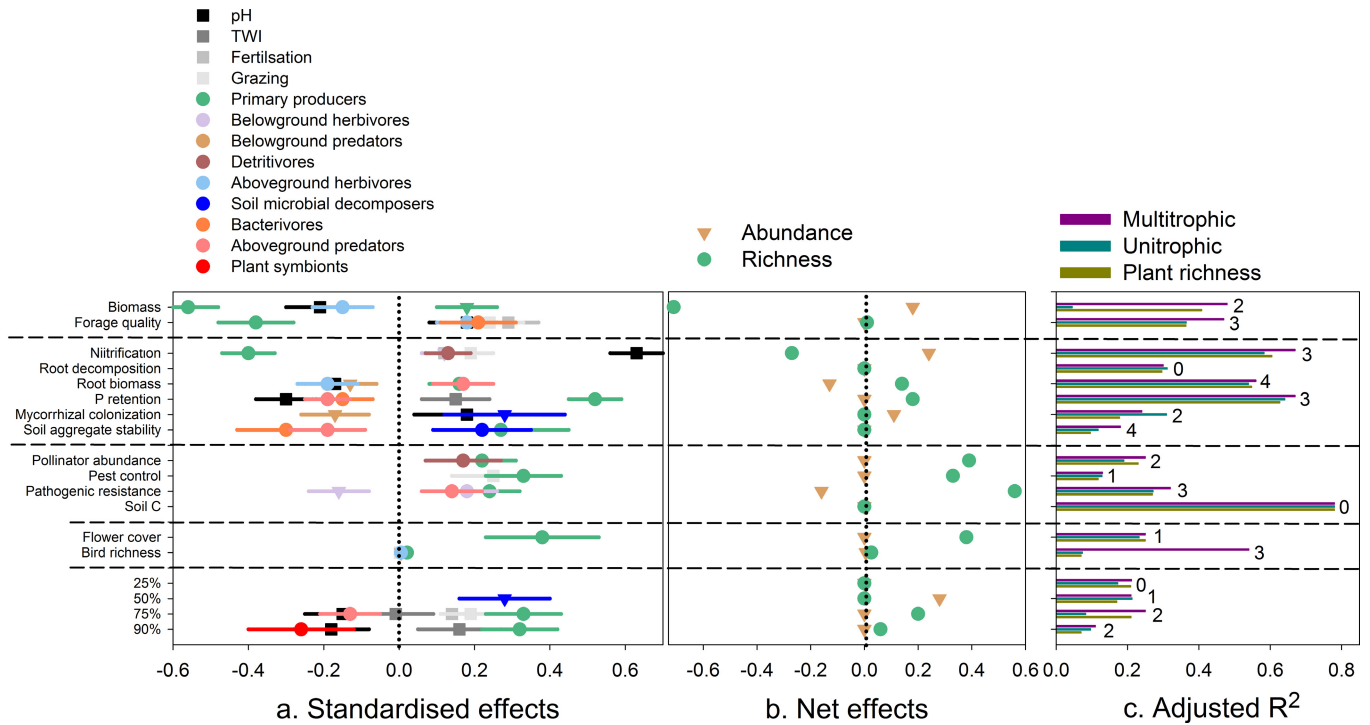
Review of multitrophic manipulative approaches. Manipulative experiments including as many groups and services as we considered in this study do not yet exist. However, we compared our correlational results with available evidence from experiments manipulating the diversity of more than one trophic group. To do this we performed a bibliographic research in the Web of Knowledge and in Google Scholar using all combinations of the terms 'multitrophic' or 'trophic groups' + 'functioning' or 'multifunctionality' or 'biomass' or 'ecosystem services' or 'diversity'. We also screened references within available reviews on multitrophic diversity–ecosystem functioning relationships^{10,27,45}. Of the papers found, we selected those which fulfilled the following criteria: i) it was a manipulative study, ii) it included a range in species richness (not only presence or absence) of, at least, two different trophic groups and iii) it provided enough information to calculate the increase in variance explained by the addition of a second trophic group. Only four studies, including seven ecosystem functions, fulfilled these criteria (Extended Data Table 1). Some of these manipulative studies did not include plants, so we calculated the percentage increase in variance seen when comparing a model with the trophic group that had the strongest explanatory power in models containing two trophic groups. When the same function was measured across several studies (that is, biomass), we calculated the average increase in variance explained for this variable when another trophic level was added. These results were used to qualitatively compare the limited evidence from multitrophic manipulations with our results.

