

# Interannual variation in land-use intensity enhances grassland multidiversity

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Although temporal heterogeneity is a well-accepted driver of biodiversity, effects of interannual variation in land-use intensity (LUI) have not been addressed yet. Additionally, responses to land use can differ greatly among different organisms; therefore, overall effects of land-use on total local biodiversity are hardly known. To test for effects of LUI (quantified as the combined intensity of fertilization, grazing, and mowing) and interannual variation in LUI (SD in LUI across time), we introduce a unique measure of whole-ecosystem biodiversity, multidiversity. This synthesizes individual diversity measures across up to 49 taxonomic groups of plants, animals, fungi, and bacteria from 150 grasslands. Multidiversity declined with increasing LUI among grasslands, particularly for rarer species and aboveground organisms, whereas common species and belowground groups were less sensitive. However, a high level of interannual variation in LUI increased overall multidiversity at low LUI and was even more beneficial for rarer species because it slowed the rate at which the multidiversity of rare species declined with increasing LUI. In more intensively managed grasslands, the diversity of rarer species was, on average, 18% of the maximum diversity across all grasslands when LUI was static over time but increased to 31% of the maximum when LUI changed maximally over time. In addition to decreasing overall LUI, we suggest varying LUI across years as a complementary strategy to promote biodiversity conservation.

biodiversity loss | agricultural grasslands | Biodiversity Exploratories

**A**mple theoretical and empirical work has shown that temporal heterogeneity can promote biodiversity by creating niches that allow species with different responses to the environment to coexist stably (1, 2). Among the processes currently eroding

## Significance

Land-use intensification is a major threat to biodiversity. So far, however, studies on biodiversity impacts of land-use intensity (LUI) have been limited to a single or few groups of organisms and have not considered temporal variation in LUI. Therefore, we examined total ecosystem biodiversity in grasslands varying in LUI with a newly developed index called multidiversity, which integrates the species richness of 49 different organism groups ranging from bacteria to birds. Multidiversity declined strongly with increasing LUI, but changing LUI across years increased multidiversity, particularly of rarer species. We conclude that encouraging farmers to change the intensity of their land use over time could be an important strategy to maintain high biodiversity in grasslands.

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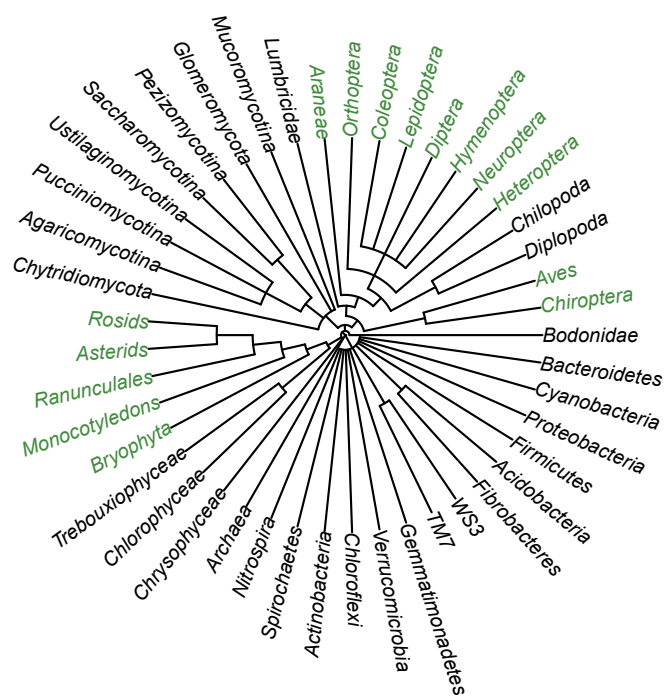
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biodiversity, land-use intensification is one of the most important (3–5), with likely feedbacks on ecosystem functioning (6). However, previous studies of land-use effects have only considered how changes in mean intensity affect biodiversity (7–9) and have neglected the question of whether interannual variation in land-use intensity (LUI) could also have an impact on biodiversity. In grasslands, farmers frequently change animal stocking densities, fertilizer application, or mowing frequencies across years (10), meaning that temporal heterogeneity in LUI can be high. Spatial heterogeneity of land use can promote biodiversity (11, 12), and we might hypothesize that interannual variation in LUI also has positive effects on biodiversity (“land-use variation hypothesis”). Changing land use across years could even mitigate some of the negative effects of high management intensity, and therefore help to develop strategies that resolve the tradeoff between high agricultural production and biodiversity conservation.

Interannual variation in LUI might generally promote biodiversity, but effects could differ between rarer and more common species or between aboveground and belowground groups. Locally abundant (common) species are often generalists and less sensitive to land use (13), whereas less abundant (rarer) species may be more sensitive to LUI because they have more specialized habitat requirements or smaller populations (14, 15). Although linkages between aboveground and belowground diversity are expected (16, 17), in grasslands, LUI and interannual variation in intensity may have more direct effects on aboveground diversity, whereas belowground diversity may be more sensitive to general soil conditions (18).

One of the main challenges when studying land-use effects on biodiversity is that responses of different taxonomic groups of organisms can differ greatly (4), making it difficult to assess overall land-use effects. One promising approach would be a synthetic index of total ecosystem biodiversity that integrates information on a wide diversity of groups of organisms and allows us to identify the conditions that simultaneously maximize the diversity of most groups. Here, we introduce and apply an index of “multidiversity,” which computes the average scaled species richness per taxonomic group. Species richness values for each group were scaled to the maximum value observed for that group across all of the grasslands, so that groups differing in the total number of species were weighted equally. The approach is conceptually similar to indices of multifunctionality used in biodiversity-ecosystem functioning research (6, 19) and to the World Wildlife Fund’s living planet index, which quantifies the overall state of biodiversity at the global scale (20). We apply the multidiversity index to a large set of biodiversity data from 150 grasslands to examine how changes in the mean and interannual variance of land use affect multidiversity and to what degree land-use effects differ between aboveground and belowground, as well as between locally rare vs. common, organisms.

We addressed these questions with the unique set of comprehensive biodiversity and land-use data of our German Biodiversity Exploratories project (21). We investigated land-use effects, first using a set of 150 plots on which the species richness of 18 taxonomic groups were measured and then using a subset of 27 plots on which 49 taxonomic groups were surveyed (Fig. 1). We modeled the response of multidiversity to an integrated measure of LUI (10), which is the sum of the standardized intensities of grazing (duration and type of grazing animals), mowing (number of cuts per year), and fertilization [kilograms of nitrogen (N) per hectare]. The shape of the relationship between LUI and biodiversity has important management implications; for instance, if the relationship is saturating rather than linear, this would suggest that large losses of biodiversity occur even at modest levels of intensification (9). We therefore fitted a series of models (Table S1) that differed in the shape of the relationship

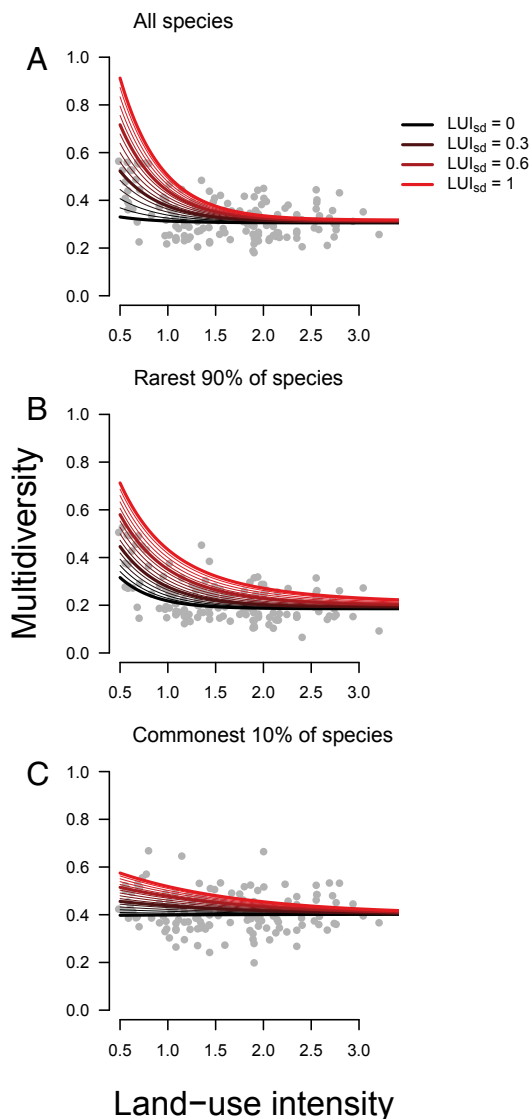


**Fig. 1.** Organism groups used to calculate multidiversity. Of 49 taxonomic groups surveyed on 27 grasslands, 45 are shown on the tree. Eighteen groups were measured on all 150 grasslands, and 16 of them are shown in green on the tree. The groups WS3 and TM7 are candidate bacterial phyla. In addition to the groups shown on the tree, our analyses included lichens (150 plots), Homoptera (now considered paraphyletic but used as a group for convenience, 150 plots), viruses (27 plots), and a fungal subphylum *incertae sedis* (27 plots), which could not be placed on the tree. The tree was created based on National Center for Biotechnology Information taxonomy ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov)), and therefore shows relationships among groups but without true branch lengths.

between LUI and multidiversity, whether they contained interannual variation in LUI [SD in LUI ( $LUI_{sd}$ )] and whether they modeled LUI as an integrated index or fitted individual land-use components separately. We used Akaike’s information criterion corrected for small sample size (AICc) to select the best-fitting models (95% confidence set; *Methods*).