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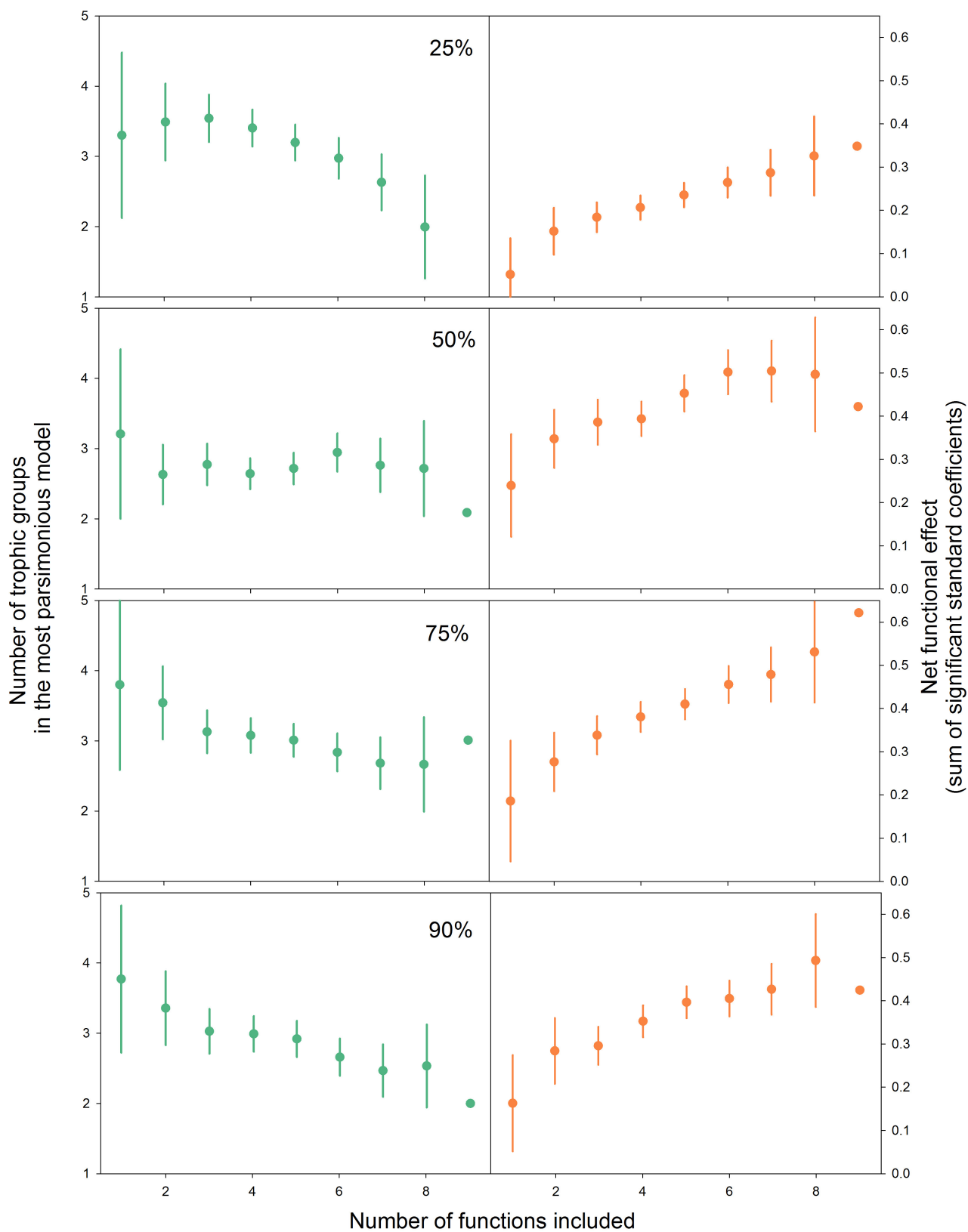
Extended Data Figure 1 | Functional effects of multitrophic richness and abundance on 14 grassland ecosystem services. a, Standardized coefficients (mean \pm s.e.m.) of the abundances (triangles) and richness (circles) of those trophic groups that significantly affect a given function are shown. **b,** The net effect (that is, the sum of significant standardized effects). **c,** Difference in adjusted R^2 between the final multitrophic models and those models using the abundance and richness of the best

performing individual trophic group (unitrophic) or plant species richness (plant richness). Ecosystem services are organized by the main four types of services they associate with (provisioning, supporting, regulating and cultural). The number of trophic groups included in the most parsimonious model is given next to their adjusted R^2 . Multifunctionality results at 25%, 50%, 75% and 90% thresholds are also shown (see Methods).



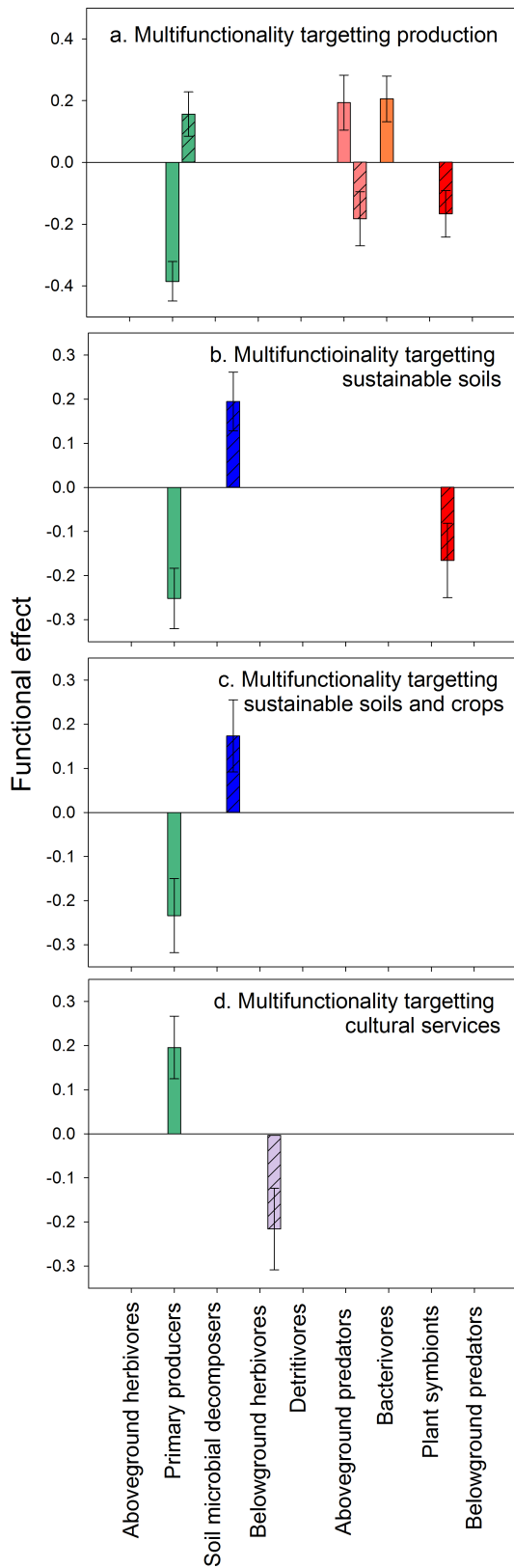
Extended Data Figure 2 | Functional effects of environmental factors and multitrophic richness and abundance on 14 grassland ecosystem functions. **a**, Standardized slope estimates (mean \pm s.e.m.) for each significant predictor are shown, with the exception of study region and soil type, which were retained in all models. **b**, Net effect (sum of significant standardized effects) for multitrophic richness and abundance. **c**, The total amount of variance explained by either environmental + plant species richness, environmental + the abundance and richness of the best individual trophic predictor, or by environmental + multitrophic diversity and abundance are shown for each function (adjusted R^2 , to control for the high number of predictors included). The number of trophic