## Results and Discussion

Our analysis of the species richness of 18 taxa across 150 grasslands showed a clear negative response of multidiversity to increasing LUI (Fig. 24). Multidiversity followed a negative asymptotic exponential relationship, which indicates that intensification of land use will have particularly negative consequences for biodiversity in extensively managed grasslands (9). The asymptote of the curve was 0.3, indicating that species richness declined to 30% of the maximum across taxonomic groups. Although there were many “losers” (13) under land-use intensification, some (mostly animal) groups were hardly affected: Diptera, arbuscular mycorrhizal fungi, and bats did not decline with increasing LUI (Fig. 3). In contrast, plants and lichens, as well as Orthoptera, Araneae, and Lepidoptera, all declined strongly. In general, animal groups showed a wider range of responses to LUI than did plant groups; however, calculating multidiversity for plants and animals separately revealed that the overall response was the same for both groups (all best models were asymptotic exponentials), although LUI explained less of the variation in animal multidiversity (pseudo- $R^2$  of 0.2 for animals and 0.7 for plants; Fig. S1 A and B and Table S2) because of the more variable responses of the animals. Modeling

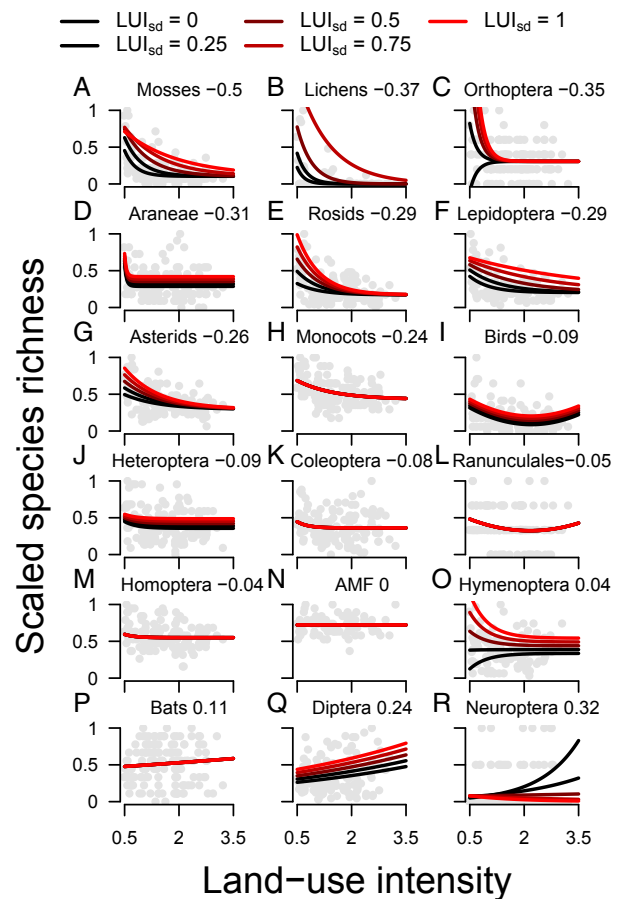


**Fig. 2.** Effect of LUI on multidiversity of 18 taxonomic groups of all species (A), relatively rare species (i.e., the 90% of species with the lowest total abundance) (B), and relatively common species (i.e., the 10% of species with the highest total abundance across plots) (C). Lines show model fits for different values of  $LUI_{sd}$ , from  $LUI_{sd} = 0$  to the maximum interannual land-use change observed in any plot,  $LUI_{sd} = 1$ . In all cases, model predictions were calculated using multimodel averaging across all models in the 95% confidence set and were averaged across regions (more details are provided in *Methods*). In C, not all models in the 95% confidence set could be used for multimodel averaging because it would not be possible to average across different types of models (e.g., those with the compound LUI and those with individual components). AICc weights of models that could be used for multimodel averaging summed to 78%.

LUI using the integrated index proved better than modeling it using the individual intensities of grazing, mowing, and fertilization. Of the individual components, however, grazing and mowing seemed to be more important than fertilization in driving declines in multidiversity (*SI Methods* and *Fig. S2*). High rates of fertilization mostly occur in frequently mown grasslands (10), but these results suggest that fertilization may not have as many negative effects as high mowing intensity. As with all nonexperimental studies, it is impossible to identify LUI categorically as the driver of these differences in multidiversity among grasslands; however, great care was taken during plot selection to

minimize confounding between environmental variables and LUI (21). Loss of multidiversity could be driven by effects on abundance, or there could be effects on species richness per se. Land-use intensification might cause a reduction in abundance, and this, in turn, could cause a loss of species richness. Alternatively, higher LUI could reduce species richness more than would be expected based on changing abundance, which would be an effect on species richness per se. Further analyses (*SI Methods* and *Figs. S3* and *S4*) suggest that both processes are important: The relative importance varies among groups, but the overall effect on multidiversity seems principally driven by an effect on species richness per se. LUI also reduced the evenness of species abundances, but the effects on evenness were less pronounced than those on species richness (*Fig. S1C* and *Table S2*), supporting the idea that richness and evenness may show different responses (22) and that LUI has smaller effects on abundance and principally reduces species numbers.

Interannual changes in LUI were beneficial for biodiversity (*Fig. 2A*), supporting our land-use variation hypothesis. In the analysis of 18 groups of organisms in 150 grasslands, all of the



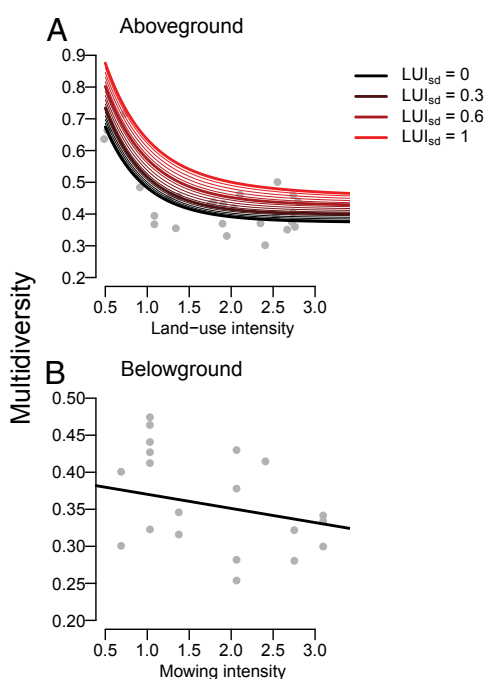
**Fig. 3.** Response to LUI of scaled species richness for the 18 taxonomic groups measured on 150 plots. For each group, the predictions from the best-fit model are shown (*Methods* and *Table S2*). Where temporal variation in LUI ( $LUI_{sd}$ ) appeared in the model, model fits are shown for different values of  $LUI_{sd}$ . (A–R) The groups are sorted in order of their response to LUI, from the group showing the strongest decline (A) to the strongest increase (R). For each group, changes in species richness with increasing LUI are shown beside the name of the group on the graph and were calculated as the difference between the relative species richness predicted by the model at minimum LUI ( $LUI = 0.5$ ) and the predicted species richness at maximum LUI ( $LUI = 3.5$ ). Model predictions were evaluated at the mean  $LUI_{sd}$  and were averaged across regions. AMF, arbuscular mycorrhizal fungi.

best-fit models (Table S2) modeled the intercept as a function of  $LUI_{sd}$ . The effect of  $LUI_{sd}$  on the intercept indicates that interannual change in land use has the greatest positive effect on multidiversity at low levels of mean LUI (Fig. 2A). Temporal variation in LUI was also beneficial for most (11 of 18; Fig. 3) of the individual taxonomic groups, and it was only negative for one species-poor group (Neuroptera, Fig. 3R). It has been shown that spatial variation in land use is beneficial for biodiversity (11, 12), and our results show that temporal heterogeneity can also be important. In natural systems, temporal variation in environmental conditions can be a mechanism promoting species coexistence (1, 2). Species might therefore vary in their response to temporal changes in LUI (23) but could persist in the grassland, or in the surrounding landscape, during years in which the management intensity is not suitable. In this case, a grassland management regime with some years of low LUI and some years with higher intensity might maintain more biodiversity than in grasslands where LUI does not change across years.

Temporal variation in overall LUI was a much better predictor of multidiversity than variation in individual components of land use. Of the components, however, temporal variation in grazing intensity had the strongest positive effect (*SI Methods*), suggesting that altering grazing regimes over time would be best for increasing biodiversity. This supports previous recommendations to increase heterogeneity in grazing intensity in rangelands as a management strategy to promote biodiversity (12). Within the observed range of land-use variation, temporal variation in grazing, mowing, and fertilization always increased multidiversity. However, because fertilization can have long-term negative effects on biodiversity (24), it seems unlikely that varying fertilizer inputs in extensively managed grasslands would promote biodiversity. Indeed, very few of our extensively managed grasslands experienced high variation in fertilization (Fig. S5). Thus, we suggest that varying grazing or mowing would be beneficial for biodiversity.

Species that were relatively rare across the grasslands benefited strongly from increased interannual variation in LUI. For each taxonomic group, we classified as common the 10% of species with the highest total abundance across plots; all other species were rare [other thresholds gave similar results (*SI Methods* and Table S3)]. The multidiversity of rarer species was very sensitive to higher mean LUI (Fig. 2B and Table S2), probably because rare species have smaller populations and more restricted niches, and are therefore vulnerable to any increase in disturbance (14, 15). However, high interannual variation in LUI slowed the decline in rare species multidiversity with increasing mean LUI. Therefore, unlike overall multidiversity, interannual variation in LUI also increased rare species multidiversity at high or intermediate mean LUI: At intermediate LUI ( $LUI = 2$ ), multidiversity of rarer species was almost twice as high under maximum interannual variation in LUI (31%) compared with no change in LUI (18%) (Fig. 2B). High interannual variation in LUI could be produced by altering the intensity of grazing, mowing, or fertilizing, or by switching the combination of these components across years, for instance, changing from grazing and mowing to only light grazing (Fig. S5). Therefore, rare species, as expected, did best in grasslands of low LUI, but some groups could occur at high diversity in more intensively managed systems if LUI was varied across years. This shows that the way intensively used systems are managed also matters very much for biodiversity. It is important to find strategies that promote both conservation and agricultural production (3, 25, 26), and our results suggest that varying land use over time could be such a strategy because it reduced some of the negative effects of intensive grassland management on the biodiversity of rarer species.

The response of common species multidiversity differed from that of rarer species. Higher LUI had much smaller effects on



**Fig. 4.** Response of the multidiversity of all 49 groups across 27 grasslands differed between the aboveground (A, 17 taxonomic groups) and belowground (B, 32 taxonomic groups) compartments. (A) Model predictions were calculated using multimodel averaging across all models in the 95% confidence set and were averaged across regions. (B) Best-fit model contained only mowing intensity.

common species multidiversity (Fig. 2C and Table S2). Many common species may be adapted to anthropogenic environments, and therefore relatively insensitive to increased management intensity. However, changing land use over time did promote common species multidiversity at low mean LUI, although the effect size was smaller than for rare species. Interannual variation in LUI also had a smaller effect on multidiversity calculated with species evenness than with species richness (AICc weights for  $LUI_{sd}$ : 100% for species richness and 49% for evenness; Fig. S1C and Table S2). Because evenness is principally driven by common species and may be negatively correlated with rarity (22), this supports the idea that varying land use over time is particularly beneficial for rarer species.

LUI had different effects on aboveground and belowground multidiversity. Using the subset of 27 grasslands in which 49 taxonomic groups had been measured, we found that aboveground multidiversity followed a similar pattern as in the 150 grasslands (Fig. 4A). Belowground multidiversity, however, was much less affected by land-use intensification or by interannual variation in LUI (Fig. 4B): Only higher mowing frequency slightly reduced belowground multidiversity. One possible explanation could be that belowground multidiversity generally responds on different spatial or temporal scales than aboveground diversity (17). Another explanation could be that land-use intensification homogenizes microbial communities, lowering  $\beta$ -diversity but without reducing  $\alpha$ -diversity (27). Thus, belowground  $\alpha$ -diversity does not appear to be mainly driven by land-use intensification in grasslands.

Our integrated index of multidiversity provides a simple quantitative measure of total ecosystem biodiversity that is superior to vote counting and facilitates comparison among different systems. A vote-counting approach, which analyzes responses of individual taxonomic groups to LUI and counts the shapes of response that are most common, would not have shown a clear

pattern because individual responses differed in magnitude and shape (Fig. 3). Earlier, taxonomically less comprehensive studies have also reported idiosyncratic land-use responses of different groups of organisms (28, 29). However, our study, which covers a large number of groups of organisms, including taxa not normally assessed in environmental monitoring, shows that there is a consistent pattern in a comprehensive measure of the biodiversity of the ecosystem. The multidiversity index could facilitate efforts to identify areas of high conservation priority or to assess the effectiveness of restoration efforts. In our analysis, we assumed that all of the taxonomic groups were of equal importance. However, future uses of the index could consider weighting the groups differently. For instance, groups could be weighted by their conservation relevance, by their importance in providing certain ecosystem services, by their phylogenetic distinctiveness, or by aesthetic/cultural value.

Using the newly developed multidiversity index and our uniquely comprehensive grassland biodiversity data, we not only provide strong support for the importance of extensively managed grasslands for nature conservation (30) but, importantly, show that increased interannual variation in LUI maintains higher biodiversity and slows the rate at which rarer species are lost with increasing LUI. Varying LUI across time might also promote ecosystem service delivery if higher plant diversity increases forage production (31) or higher pollinator diversity promotes pollination of surrounding crops (32). One way of ameliorating the adverse effect of land-use intensification on biodiversity could therefore be to encourage farmers to alter the intensity of their land use somewhat across years. This could contribute to reconciling the need to produce high levels of biomass in grasslands with the maintenance of biodiversity.

## Methods

**Study Design.** The study grasslands are located in three regions in Germany and are part of the Biodiversity Exploratories project ([www.biodiversity-exploratories.de](http://www.biodiversity-exploratories.de)). The study regions are (i) the United Nations Educational, Scientific, and Cultural Organization (UNESCO) Biosphere Area of Schwäbische Alb in southwestern Germany, (ii) the National Park of Hainich-Dün and the surrounding area in central Germany, and (iii) the UNESCO Biosphere Reserve of Schorfheide-Chorin in northeastern Germany. The three regions differ in climate, geology, and topography and are representative of large parts of Central Europe, spanning a range of almost 3 °C in mean annual temperature and 500–1,000 mm of precipitation [details are provided by Fischer et al. (21)]. Grasslands in all three regions span a similar gradient in land-use intensity (LUI) (21). Because natural grasslands, those not requiring management to prevent succession to forest, are almost absent from Western and Central Europe, the land-use gradient is from seminatural to intensively managed grasslands. In each region, 50 permanent grassland plots (50 × 50 m) were established (150 in total) along a gradient of increasing LUI. A smaller number of plots, spanning the same range in LUI, on which more labor-intensive measurements could be carried out were also established: There were nine of these in each exploratory region (27 in total). All of the plots had been grassland for at least 20 y before the start of the project.

**Land Use.** Land use in these grasslands comprises fertilization, mowing, and grazing at different intensities. Land use was quantified based on a questionnaire submitted to farmers and landowners each year from 2006 to 2008 (10, 21). Grasslands could be grazed by cattle, horses, or sheep, and farmers reported the number of animals and the duration of grazing in each plot. Farmers were also asked about the number of mowing events per year (from one to three cuts) and the amount of N in fertilizer (organic and inorganic) added to the grassland.

Land use was quantified using a compound index of LUI (10), which does not suffer information loss due to categorization and makes different management types comparable. LUI integrates the intensity of fertilization ( $F$ ), the mowing frequency ( $M$ ), and the intensity of grazing ( $G$ ) for each grassland plot. Grazing livestock were translated into livestock units weighted for their impact on grasslands (21). For each plot, an individual LUI component ( $F$ ,  $M$ , or  $G$ ) was standardized relative to its mean across all three regions and across all 3 y (details are provided in *SI Methods*). The compound

LUI is the sum of the three standardized components. The minimum LUI of 0.5 could be produced by mowing every 2 y, fertilizing at the rate of 6 kg of  $N\text{-ha}^{-1}\text{-y}^{-1}$ , or grazing one cow (>2 y old) per hectare for 30 d (or one sheep per hectare for the whole year). An intermediate LUI of 1.5 would equate to around two cuts per year, the addition of 60 kg of  $N\text{-ha}^{-1}\text{-y}^{-1}$ , or grazing one cow per hectare for most of the year (300 d). A high LUI of 3.0 could be produced by grazing three cows per hectare for most of the year (300 d) and fertilizing at the rate of 50 kg of  $N\text{-ha}^{-1}\text{-y}^{-1}$  or by cutting three times and fertilizing with 130 kg of  $N\text{-ha}^{-1}\text{-y}^{-1}$ . For the analyses here, we used the average LUI across 3 y and the  $LUI_{sd}$  across 3 y (2006–2008). In addition to using the LUI (i.e., where all three types of land use are given equal weight), we tested the individual standardized land use components in our models to determine whether certain types of land use had a larger effect on biodiversity.

The intensity of land use in the grasslands changed considerably over time (10). We quantified this using the  $LUI_{sd}$  across the 3 y. This  $LUI_{sd}$  was uncorrelated with the mean LUI across the 3 y (Fig. S5). Because most of the data were collected in 2008 or 2009 (Table S4),  $LUI_{sd}$  calculates the change in land use in the years preceding data collection. We also calculated the SD in mowing, grazing, and fertilization intensity across the 3 y (*SI Methods*).

**Species Richness Data.** Data on the species richness of 18 taxonomic groups were collected with different standardized sampling methods on the 150 plots (Table S4). In some cases, more labor-intensive methods were used to sample the same groups on the subset of 27 plots; however, the intensity of sampling did not affect the results (Fig. S6A). Note that we use the term “species richness” throughout, although for the microbial and fungal groups, these are phylotypes and not necessarily true species.

**Calculation of Multidiversity.** We calculated multidiversity as the average proportional species richness across taxonomic groups. Species richness values were standardized for each taxonomic group by scaling them to the maximum observed value across all grasslands. Note that we could not simply sum species richness values to calculate multidiversity because this would have given higher weighting to species-rich groups. For instance, the bacterial groups had phylotype richness values of several thousand. However, we also conducted a range of sensitivity analyses to test other ways of calculating multidiversity (*SI Methods*). We used a different standardizations of species richness, we used a range of thresholds, and we calculated multidiversity using alternative taxonomic groupings (Fig. S6). The code used to calculate multidiversity is available at <https://github.com/eric-allan/multidiversity>.

We calculated multidiversity values for all 150 plots using 18 groups, and we also calculated multidiversity for the six plant groups (including lichens) and 11 animal groups separately. Furthermore, we calculated multidiversity based on Pielou's evenness index ( $J$ ) rather than based on species richness. On the subset of 27 plots, we calculated multidiversity for the 17 above-ground groups and the 33 below-ground groups separately.