groups included in the best models (2.15 ± 1.2 across functions, and 1.94 ± 1.2 across functions and multifunctionality indices) is given next to the adjusted R^2 value. The increase in the adjusted R^2 values in models with plant-species-richness averaged 0.07 ± 0.12 (across functions) and 0.06 ± 0.11 (across functions and multifunctionality indices). Ecosystem services are organized by the main four types of services they associate with (top–bottom: provisioning, supporting, regulating and cultural). TWI, topographic wetness index, based on the aspect and position in the slope, and the inclination of the slope. Multicollinearity between the predictors introduced is unlikely (Extended Data Table 3).

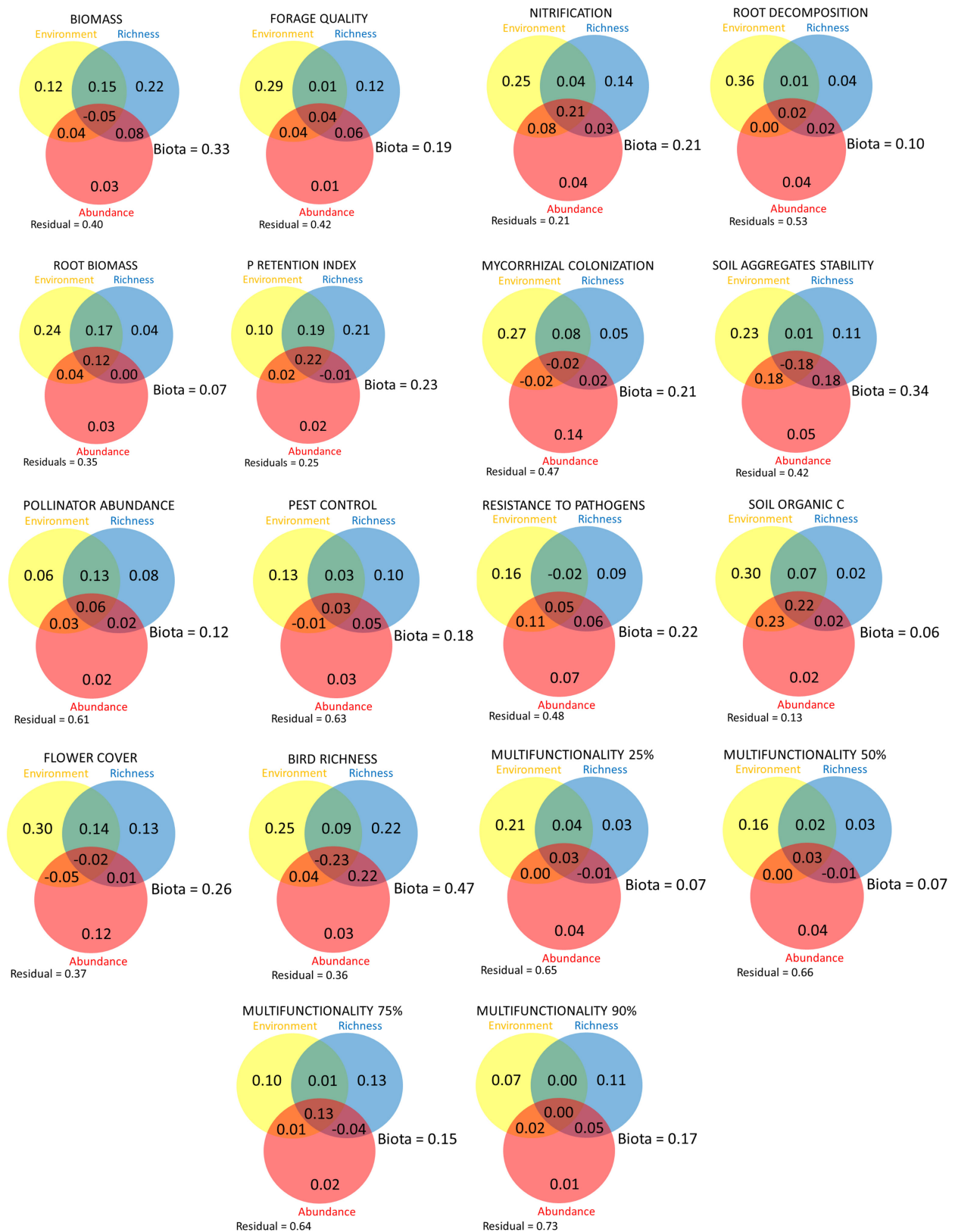


Extended Data Figure 3 | Number of trophic groups necessary to predict multifunctionality measures calculated with all possible combinations of 1–9 services, and their net effects. The number of predictors selected in the best models (left) and their overall