Additionally, we calculated multidiversity on all 150 plots for common and rare species separately. For each species, we calculated its total abundance across plots. Within each of 17 groups (we did not have data on the occurrence of each mycorrhizal fungal phylotype in each plot, so they were excluded from this analysis), we split the species into two categories: Common species were the top 10% in terms of total abundance, and the species we refer to as “rare” were the bottom 90% of species. Species abundances followed approximately lognormal distributions, so this split ensured that only abundant species were counted as common. Classifying rare species as the least abundant 50% of species or defining rare and common species separately for each region gave similar results (*SI Methods* and Table S3). Using a threshold in this way means that the species we classified as rare were only relatively rare (i.e., across the study plots) and not necessarily generally rare in the landscape. We analyzed multidiversity for the 17 groups of rare species and the 17 groups of common species separately.

**Statistical Analysis.** We first analyzed the response to LUI for each of the 18 taxonomic groups measured on all plots; all analyses were conducted with R version 2.15 (33). We used an approach similar to that of Scherber et al. (16) and scaled the species richness of each group between 0 and 1. We then fitted a series of models to estimate the shape of the response of each taxonomic group to LUI. We fitted “region” in all models to account for regional differences in species richness. We tested polynomial models with linear, quadratic, or cubic terms for LUI. These models test for a linear change in species richness with land use, a unimodal relationship, or a relationship with two turning points. We also used nonlinear regressions [fitted with the `gnls` function in `nlme` (34)] and tested for three further shapes of response: (i) negative exponential models, which model an

exponential decay of species richness with increasing LUI, asymptoting at 0; (ii) asymptotic exponential models in which species richness can asymptote at values greater than 0; and (iii) power law models, which allow a diversity of shapes of response to be modeled. In the nonlinear regressions, we modeled the intercept of each model as a function of region, which is therefore equivalent to fitting region as a categorical factor in the polynomial regressions. We also fitted a null model with only a main effect for region.

To model the influence of temporal changes in LUI, we fitted the same models as above but with covariates for LUI<sub>sd</sub>. For the linear regressions (linear, quadratic, or cubic), we either fitted a main effect only for LUI<sub>sd</sub> or an interaction between LUI<sub>sd</sub> and all other parameters. For the nonlinear regressions, we modeled all of the possible combinations of each of the individual parameters as a function of LUI<sub>sd</sub>. This resulted in 25 different models (Table S1). For each taxonomic group, the best-fit model was selected using AICc (35).

To analyze the shape of the relationship between LUI and multidiversity, we used the same series of models as above; in addition, we tested models with each of the three land-use components (fertilization, grazing, and mowing) fitted individually. We did not use models with individual land-use components for the analysis of individual diversities because we wanted to be able to compare the response of the different taxonomic groups to the same measure of LUI. In the analysis of multidiversity, we fitted all possible combinations of linear or linear and quadratic terms for each land-use component, while obeying the principle of marginality (36). All models contained a main effect for region. We did not conduct nonlinear regressions for the different land-use components

because models could not include nonlinear terms for more than one land-use component at a time (all 76 models are listed in Table S1).

To model multidiversity on the subset of 27 plots with fewer degrees of freedom, we used a reduced set of models. We did not include linear models with interactions between LUI<sub>sd</sub> and LUI or nonlinear models with more than one parameter modeled as a function of LUI<sub>sd</sub> (67 models).

We calculated AICc weights for each model: These weight the explanatory power of each model relative to the others tested. For the analysis of multidiversity, we present the models that account for 95% of the AICc weights as the set of best models (95% confidence set). We also calculated parameters for the relationships shown in Figs. 2 and 4A with multimodel averaging (35), using the MuMIn package in R (37). This averages the parameters across all models in the 95% confidence set, weighing each value by the model's AICc weight. We further calculated the square of the Pearson correlation coefficient between observed and model fitted values (pseudo- $R^2$ ). Although this measure may not be appropriate for nonlinear models, it conveys an idea of the goodness of fit.

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- Adler PB, HilleRisLambers J, Kyriakidis PC, Guan Q, Levine JM (2006) Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc Natl Acad Sci USA* 103(34):12793–12798.
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366.
- Foley JA, et al. (2005) Global consequences of land use. *Science* 309(5734):570–574.
- Flynn DFB, et al. (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecol Lett* 12(1):22–33.
- Laliberté E, et al. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecol Lett* 13(1):76–86.
- Isbell F, et al. (2011) High plant diversity is needed to maintain ecosystem services. *Nature* 477(7363):199–202.
- Clough Y, et al. (2011) Combining high biodiversity with high yields in tropical agroforests. *Proc Natl Acad Sci USA* 108(20):8311–8316.
- Geiger F, et al. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic Appl Ecol* 11(2):97–105.
- Kleijn D, et al. (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc Biol Sci* 276(1658):903–909.
- Blüthgen N, et al. (2012) A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic Appl Ecol* 13(3):207–220.
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: Is habitat heterogeneity the key? *Trends Ecol Evol* 18(4):182–188.
- Fuhlendorf SD, Engle DM (2001) Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *Bioscience* 51(8):625–632.
- McKinney ML, Lockwood JL (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14(11):450–453.
- Fischer M, Stöcklin J (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conserv Biol* 11(3):727–737.
- Lavergne S, Thuiller W, Molina J, Debussche M (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: A 115-year study in the Mediterranean region. *J Biogeogr* 32(5):799–811.
- Scherber C, et al. (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468(7323):553–556.
- De Deyn GB, Van der Putten WH (2005) Linking aboveground and belowground diversity. *Trends Ecol Evol* 20(11):625–633.
- Bardgett RD, Bowman WD, Kaufmann R, Schmidt SK (2005) A temporal approach to linking aboveground and belowground ecology. *Trends Ecol Evol* 20(11):634–641.
- Maestre FT, et al. (2012) Plant species richness and ecosystem multifunctionality in global drylands. *Science* 335(6065):214–218.
- Loh J, et al. (2005) The Living Planet Index: Using species population time series to track trends in biodiversity. *Philos Trans R Soc Lond B Biol Sci* 360(1454):289–295.
- Fischer M, et al. (2010) Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic Appl Ecol* 11(6):473–485.
- Wilsey BJ, Chalcraft DR, Bowles CM, Willig MR (2005) Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology* 86(5):1178–1184.
- Thies C, Steffan-Dewenter I, Tscharntke T (2008) Interannual landscape changes influence plant-herbivore-parasitoid interactions. *Agric Ecosyst Environ* 125(1–4):266–268.
- Isbell F, Tilman D, Polasky S, Binder S, Hawthorne P (2013) Low biodiversity state persists two decades after cessation of nutrient enrichment. *Ecol Lett* 16(4):454–460.
- Phalan B, Onial M, Balmford A, Green RE (2011) Reconciling food production and biodiversity conservation: Land sharing and land sparing compared. *Science* 333(6047):1289–1291.
- Tscharntke T, et al. (2012) Landscape moderation of biodiversity patterns and processes—Eight hypotheses. *Biol Rev Camb Philos Soc* 87(3):661–685.
- Rodrigues JLM, et al. (2013) Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil bacterial communities. *Proc Natl Acad Sci USA* 110(3):988–993.
- Billetter R, et al. (2008) Indicators for biodiversity in agricultural landscapes: A pan-European study. *J Appl Ecol* 45(1):141–150.
- Dormann CF, et al. (2007) Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Glob Ecol Biogeogr* 16(6):774–787.
- Krauss J, et al. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. *Ecol Lett* 13(5):597–605.
- Isbell F, et al. (2013) Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proc Natl Acad Sci USA* 110(29):11911–11916.
- Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. *Proc Natl Acad Sci USA* 99(26):16812–16816.
- R Core Team (2012) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna).
- Pinheiro J, Bates D, DebRoy S, Sarkar D; R Development Core Team (2012) *lme4: Linear and Nonlinear Mixed Effects Models*.
- Burnham K, Anderson D (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer, Berlin).
- Nelder JA (1977) A reformulation of linear models. *J R Stat Soc Ser A Stat Soc* 140(1):48–77.
- Bartoň K (2012) *MuMIn: Multi-Model Inference*. R Package Version 1.

# Supporting Information

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## SI Methods

**Land-Use Intensity Index.** The land-use intensity index (LUI) sums the intensity of fertilization ( $F$ ), the frequency of mowing ( $M$ ), and the intensity of livestock grazing ( $G$ ) in each plot. Pesticides were not applied to any of the plots, and were therefore not included.  $F$  was quantified as kilograms of nitrogen (N) applied per hectare and included both organic and inorganic N; rates varied between 0 and 163 kg of N·ha<sup>-1</sup>. To convert organic fertilizer inputs to kilograms of N per hectare, the volume of cattle slurry was multiplied by 3.2 kg of N·m<sup>-3</sup> and that of cattle manure was multiplied by 0.6 kg of N·m<sup>-3</sup>.  $G$  was calculated based on the number of days of grazing, the density of grazing animals per hectare, and the type of grazing animal, which was expressed as livestock units (LU), and varied between 0 and 1,430 LU. Grazing animals were converted to LU as follows: cattle <1 y old, 0.3 LU; cattle aged 2 y, 0.6 LU; cattle >2 y old, 1 LU; sheep and goats <1 y old, 0.05 LU; sheep and goats >1 y old, 0.1 LU; horses <3 y old, 0.7 LU; horses >3 y old, 1.1 LU.  $M$  was the number of cuts per year and ranged from one to three. The intensities of these three land-use components were standardized by their means across regions and across 3 y (2006–2008) and summed to produce the LUI:

$$\text{LUI} = \sqrt{\frac{F}{F_{G\ 2006-2008}} + \frac{G}{G_{G\ 2006-2008}} + \frac{M}{M_{G\ 2006-2008}}},$$

where  $F_{G\ 2006-2008}$ ,  $G_{G\ 2006-2008}$ , and  $M_{G\ 2006-2008}$  are the global mean values for fertilization, grazing, and mowing across all regions and across 3 y:  $F_{G\ 2006-2008} = 23$  kg of N·ha<sup>-1</sup>,  $G_{G\ 2006-2008} = 129$  grazing days (i.e., equivalent to grazing one cow >2 y old per hectare for 129 d), and  $M_{G\ 2006-2008} = 1.0$  cut per year. The square-root transformation was applied to produce a more even distribution and to reduce the influence of outliers. Standardizing by means within regions gave almost identical values ( $R^2 = 0.97$ ), as did standardizing by the maximum rather than the mean ( $R^2 = 0.86$ ) (1).

**Sensitivity Analyses.** In addition to the main analysis using a mean of scaled species richness values, we used a threshold-based approach to calculate multidiversity because it has been argued that this is more appropriate for multifunctionality indices (2, 3). In each plot, the species richness of each taxonomic group was scored as to whether it passed a certain threshold, which was defined as a proportion of the maximum species richness attained by that group in any plot across all regions. For each plot, the multidiversity score was the proportion of groups that exceeded the given threshold (i.e., the proportion of taxonomic groups that were at high diversity). We used thresholds of 30%, 50%, 60%, and 70% of the maximum species richness for each group (Table S3). Using these different thresholds resulted in very similar model selection. In all cases, asymptotic exponential models were the best (all models in the 95% confidence set modeled an asymptotic exponential relationship between LUI and multidiversity) and the SD in LUI ( $\text{LUI}_{\text{sd}}$ ) was included in the best-fit models (Table S3). This shows that using a threshold did not qualitatively change our results. In addition to using a threshold, we tested whether standardizing species richness values by calculating z-scores (i.e., subtracting the mean and dividing by the SD) changed the results compared with standardizing by the maximum. The alternative standardization gave almost exactly the same results (Table S3).

We also calculated multidiversity of rare (bottom 90%) and common (top 10%) species separately for each region. Species that are restricted to a single region might, in fact, be common within a region but appear rare across regions. To account for this, we designated species as rare or common for each of the three regions and then calculated multidiversity of rare and common species separately per region. We then combined the multidiversity values from the different regions and analyzed them in a single analysis using the same models as before. This gave similar results to defining the rare and common species across regions. Regardless of whether rare species were defined across regions or separately within regions, multidiversity was best predicted with an asymptotic exponential model and changing land use over time was beneficial for rare species multidiversity (Table S3). For the multidiversity of common species, variation in LUI over time had positive effects when the common species were defined across or within regions. In both cases, overall mean LUI did not have strong effects on multidiversity, but the shape of the relationship varied, the model with the lowest Akaike's information criterion (corrected for small sample sizes), AICc, in the analysis of multidiversity of common species defined within regions had a quadratic term for LUI (Table S3). This model predicted that the lowest multidiversity was found at intermediate LUI; however, the quadratic relationship was not well supported, because the second best model (<1 AICc unit higher than the best model) suggested a continuous, decelerating decline in multidiversity with LUI. Because it is not possible to separate models that differ in <2 AICc units, we can only conclude that the common species multidiversity, defined within regions, declines nonlinearly with increasing LUI and that variation in LUI has an important effect. Thus, both methods of defining common species gave similar results, although the species that are common across regions seem less sensitive to overall LUI.

Our measure of multidiversity gives equal weight to all of the groups used to calculate it; therefore, we also explored the sensitivity of our measure to alternative groupings. Using the subset of 27 plots, we aggregated the data into progressively larger taxonomic groups and checked whether calculating multidiversity among these larger groups changed the result. Multidiversity values calculated using these different groupings were very closely correlated (Fig. S6).

**Individual Components of Land Use and Land-Use Variation.** Although the models containing the integrated index of LUI had better fits than the models with the individual components of land use (grazing, fertilization, and mowing) fitted separately (Table S2), we did some additional modeling to determine which of these components was most important in affecting multidiversity. We therefore analyzed multidiversity only with models containing the individual land-use components: All possible combinations of linear and quadratic terms for grazing, fertilization, and mowing were fitted, along with the  $\text{LUI}_{\text{sd}}$ , which was fitted only as a linear term (all the models containing the individual components are listed in Table S1). All of the variables seemed to be important, because the best-fit model contained linear terms for mowing and grazing and a quadratic term for fertilization, along with the  $\text{LUI}_{\text{sd}}$ . Examining the AICc weights of the terms revealed some differences, with grazing and mowing having higher weights than fertilization (Fig. S2). Variation in LUI remained important in this set of models. We also plotted the effects of the different components of LUI using partial regression plots, which is the most appropriate way to show the effects of variables that are

correlated with each other (4) (Fig. S2). This showed that mowing and grazing had strong negative effects on multidiversity, whereas fertilization had much smaller effects, with high rates of fertilization not negative for multidiversity. High fertilization is usually associated with high mowing frequency (1), but these results show that the high rates of fertilization themselves may not have as negative effects as high mowing intensity. It is often predicted that diversity is maximized at intermediate grazing intensity and not at the lowest grazing intensities (5). We do not find evidence for this here, but we note that we have no grasslands that are never grazed or mown and that cessation of grazing in our species-rich, lightly grazed grasslands would likely lead to shrub encroachment and a decline in the diversity of many groups.

To investigate the effects of  $LUI_{sd}$  further, we fitted a series of asymptotic exponential models with parameters modeled as a function of the SD in the individual components of land use (grazing, fertilization, and mowing). We selected all of the models in the 95% confidence set (Table S2), and as well as fitting models in which the intercept, intercept and asymptote, intercept and rate constant, or all three parameters depended on the  $LUI_{sd}$ , we also fitted sets of models in which these parameters depended on all possible combinations of SD in fertilization, mowing, or grazing: a total of 33 models. This led to the same model selection as in the overall analysis (i.e., models containing variation in the individual components provided much worse fits than models with  $LUI_{sd}$ ). This indicates that temporal variation in LUI is much better captured with our overall metric than with measures of variability in different types of land use. However, to identify whether variation in some types of land use was more important, we removed the models containing  $LUI_{sd}$  from the set of models and selected only among models with the temporal SDs of the individual components. This revealed that the SD in grazing intensity over time was most important (100% of AICc weights) and that variation in the other components was less important (SD of fertilization intensity = 43% and SD of mowing intensity = 57%). The effect size of the SD of grazing intensity was also larger, because it increased the intercept of the asymptotic exponential by  $1.71 \pm 1.1$ , which is larger than the effect of fertilization ( $1.05 \pm 1.1$ ) or mowing ( $0.83 \pm 0.82$ ); these parameters come from a model with the intercept modeled as a function of the SD in grazing, mowing, and fertilization.

**Effect of Changes in Abundance.** We further investigated whether the patterns in species richness that we found could have been driven only by changes in abundance or whether there was an effect on species richness, per se. Typically, rarefaction would be

used to correct species richness values for abundance, but in our dataset, minimum abundance values in a plot were low (often one or two individuals) for many taxonomic groups, making rarefaction problematic. We therefore used the approach of Richardson and Richards (6), which generates an expected diversity for each group in each plot, assuming that only abundance drives the species richness patterns. This approach pools all individuals of every species into one large group and then randomly samples individuals from this species pool to form the local communities. The randomization is constrained so that total abundance in each sample and for each species remains fixed at observed values. We used this randomization to produce expected species richness values for each group in each plot. We used the data from the 17 groups (minus mycorrhizal fungi, for which there were no abundance data) measured on the 150 grassland plots for this analysis.

Having derived expected species richness values, we then calculated multidiversity using the expected species richness. If changes in abundance drive the multidiversity pattern, multidiversity calculated from expected values should show the same pattern as the original multidiversity index. Multidiversity calculated from expected values was not correlated with LUI (Fig. S3A). We also calculated observed and expected species richness for each group in each plot. This is the species richness value, corrected for abundance. We plotted observed minus expected values for each group against LUI (Fig. S4). For many of the groups, these observed minus expected values did still decrease with increasing LUI, indicating that there is an LUI effect on species richness, per se, for these groups. However, for other taxonomic groups (butterflies and birds), the species richness response did seem to be driven by abundance because observed minus expected values did not decline with increasing LUI. We then calculated multidiversity from the observed minus expected values. Because many of these values were negative (observed species richness less than expected), we first recoded negative values as 0. These multidiversity values did show a similar pattern to the overall index: an exponential decline with increasing LUI and a positive effect of  $LUI_{sd}$  (Fig. S3B and Table S3). These analyses indicate that the species richness response of some of the groups was driven by abundance and, therefore, that some of the response of multidiversity was driven by abundance changes in these groups. However, there were also effects on species richness, per se, and our overall conclusions about the response of multidiversity to LUI were not solely driven by abundance changes.

1. Blüthgen N, et al. (2012) A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic Appl Ecol* 13(3):207–220.
2. Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proc Natl Acad Sci USA* 107(4):1443–1446.
3. Gamfeldt L, Hillebrand H, Jonsson PR (2008) Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology* 89(5):1223–1231.