effects (sum of standardized coefficients; right) across all possible combinations of 1–9 services ($N=501$) are shown. Error bars show the 95% confidence intervals, estimated for all possible combinations of n (1 to 9) functions

in both cases. Only the 9 services with fewer than 20 data gaps were considered in these analyses (see details in Methods). Multifunctionality for these combinations was calculated at the 25% (upper panel), 50%, 75% and 90% (bottom panel) thresholds. Services removed were flower cover, arbuscular mycorrhizal colonization, soil aggregate stability, phosphorous retention index and pest control.

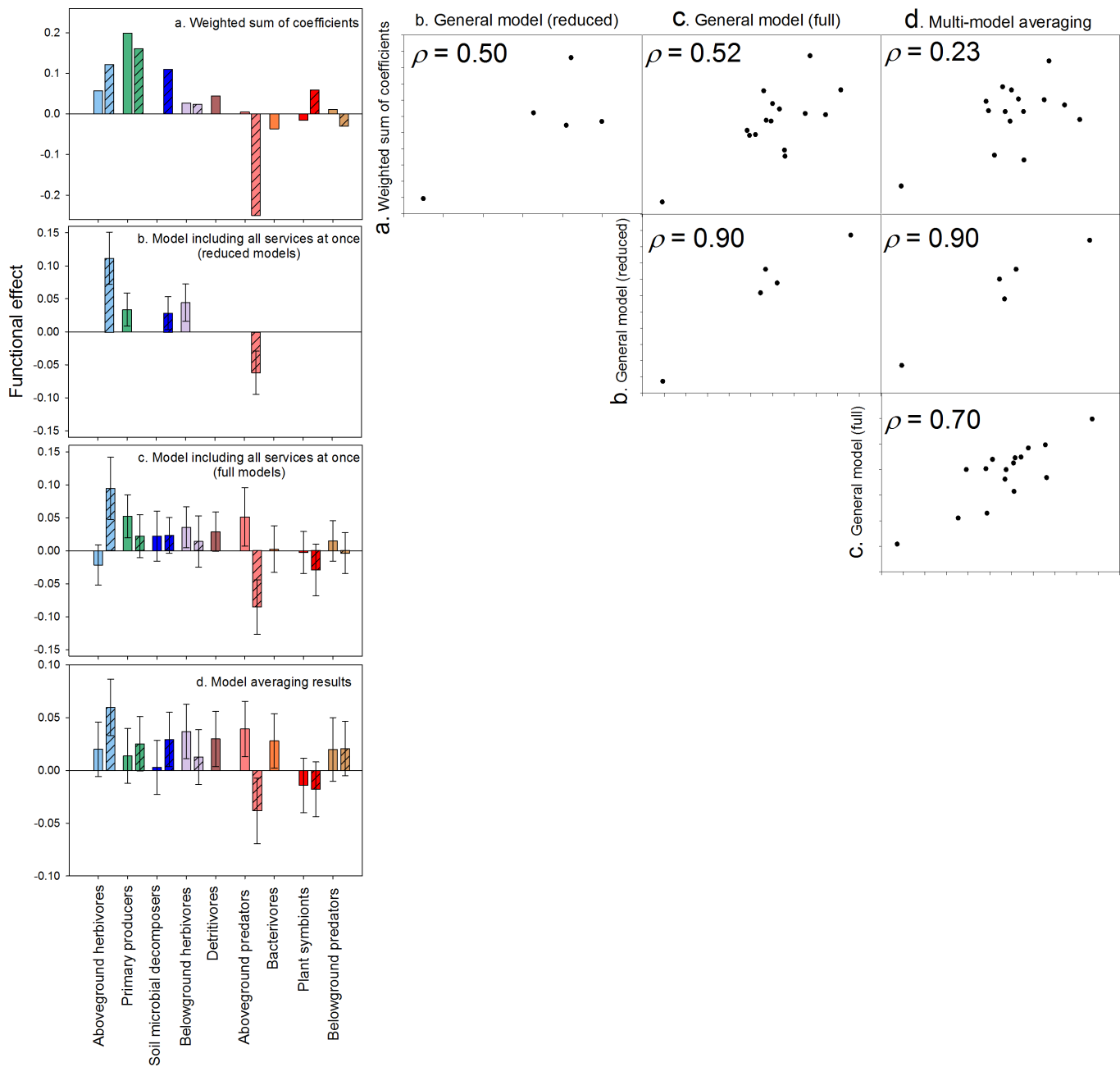


Extended Data Figure 4 | Functional effect of the different trophic groups on contrasting multifunctionality scenarios. Overall functional effects (significant standardized coefficients; mean \pm s.e.m.) from the most parsimonious model) of the richness (open bars) and abundance (hatched bars) of each group are shown according to ref. 34.



Extended Data Figure 5 | Functional importance of species richness and abundance compared to environmental drivers. Venn diagrams showing the variance partition for the four components of our statistical models (environment: climate, soil and land-use intensity; species richness models (environment: climate, soil and land-use intensity; species richness and abundance of primary producers, above- and

below-ground predators, below-ground herbivores and soil microbial decomposers). The variance not explained by the model (the residual) is also shown. The variance explained by richness, abundance and their overlap is summed up as Biota. Each panel represents an individual function or multifunctionality metric.



Extended Data Figure 6 | Functional effect of the different trophic groups. Overall functional effects (mean \pm s.e.m. of the standardized slopes obtained from the model; with the exception of **a**, where error could not be estimated) of the richness (open bars) and abundance (hatched bars) of each group. **a**, The values were calculated after weighting each standardized coefficient (those in Extended Data Fig. 1) by the adjusted R^2 of the model to account for differences in model performance.

b, c, The values were calculated as the standardized coefficients in a general model fitted to all services at once, including 'service identity' as an extra predictor and 'plot' as random factor to control for pseudo-replication (reduced models (**b**); the ones presented in the main text), or full models (**c**) and **d**, calculated as multi-model average parameters from a model fitted to all services at once. Correlations (Spearman's rank correlation coefficients) between the different approaches are given.

Extended Data Table 1 | Re-analysis of manipulative multitrophic studies

Study ID	Reference	System	# trophic groups manipulated	Approach	Response variable	Variance explained best group	Variance explained two trophic groups	% increase with multitrophic approach	comment
1	Douglass et al. 2008 Ecolett	aquatic	2	mesocosm	grazer abundance	55.0	61.0	10.9	based on ω^2
1	Douglass et al. 2008 Ecolett	aquatic	2	mesocosm	predator abundance	5.0	7.0	40.0	based on ω^2
2	Bruno et al. 2008. Ecology	aquatic	2	mesocosm	autotroph biomass	19.5	42.7	119.0	based on F
3	Naeem et al. 2000. Nature	terrestrial	2	microcosm	autotroph biomass	13.6	23.5	72.8	based on F
3	Naeem et al. 2000. Nature	terrestrial	2	microcosm	detritivore biomass	5.6	11.3	101.8	based on F
3	Naeem et al. 2000. Nature	terrestrial	2	microcosm	# C sources used	7.2	13.5	87.5	based on F
4	Handa et al. 2014 Nature	both	2	field.expt	Litter C loss	5.8	6.6	13.8	based on %SS

For each study, an ID number and full reference are given. The system in which each study was performed (aquatic or terrestrial), the number of trophic groups manipulated and the approach used (controlled mesocosms or field studies) are provided. The ecosystem functions ('response variable') measured within each study were grouped in biomass production (the first five rows), nutrient cycling (sixth row) and decomposition (seventh row). Variance explained (according to the statistic mentioned in comments; ω^2 = proportion of variance explained according to the authors; F = Fisher's F , SS = sum of squares) for the single trophic group with the most explanatory power, and the difference between the variance explained by this group and the inclusion of a second group are given (grey column).

Extended Data Table 2 | Details of the sampling procedure for each trophic group and function