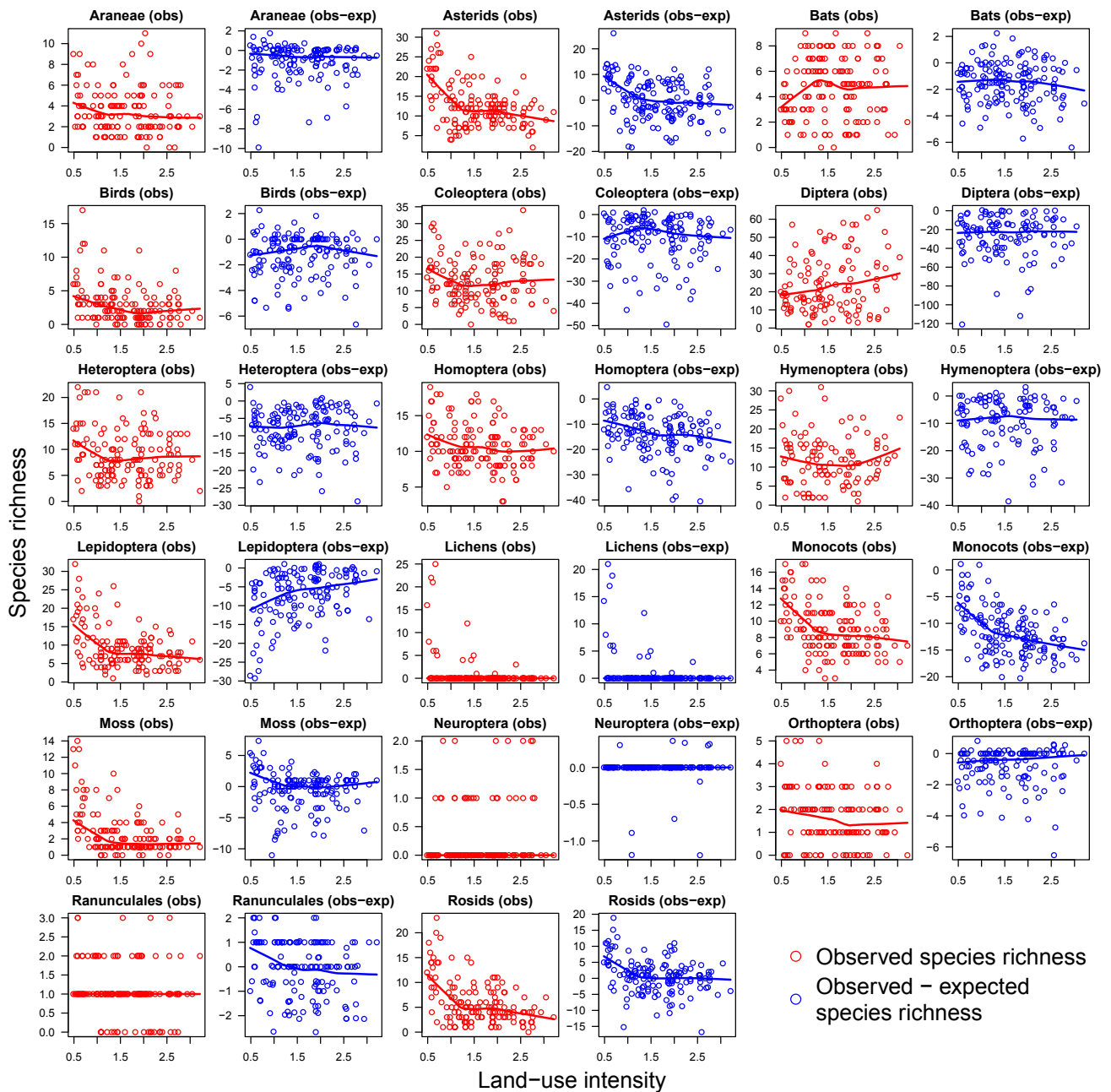
4. Moya-Laraño J, Corcobado G (2008) Plotting partial correlation and regression in ecological studies. *Web Ecol* 8:35–46.
5. Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol Monogr* 63(4):327–366.
6. Richardson JML, Richards MH (2008) A randomisation program to compare species-richness values. *Insect Conservation and Diversity* 1(3):135–141.



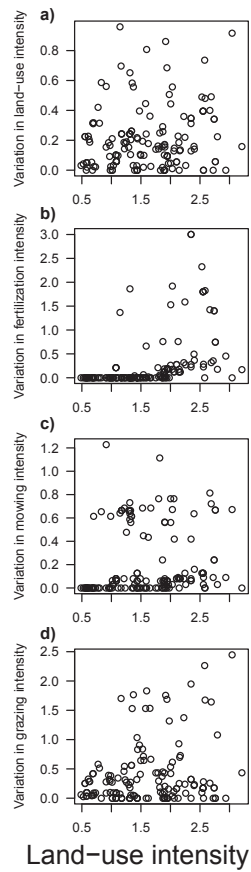




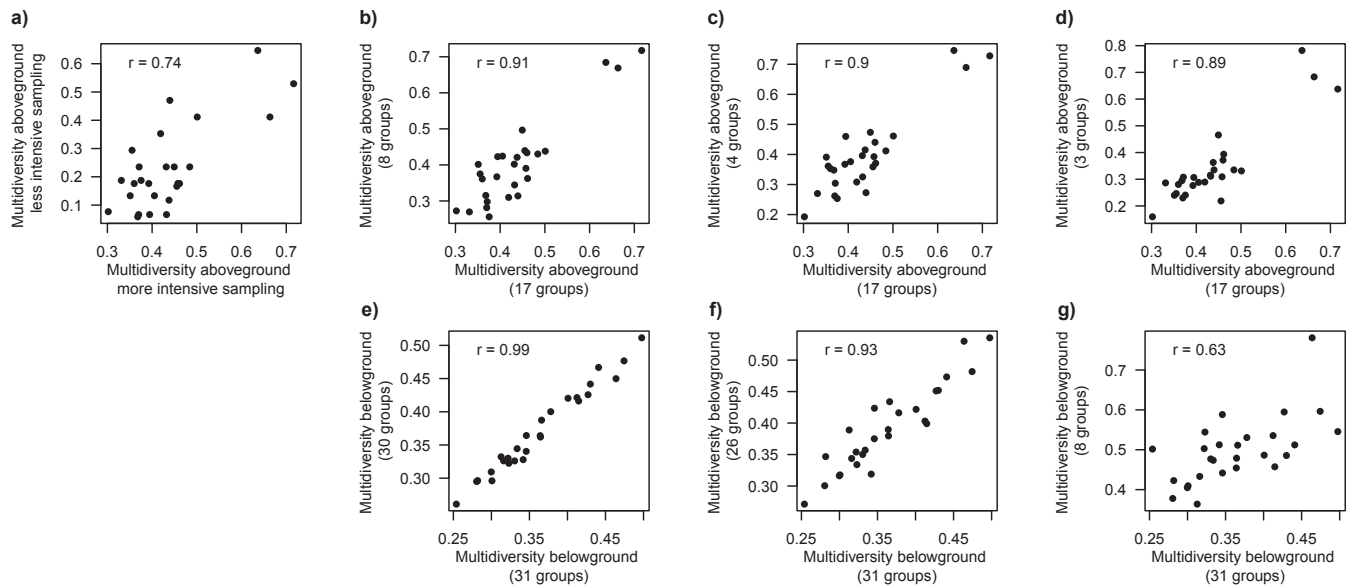




**Fig. S4.** Observed and abundance-corrected species richness for each of 17 taxonomic groups measured in the 150 grasslands. For each group, the points in red show the observed species richness against LUI. The points in blue show the observed (obs) minus expected (exp) species richness (more information regarding the calculation of expected values is provided in *SI Methods*). The solid line shows a locally weighted polynomial regression fitted to the data with  $\text{span} = 2/3$ , function “*lowess*” in R.



**Fig. S5.** Relationship between mean LUI and  $LUI_{sd}$  across 3 y (*A*,  $\rho = 0.12$ ), SD in mowing frequency across 3 y (*C*,  $\rho = 0.33$ ), SD in grazing intensity (*D*,  $\rho = 0.12$ ), and SD in fertilization intensity (*B*,  $\rho = 0.73$ ). Examples of plots with high interannual variation in LUI are shown: to produce a  $LUI_{sd}$  of 0.9 and a mean LUI of 3: 2 y of heavy grazing ( $1,428 \text{ LU}\cdot\text{ha}^{-1}$ ) and mowing once a year, and 1 y of grazing moderately ( $461 \text{ LU}\cdot\text{ha}^{-1}$ ); to produce a  $LUI_{sd}$  of 0.8 and a mean LUI of 1.9: 2 y of grazing at  $671 \text{ LU}\cdot\text{ha}^{-1}$  and 1 y of grazing at  $80 \text{ LU}\cdot\text{ha}^{-1}$ ; and to produce a  $LUI_{sd}$  of 0.65 and a mean LUI of 1.3: 1 y of grazing lightly ( $56 \text{ LU}\cdot\text{ha}^{-1}$ ), 1 y of mowing once a year, and 1 y of fertilizing at  $62 \text{ kg of N}\cdot\text{ha}^{-1}$  and mowing once per year.



**Fig. S6.** Relationship among different measures of multidiversity on the subset of 27 plots for multidiversity aboveground (A–D) and multidiversity belowground (E–G). In each graph,  $r$  values show Pearson correlation coefficients. (A) No extra taxonomic groups were measured aboveground on the subset of 27 plots; however, several insect groups were measured more intensively on the subset of 27 plots than they were on all 150 plots (full details are provided in Table S4). Multidiversity is calculated with the species richness values from the more intensive sampling “Multidiversity aboveground 27 plots” and is calculated with the same 17 groups but with species richness values from the less intensive sampling “Multidiversity aboveground 150 plots.” The high correlation between the two measures shows that the intensity of sampling does not affect the overall results. (B–G) Multidiversity was also calculated using different taxonomic groups, progressively aggregating groups into larger ones and summing the species richness values within the groups. Three different levels were used, and these are shown in Table S4. For example, Coleoptera formed one group in the main analysis of multidiversity. For aggregation level 1, they were aggregated with other insects and the total species richness of Hexapoda was included in the analysis; for aggregation level 2, they were aggregated with all other arthropods (insects and arachnids) and the species richness of Arthropoda was analyzed; and at aggregation level 3, they were aggregated with all other animals (also including vertebrate groups) and the species richness of animals was analyzed as one group. This tests whether our calculation of multidiversity is affected by the taxonomic groups that we chose; the close correlations among all of the measures indicate that the groups we chose for the analysis do not bias the results. Correlations between the multidiversity values used in the main analysis and the groups formed with the first aggregation are shown for aboveground groups (B, 17 vs. 8 groups) and belowground groups (E, 31 vs. 30 groups). Correlations between the multidiversity values used in the main analysis and the groups formed with the second aggregation are shown for aboveground groups (C, 17 vs. 4 groups) and belowground groups (F, 31 vs. 26 groups). Correlations between the multidiversity values used in the main analysis and the groups formed with the third aggregation are shown for aboveground groups (D, 17 vs. 3 groups) and belowground groups (G, 31 vs. 8 groups).