Trophic groups			
Trophic group	Subgroup	Sampling method	Author
Primary producers	Plants, bryophytes	Measurement of % cover in a 4×4 m subplot, done in 2009	Boch, Heinze, Hölzel, Klaus, Kleinebecker, Müller, Prati, Socher, Fischer
Aboveground herbivores	Herbivorous insects	Sweep netting (Hemiptera: Heteroptera/Auchenorrhyncha, Hymenoptera, Neuroptera and Orthoptera). Transects of 150m with 60 double sweeps, done twice per plot in 2008-2010.	Lange, Pašalić, Türke, Gossner, Weisser
Aboveground predators	Carnivorous insects	Sweep netting (Hemiptera: Heteroptera/Auchenorrhyncha, Hymenoptera, Neuroptera and Orthoptera). Transects of 150m with 60 double sweeps done twice per plot in 2008-2010.	Lange, Pašalić, Türke, Gossner, Weisser
	Spiders	Sweep netting. Transects of 150m with 60 double sweeps, done twice per plot in 2008-2010.	Lange, Pašalić, Türke, Gossner, Weisser
	Chilopoda	Kempson extraction from one soil core of 20 × 5 cm per plot, done in 2008	Birkhofer, Diekötter, Wolters
Detritivores	Annelids	Hand sorting from two soil cores of 20 × 10 cm per plot, done in 2008	Birkhofer, Diekötter, Wolters
	Diplopoda	Kempson extraction from one soil core of 20 × 5 cm per plot, done in 2008	Birkhofer, Diekötter, Wolters
	Detritivorous insects	Sweep netting (Hemiptera: Heteroptera/Auchenorrhyncha, Hymenoptera, Neuroptera and Orthoptera). Transects of 150m with 60 double sweeps, done twice per plot in 2008-2010.	Lange, Pašalić, Türke, Gossner, Weisser
Microbial decomposers	Soil bacteria	cDNA amplicon sequencing of partial (V3) 16S rRNA gene transcripts, done in 2011	Baumgartner, Sikorski, Overmann
Bacterivores	Bacterivorous protists	18S rDNA gene PCR and amplicon sequencing (454) filtering for rhizarians, alveolates, stramenopiles and opisthokonts, done in 2011	Venter, Arndt
Symbionts	Arbuscular mycorrhizal fungi	Pyrotag sequencing of the NS31 - AM1 fragment of the 18S rDNA genes, done in 2011	Klemmer, Wubet, Buscot
Belowground herbivores	Insect larvae	Extracted from a heat/moisture gradient in one soil core of 20 × 5 cm per site, done in 2011 over a period of eight days.	Sonnemann, Wurst
Belowground predators	Insect larvae	Extracted from a heat/moisture gradient in one soil core of 20 × 5 cm per site, done in 2011 over 8 days.	Sonnemann, Wurst
Functions			
Function	Sampling method		Author
Aboveground plant biomass	Harvested in four 0.5 m × 0.5 m quadrats per plot, done in May-June in 2008-2012.		Schmitt, Prati, Fischer, Klaus, Kleinebecker, Hölzel
Belowground plant biomass	Measured in 14 soil cores (0-10 cm). Fine roots were sorted and weighted after drying in the oven, done in samples collected in May 2011		Solly, Schöning, Schrupf
Root decomposition rate	Measured as the mass loss from root litter bags after 6 months, from October 2011 to April 2012.		Solly, Schöning, Schrupf
Potential nitrification	10 mM ammonium sulphate solution was added as substrate to 2.5g of soil composite samples (i.e. the same samples as for soil carbon; see below).		Stempfhuber, Schloter
Phosphorus uptake and retention	Proportion of P in plants and microbes (shoot P stock + microbial P stock) / (shoot P stock + microbial P stock + soil extractable P [NaHCO ₃]).		Alt, Sorkau, Oelman, Wilcke, Klaus, Kleinebecker, Hölzel
Arbuscular mycorrhizal fungal root colonization	Cultured in sterile soil in the field from April to October 2011 and then extracted with sodium hexametaphosphate (35 g l ⁻¹). Hyphal length was quantified after staining with trypan blue.		Morris, Rillig
Stability of soil aggregates	A subsample of the same soil than above (AMF colonization) was passed through a 250 µm sieve under water to determine the percentage of water stable macroaggregates.		Morris, Rillig
Soil organic Carbon	Measured in 14 soil cores (0-10 cm). Calculated as the difference between total carbon (measured with a CN analyzer "Vario Max" [Elementar Analysensysteme GmbH, Hanau, Germany]) and inorganic carbon (determined after combustion of organic carbon in a muffle furnace, 450°C for 16 h), done in samples collected in May 2011		Schöning, Solly, Schrupf
Forage quality	Was calculated as a function of mean of scaled crude protein concentration and scaled relative forage value, done in May-June in 2008-2012.		Klaus, Kleinebecker, Hölzel
Resistance to plant pathogens	Calculated as the inverse of the total cover of foliar fungal pathogens. The cover of pathogens was measured in four 25 × 1 m transects per plot, were proportion of plants infected, and leaf area infected of these individuals was measured; done in October 2011.		Blaser, Prati, Fischer
Pest control	Number of trap nesting wasps known to feed on pest insects, done between April and October 2008.		Steckel, Westphal, Steffan-Dewenter
Pollinator abundance	Estimated as the total abundance of flower visitors, measured in one 200 × 3 m transect per plot, done in May 2008		Krauss, Klein, Weiner, Werner, Blüthgen
Bird diversity	Measured as the cumulative species richness estimated by audio-visual point-counts, done in May-June 2008-2010		Renner, Böhm, Tschapka
Flower cover	Measured as the number of inflorescences in four 50 × 3 m transects per plot. Flower area for each species was obtained from the literature.		Binkenstein, Schaefer

Note that for some groups the taxonomic unit was either operational taxonomic units (OTU: fungi and protists) or families (bacteria and below-ground insect larvae). Abundance measures were: per cent cover (plants, bryophytes), number of individuals captured (arthropods) and relative proportion of sequence reads assigned to each family among all reads within each plot (protists, soil bacteria and mycorrhiza).

Extended Data Table 3 | Correlations between diversity predictors from the models in the main text

Models using residuals after controlling for environmental predictors

	Belowground herbivores	Belowground predators	Detritivores	Aboveground herbivores	Soil microbial decomposers	Bacterivores	Aboveground predators	Plant symbionts	Primary producers	Belowground herbivores	Belowground predators	Detritivores	Aboveground herbivores	Soil microbial decomposers	Bacterivores	Aboveground predators	Plant symbionts
Abundance																	
Primary producers	-0.06	0.09	0.03	-0.07	-0.01	0.01	-0.13	-0.05	0.06	0.06	-0.05	0.05	-0.06	0.10	-0.02	-0.04	-0.16
Belowground herbivores		0.21	0.08	0.19	0.00	0.18	-0.02	-0.02	-0.15	0.37	0.10	0.13	0.08	0.06	0.18	-0.05	0.10
Belowground predators			0.14	-0.16	0.05	0.09	-0.23	-0.04	-0.16	0.22	0.54	0.12	0.09	0.20	0.15	-0.09	0.12
Detritivores				0.12	-0.10	-0.02	0.20	-0.02	0.04	0.15	0.09	0.74	0.12	-0.13	0.02	0.03	-0.15
Aboveground herbivores					0.01	0.16	0.32	-0.05	-0.05	0.05	0.08	0.22	0.54	-0.04	0.14	0.34	-0.06
Soil microbial decomposers						0.27	-0.02	0.05	0.00	0.01	0.04	-0.05	-0.11	0.17	0.25	-0.05	0.08
Bacterivores							-0.13	0.06	-0.24	0.11	0.12	0.00	-0.10	0.13	0.76	-0.14	0.25
Aboveground predators								-0.04	0.14	0.02	-0.11	0.14	0.38	-0.16	-0.18	0.59	-0.18
Plant symbionts									-0.06	0.03	-0.10	0.04	-0.12	0.03	-0.06	0.03	0.46
Richness																	
Primary producers										-0.13	-0.13	-0.09	0.16	-0.38	-0.26	0.02	-0.22
Belowground herbivores											0.24	0.18	0.11	-0.03	0.09	0.11	0.13
Belowground predators												0.08	0.13	0.19	0.25	-0.02	-0.07
Detritivores													0.19	-0.12	0.02	0.09	-0.08
Aboveground herbivores														0.02	-0.03	0.48	-0.15
Soil microbial decomposers															0.21	-0.06	0.17
Bacterivores																-0.17	0.21
Aboveground predators																	-0.17

Models including environmental predictors

	Soil depth	Fertilisation	Mowing	Grazing	Elevation	TWI	Primary producers	Belowground herbivores	Belowground predators	Detritivores	Aboveground herbivores	Soil microbial decomposers	Bacterivores	Aboveground predators	Plant symbionts	Primary producers	Belowground herbivores	Belowground predators	Detritivores	Aboveground herbivores	Soil microbial decomposers	Bacterivores	Aboveground predators	Plant symbionts	
Environment																									
pH	0.05	0.07	0.05	-0.17	-0.24	0.22	-0.19	-0.22	-0.09	0.12	-0.21	-0.40	-0.30	0.25	-0.03	0.08	-0.18	0.00	0.21	-0.07	-0.05	-0.35	0.21	-0.07	
Soil depth		-0.21	0.02	-0.01	-0.82	0.52	-0.28	-0.22	-0.11	0.22	-0.29	-0.15	-0.06	-0.10	0.60	-0.62	-0.16	0.20	0.26	-0.39	0.42	0.10	-0.02	0.37	
Fertilisation			0.61	-0.22	0.15	0.00	0.01	-0.06	0.22	0.06	-0.06	0.00	0.10	0.01	-0.16	-0.23	-0.04	0.09	0.13	-0.06	-0.08	-0.01	-0.10	-0.06	
Mowing				-0.68	0.05	0.18	-0.03	-0.09	0.19	0.09	-0.15	-0.17	-0.01	-0.04	-0.12	-0.40	-0.13	0.10	0.09	-0.24	-0.02	-0.04	-0.17	-0.16	
Grazing					-0.09	-0.13	0.01	0.04	-0.02	-0.04	0.16	0.26	0.27	0.01	0.11	0.13	0.12	0.14	-0.04	0.11	0.07	0.32	0.12	0.25	
Elevation						-0.55	0.31	0.18	0.11	-0.28	0.29	0.22	0.05	-0.04	-0.61	0.60	0.19	-0.20	-0.33	0.39	-0.32	-0.13	-0.10	-0.42	
TWI							-0.19	-0.20	-0.02	0.15	-0.28	-0.36	-0.19	0.09	0.35	-0.50	-0.11	0.19	0.27	-0.28	0.41	-0.08	0.14	0.10	
Abundance																									
Primary producers							-0.06	0.13	-0.06	0.22	0.06	-0.08	-0.27	-0.21	0.12	0.06	-0.15	-0.11	0.10	-0.10	-0.13	-0.14	-0.41		
Belowground herbivores								0.26	-0.02	0.11	0.26	0.28	-0.05	-0.08	0.19	0.48	0.08	-0.03	0.22	-0.09	0.24	-0.12	0.20		
Belowground predators									0.09	-0.01	0.08	0.14	-0.19	-0.09	-0.08	0.24	0.51	0.06	0.09	0.09	0.13	-0.13	0.05		
Detritivores										0.02	-0.15	-0.05	0.16	0.15	-0.16	0.09	0.20	0.88	0.01	-0.06	0.02	0.08	0.03		
Aboveground herbivores											0.07	0.06	0.23	-0.25	0.17	0.05	-0.06	-0.01	0.64	-0.14	0.03	0.31	-0.29		
Soil microbial decomposers												0.47	-0.18	0.05	0.17	0.17	0.01	-0.21	0.09	-0.11	0.46	-0.18	0.32		
Bacterivores													-0.17	0.05	-0.07	0.15	0.12	-0.08	-0.07	0.08	0.82	-0.20	0.40		
Aboveground predators														-0.11	0.23	-0.03	-0.09	0.18	0.32	-0.13	-0.15	0.68	-0.07		
Plant symbionts															-0.38	0.01	0.06	0.19	-0.29	0.28	0.13	-0.05	0.64		
Richness																									
Primary producers																0.14	-0.22	-0.24	0.42	-0.31	-0.13	0.14	-0.14		
Belowground herbivores																	0.22	0.08	0.18	-0.08	0.11	0.03	0.19		
Belowground predators																		0.17	-0.01	0.27	0.20	-0.02	0.12		
Detritivores																			0.04	-0.01	-0.05	0.15	0.08		
Aboveground herbivores																				-0.17	-0.09	0.41	-0.22		
Soil microbial decomposers																					0.14	-0.04	0.24		
Bacterivores																						-0.18	0.46		
Aboveground predators																							-0.09		