**Table S1. All the models fit in the analyses**

Model description	R code
<b>Model with compound LUI: used for all analyses</b>	
No LUI <sub>sd</sub>	
Null	lm(y ~ Exploratory)
Linear LUI	lm(y ~ Exploratory + LUI)
Quadratic LUI	lm(y ~ Exploratory + poly(LUI,2))
Cubic LUI	lm(y ~ Exploratory + poly(LUI,3))
Negative exponential LUI	gnls(y ~ a * exp(-b * LUI), params = list(a ~ Exploratory, b ~ 1), start = c(1, 1, 1, 1))
Asymptotic exponential LUI	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym + lrc ~ 1, R0 ~ Exploratory), start = c(p[c(1, 3)], p[2], 1, 1))
Power law LUI	gnls(y ~ a + b * (LUI^c), params = list(a ~ Exploratory, b + c ~ 1), start = c(p2[1], 0, 0, p2[2], p2[3]))
LUI <sub>sd</sub> main effect	
LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd)
Linear LUI + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI + LUI.sd)
Quadratic LUI + LUI <sub>sd</sub>	lm(y ~ Exploratory + poly(LUI,2) + LUI.sd)
Cubic LUI + LUI <sub>sd</sub>	lm(y ~ Exploratory + poly(LUI,3) + LUI.sd)
Negative exponential intercept as function of LUI <sub>sd</sub>	gnls(y ~ a * exp(-b * LUI), params = list(a ~ Exploratory + LUI.sd, b ~ 1), start = c(1, 1, 1, 1, 1))
Asymptotic exponential intercept as function of LUI <sub>sd</sub>	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym + lrc ~ 1, R0 ~ Exploratory + LUI.sd), start = c(p[c(1, 3)], p[2], 1, 1, 0), control = nlc)
Asymptotic exponential asymptote as function of LUI <sub>sd</sub>	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym ~ LUI.sd, lrc ~ 1, R0 ~ Exploratory), start = c(p[1], 0, p[3], p[2], 1, 1), control = nlc)
Asymptotic exponential rate constant as function of LUI <sub>sd</sub>	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym ~ 1, lrc ~ LUI.sd, R0 ~ Exploratory), start = c(p[c(1, 3)], 0, p[2], 1, 1), control = nlc)
Power law intercept as function of LUI <sub>sd</sub>	gnls(y ~ a + b * (LUI^c), params = list(a ~ Exploratory + LUI.sd, b + c ~ 1), start = c(p2[1], 0, 0, p2[2], p2[3]))
LUI <sub>sd</sub> interaction	
Linear LUI × LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI * LUI.sd)
Quadratic LUI × LUI <sub>sd</sub>	lm(y ~ Exploratory + poly(LUI,2) * LUI.sd)
Cubic LUI × LUI <sub>sd</sub>	lm(y ~ Exploratory + poly(LUI,3) * LUI.sd)
Negative exponential all parameters as function of LUI <sub>sd</sub>	gnls(y ~ a * exp(-b * LUI), params = list(a ~ Exploratory + LUI.sd, b ~ LUI.sd), start = c(1, 1, 1, 1, 1))
Asymptotic exponential asymptote and rate constant as function of LUI <sub>sd</sub>	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym + lrc ~ LUI.sd, R0 ~ Exploratory), start = c(p[1], 0, p[2], 0, p[3], 1, 1), control = nlc)
Asymptotic exponential asymptote and intercept as function of LUI <sub>sd</sub>	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym ~ LUI.sd, lrc ~ 1, R0 ~ Exploratory + LUI.sd), start = c(p[1], 0, p[3], p[2], 1, 1, 0), control = nlc)
Asymptotic exponential rate constant and intercept as function of LUI <sub>sd</sub>	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym ~ 1, lrc ~ LUI.sd, R0 ~ Exploratory + LUI.sd), start = c(p[1], p[3], 0, p[2], 1, 1, 0), control = nlc)
Asymptotic exponential all parameters as function of LUI <sub>sd</sub>	gnls(y ~ Asym + (R0 - Asym) * exp(-exp(lrc) * LUI), params = list(Asym + lrc ~ LUI.sd, R0 ~ Exploratory + LUI.sd), start = c(p[1], 0, p[3], 0, p[2], 1, 1, 0), control = nlc)
Power law all parameters as function of LUI <sub>sd</sub>	gnls(y ~ a + b * (LUI^c), params = list(a ~ Exploratory + LUI.sd, b + c ~ LUI.sd), start = c(p2[1], 0, 0, 0, p2[2], 0, p2[3], 0))
<b>Models with individual components: used for analysis of multidiversity</b>	
Fertilization	lm(y ~ Exploratory + Fstd)
Mowing	lm(y ~ Exploratory + Mstd)
Grazing	lm(y ~ Exploratory + Gstd)
Fertilization + grazing	lm(y ~ Exploratory + Fstd + Gstd)
Fertilization + mowing	lm(y ~ Exploratory + Fstd + Mstd)
Mowing + grazing	lm(y ~ Exploratory + Mstd + Gstd)
Fertilization + mowing + grazing	lm(y ~ Exploratory + Fstd + Mstd + Gstd)
Fertilization <sup>2</sup>	lm(y ~ Exploratory + poly(Fstd,2))
Mowing <sup>2</sup>	lm(y ~ Exploratory + poly(Mstd,2))
Grazing <sup>2</sup>	lm(y ~ Exploratory + poly(Gstd,2))
Fertilization <sup>2</sup> + mowing	lm(y ~ Exploratory + poly(Fstd,2) + Mstd)
Fertilization <sup>2</sup> + mowing + grazing	lm(y ~ Exploratory + poly(Fstd,2) + Mstd + Gstd)
Fertilization <sup>2</sup> + grazing	lm(y ~ Exploratory + poly(Fstd,2) + Gstd)
Mowing <sup>2</sup> + fertilization	lm(y ~ Exploratory + poly(Mstd,2) + Fstd)
Mowing <sup>2</sup> + fertilization + grazing	lm(y ~ Exploratory + poly(Mstd,2) + Fstd + Gstd)
Mowing <sup>2</sup> + grazing	lm(y ~ Exploratory + poly(Mstd,2) + Gstd)
Grazing <sup>2</sup> + fertilization	lm(y ~ Exploratory + poly(Gstd,2) + Fstd)
Grazing <sup>2</sup> + fertilization + mowing	lm(y ~ Exploratory + poly(Gstd,2) + Fstd + Mstd)
Grazing <sup>2</sup> + mowing	lm(y ~ Exploratory + poly(Gstd,2) + Mstd)
Fertilization <sup>2</sup> + mowing <sup>2</sup>	lm(y ~ Exploratory + poly(Fstd,2) + poly(Mstd,2))
Fertilization <sup>2</sup> + grazing <sup>2</sup>	lm(y ~ Exploratory + poly(Fstd,2) + poly(Gstd,2))

**Table S1. Cont.**

Model description	R code
Mowing <sup>2</sup> + Grazing <sup>2</sup>	lm(y ~ Exploratory + poly(Mstd,2) + poly(Gstd,2))
Fertilization <sup>2</sup> + mowing <sup>2</sup> + grazing	lm(y ~ Exploratory + poly(Fstd,2) + poly(Mstd,2) + Gstd)
Fertilization <sup>2</sup> + grazing <sup>2</sup> + mowing	lm(y ~ Exploratory + poly(Fstd,2) + poly(Gstd,2) + Mstd)
Mowing <sup>2</sup> + grazing <sup>2</sup> + fertilization	lm(y ~ Exploratory + poly(Mstd,2) + poly(Gstd,2) + Fstd)
Mowing <sup>2</sup> + grazing <sup>2</sup> + fertilization <sup>2</sup>	lm(y ~ Exploratory + poly(Fstd,2) + poly(Mstd,2) + poly(Gstd,2))
With LUI <sub>sd</sub>	
Fertilization + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + Fstd)
Mowing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + Mstd)
Grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + Gstd)
Fertilization + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + Fstd + Gstd)
Fertilization + mowing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + Fstd + Mstd)
Mowing + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + Mstd + Gstd)
Fertilization + mowing + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + Fstd + Mstd + Gstd)
Fertilization <sup>2</sup>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2))
Mowing <sup>2</sup> + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Mstd,2))
Grazing <sup>2</sup> + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Gstd,2))
Fertilization <sup>2</sup> + mowing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + Mstd)
Fertilization <sup>2</sup> + mowing + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + Mstd + Gstd)
Fertilization <sup>2</sup> + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + Gstd)
Mowing <sup>2</sup> + fertilization + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Mstd,2) + Fstd)
Mowing <sup>2</sup> + fertilization + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Mstd,2) + Fstd + Gstd)
Mowing <sup>2</sup> + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Mstd,2) + Gstd)
Grazing <sup>2</sup> + fertilization + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Gstd,2) + Fstd)
Grazing <sup>2</sup> + fertilization + mowing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Gstd,2) + Fstd + Mstd)
Grazing <sup>2</sup> + mowing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Gstd,2) + Mstd)
Fertilization <sup>2</sup> + mowing <sup>2</sup> + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + poly(Mstd,2))
Fertilization <sup>2</sup> + grazing <sup>2</sup> + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + poly(Gstd,2))
Mowing <sup>2</sup> + grazing <sup>2</sup> + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Mstd,2) + poly(Gstd,2))
Fertilization <sup>2</sup> + mowing <sup>2</sup> + grazing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + poly(Mstd,2) + Gstd)
Fertilization <sup>2</sup> + grazing <sup>2</sup> + mowing + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + poly(Gstd,2) + Mstd)
Mowing <sup>2</sup> + grazing <sup>2</sup> + fertilization + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Mstd,2) + poly(Gstd,2) + Fstd)
Mowing <sup>2</sup> + grazing <sup>2</sup> + fertilization <sup>2</sup> + LUI <sub>sd</sub>	lm(y ~ Exploratory + LUI.sd + poly(Fstd,2) + poly(Mstd,2) + poly(Gstd,2))

A model description is given, along with the code used to fit the models in the statistical package R. The formula for the asymptotic exponential model was:

$$y = a + (b - a)e^{-e^c x}$$

where  $a$  is the asymptote (Asym in R code),  $b$  is the intercept (R0), and  $c$  is the natural log of the rate constant (lrc).