Correlations between residuals (after controlling for the effect of study region, soil type, pH, topographic wetness index and the three land-use intensity components: fertilization, mowing and grazing) of abundance and species richness of the nine different trophic groups considered (top) or of the raw data (bottom). Those predictors removed owing to multicollinearity problems are shaded grey, with the correlation responsible highlighted. TWI = topographic wetness index, obtained from P. M., unpublished data.

Extended Data Table 4 | Model selection

	Biomass	Forage quality	Potential nitrification	Root biomass	Root decomposition	Phosphorus retention	Mycorrhizal colonization	Soil aggregate stability	Soil C	Pest control	Resistance to pathogen	Pollinator abundance	Bird diversity	Flower cover	Multifunctionality 25%	Multifunctionality 50%	Multifunctionality 25%	Multifunctionality 90%	
Abundance	Primary producers	3.26	-1.92	-1.09	-1.08	-2.34	0.59	-1.90	-2.00	-1.48	-0.35	6.09	-1.84	-1.99	3.53	-1.48	-1.76	-1.48	-1.69
	Belowground herbivores	-1.85	-0.50	1.35	-2.00	-1.88	-0.13	-0.02	-1.99	-1.70	-2.00	1.88	0.13	-0.10	-1.24	-0.65	-2.00	-0.98	-1.95
	Belowground predators	-1.90	0.03	-1.95	5.88	-1.97	-1.75	3.10	-0.70	-2.00	-1.74	-1.62	-1.71	-0.19	-1.98	-1.90	-1.34	-0.30	-0.06
	Aboveground herbivores	-0.74	-1.71	11.71	0.94	-0.46	-1.96	4.83	3.71	3.26	-1.96	-0.77	-1.97	-2.00	1.29	1.46	-0.03	-0.63	-1.74
	Soil microbial decomposer	-1.57	-0.86	0.38	-0.20	-0.14	-1.29	5.10	7.13	1.45	-1.99	0.66	-0.75	1.55	-1.99	-2.00	1.68	-1.98	-1.80
	Aboveground predators	0.74	-1.25	1.18	4.38	-1.84	-1.88	-1.94	2.68	0.48	1.79	6.41	-1.97	2.10	-1.81	-0.25	0.59	2.23	-1.28
	Plant symbionts	-0.80	-1.22	5.99	0.55	-0.39	1.82	-0.93	1.39	0.03	0.49	-1.96	2.92	-1.85	-1.96	-1.87	-0.97	-1.83	-2.00
	Primary producers	14.90	5.43	12.00	1.94	0.13	16.91	-0.32	4.28	-0.97	5.01	1.56	-1.74	33.27	-1.66	-1.83	-1.35	6.88	2.45
	Belowground herbivores	-0.09	-1.95	-1.93	-0.23	-1.92	-1.94	-1.99	2.13	-1.61	-0.71	1.13	-2.00	-1.22	-1.99	-1.51	-1.88	-0.61	-1.74
	Belowground predators	-0.08	-1.78	-0.59	-1.65	-1.97	-0.56	-1.83	-1.65	-0.25	-1.59	-0.04	-1.84	-1.98	-1.02	-1.76	-1.53	-1.47	0.04
Richness	Detritivores	0.74	-1.89	2.56	-1.79	-1.63	-1.22	-1.15	-1.35	-2.00	-1.32	-1.68	-1.63	-1.63	-0.44	-1.32	-1.66	-1.70	-1.64
	Aboveground herbivores	5.68	5.14	-1.85	6.91	-1.99	-1.67	-1.66	-1.66	0.10	-1.94	-0.65	-1.57	5.90	6.40	-1.49	-0.76	-1.98	-1.98
	Soil microbial decomposer	-1.97	-0.80	0.47	-3.86	-1.77	-1.20	4.95	-1.41	-1.37	-1.99	-1.54	-1.66	-1.66	-1.63	-1.92	0.01	-0.43	-0.77
	Bacterivores	-1.93	2.98	-0.86	-1.55	-1.80	0.74	-1.84	3.58	-1.75	-1.58	-1.91	1.44	-1.87	-1.90	-1.56	-1.33	-1.05	-1.90
	Aboveground predators	2.31	-1.93	-1.43	5.79	-1.81	10.25	-0.23	-1.97	6.17	3.29	-0.75	-1.38	-1.88	-1.34	-0.53	-2.00	-0.48	-1.60
	Plant symbionts	-1.91	-1.87	-1.91	-0.35	-1.58	-1.36	-1.39	-1.38	0.55	-1.99	2.64	7.34	-2.00	-2.00	-1.32	-2.00	-0.03	1.27

Difference in AIC when subtracting each term regarding the full model according to the backward step AIC procedure used (models using the environmental-corrected residuals, as presented in Fig. 1 and Extended Data Fig. 1). Green shade indicates the terms included in the most parsimonious models. Orange shade indicates terms included in the model with the lowest AIC but further removed using *F*-ratio tests.