The formula for the negative exponential was:

$$y = ae^{-bx}$$

where  $a$  is the intercept and  $b$  is the rate constant.

The formula for the power law models was:

$$y = a + bx^c$$

For the asymptotic exponential models, starting parameters "p" were found using the self-starting function SSasym in R. For the power law models, starting parameters "p2" were found by trying a series of random starting values using the R function nl2.



**Table S2. Best-fit models in the analysis of multidiversity**

Type	LUI	LUI <sub>sd</sub>	Fertilization	Mowing	Grazing	AICc	AICc weight, %	Pseudo-R <sup>2</sup> , %
150 plots, 18 taxonomic groups								
Multidiversity measures								
Multidiversity (richness, all species)								
AE	AE	Intercept				-390	47	49
AE	AE	Intercept, asymptote				-389	26	50
AE	AE	Rate, asymptote				-388	16	49
AE	AE	Intercept, asymptote, rate				-386	8	50
Multidiversity (rare species)								
AE	AE	Rate				-387	33	53
AE	AE	Asymptote, rate				-386	22	54
AE	AE	Asymptote, intercept				-385	15	53
AE	AE	Intercept				-385	13	53
AE	AE	Rate, intercept				-384	9	53
AE	AE	Rate, intercept, asymptote				-384	7	54
Multidiversity (common species)								
AE	AE	Intercept				-376	37	29
AE	AE	Asymptote, intercept				-374	15	29
AE	AE	Rate, intercept				-374	14	29
AE	AE	Asymptote, intercept, rate				-372	5	29
AE	AE	Asymptote				-371	3	26
AE	AE	Asymptote, rate				-370	2	27
AE	AE	Rate				-370	2	26
LM		Linear	Quadratic	Linear		-370	2	27
LM		Linear		Linear		-370	2	25
AE	AE					-369	1	25
LM		Linear		Quadratic		-369	1	25
NE	NE	Intercept				-369	1	24
LM	Quadratic	Linear				-368	1	25
LM			Quadratic			-368	1	25
LM		Linear	Linear	Linear		-368	1	25
LM		Linear	Quadratic	Linear	Linear	-368	1	27
LM		Linear		Linear	Linear	-368	1	25
LM		Linear	Quadratic	Quadratic		-368	1	27
LM				Linear		-368	1	23
	Linear	Linear				-368	1	24
NE						-368	1	25
LM		Intercept, rate		Quadratic		-367	1	24
Multidiversity (Pielou evenness, J*)								
LM	Quadratic	Linear				-336	21	28
LM	Quadratic					-335	18	27
PL	PL	Intercept				-335	17	28
LM	Cubic	Linear				-335	13	29
LM	Cubic					-334	11	28
PL	PL					-334	11	26
LM	Quadratic	LUI × LUI <sub>sd</sub>				-332	4	29
Multidiversity (plants)								
AE	AE	Rate				-346	33	70
AE	AE	Intercept				-345	21	69
AE	AE	Rate, intercept				-345	19	70
AE	AE	Asymptote, rate				-344	11	70
AE	AE	Asymptote, intercept, rate				-343	7	70
AE	AE	Asymptote, intercept				-343	7	69
Multidiversity (animals)								
AE	AE	Asymptote, intercept				-297	36	20
AE	AE	Intercept				-295	13	18
AE	AE	Rate				-295	13	18
AE	AE	Asymptote, intercept, rate				-295	12	20
AE	AE	Asymptote				-294	8	18
AE	AE	Asymptote, rate				-294	7	19
AE	AE	Intercept, rate				-293	5	18
PL	PL	Intercept				-292	2	16

Table S2. Cont.

Type	LUI	LUI <sub>sd</sub>	Fertilization	Mowing	Grazing	AICc	AICc weight, %	Pseudo-R <sup>2</sup> , %
Individual groups								
Arbuscular mycorrhizal fungi								
Null						184	33	3
Araneae								
PL	PL					-56	13	10
Asterids								
AE	AE	Intercept				-228	48	63
Bats								
NE	NE					-75	12	51
Birds								
LM	Quadratic	Linear				-167	24	33
Coleoptera								
AE	AE					-66	35	12
Diptera								
NE	NE	Intercept				-16	27	19
Heteroptera								
AE	AE	Asymptote				-46	19	15
Homoptera								
AE	AE					-112	23	11
Hymenoptera								
AE	AE	Asymptote, intercept				-52	29	27
Lepidoptera								
AE	AE	Rate				-181	39	56
Lichens								
NE	NE	Asymptote, intercept, rate				-275	39	61
Monocotyledons								
AE	AE					-145	27	36
Mosses								
AE	AE	Intercept, rate				-196	52	61
Neuroptera								
NE	NE	Asymptote, intercept, rate				27	48	11
Orthoptera								
AE	AE	Intercept				-8	40	16
Ranunculales								
LM	Quadratic					-32	18	17
Rosids								
AE	AE	Intercept				-166	33	52
27 plots, 49 taxonomic groups								
Multidiversity aboveground								
AE	AE	Asymptote				-75	45	81
AE	AE					-74	23	77
AE	AE	Intercept				-73	18	80
AE	AE	Rate				-73	14	80
Multidiversity belowground (top five models are shown)								
LM				Linear		-67	13	22
Null						-66	9	10
LM					Grazing	-66	9	19
LM				Quadratic		-66	9	29
LM			Linear			-65	5	15

Different measures of multidiversity are shown for the analysis with 150 plots and 18 taxonomic groups measured and for the subset of 27 plots where 49 taxonomic groups were measured. Models in the 95% confidence set of models are shown (i.e., the set of models whose combined AIC weights sum to 95%). AICc values are corrected for small sample sizes. LUI × LUI<sub>sd</sub> indicates an interaction between the terms. All model formulae are provided in Table S1. AE, asymptotic exponential; LM, linear model; NE, negative exponential; PL, power law.

\*Calculated as  $J = \frac{-\sum_{i=1}^S p_i \ln p_i}{\ln S}$ , where  $S$  is the number of species,  $p_i$  is the proportional abundance of the  $i$ th species, and  $R$  is the total number of species.







Table S4. Cont.

Taxa	Aggregation level 1	Aggregation level 2	Aggregation level 3	Compartment	Sampling method	No. of plots measured	Year of measurement and sampling intensity	Authors
Monocotyledons	Monocotyledons	Embryophyta	Plantae	Above	% cover 4 × 4-m subplot	148	2009: once per plot	Müller, Boch, Socher, Prati, Fischer M, Klaus, Kleinebecker, Hölzel
Subset of 27 plots Araneae	Arachnida	Arthropoda	Animalia	Above	Sweep netting and pitfall trapping	27	2008: twice per plot	Lange, Pašalić, Türke, Gossner, Weisser
Coleoptera	Hexapoda	Arthropoda	Animalia	Above	Sweep netting and pitfall trapping	27	Combined data: Krauss, Lange, Pašalić, Türke, Gossner, Weisser, Rothenwöhler, Scherber, Tschardtke	Werner, Weiner, Blüthgen
Diptera	Hexapoda	Arthropoda	Animalia	Above	Flower visitor observation	22	2008: one to three times per plot	Lange, Pašalić, Türke, Gossner, Weisser
Heteroptera	Hexapoda	Arthropoda	Animalia	Above	Sweep netting and pitfall trapping	27	2008: twice per plot	Lange, Pašalić, Türke, Gossner, Weisser
Homoptera	Hexapoda	Arthropoda	Animalia	Above	Sweep netting and pitfall trapping	27	2008: twice per plot	Lange, Pašalić, Türke, Gossner, Weisser
Hymenoptera	Hexapoda	Arthropoda	Animalia	Above	Flower visitor observation and trap nesting	27	Trap nests: 2008, four surveys	Combined data: Steckel, Bellach, Westphal, Scherber, Steffan-Dewenter, Tschardtke, Werner, Weiner, Blüthgen
Lepidoptera	Hexapoda	Arthropoda	Animalia	Above	Butterfly netting along a transect	26	2008: three times per plot	Börschig, Krauss, Klein
Neuroptera	Hexapoda	Arthropoda	Animalia	Above	Sweep netting and pitfall trapping	27	2008: twice per plot	Lange, Pašalić, Türke, Gossner, Weisser
Orthoptera	Hexapoda	Arthropoda	Animalia	Above	Sweep netting and pitfall trapping	27	2008: twice per plot	Lange, Pašalić, Türke, Gossner, Weisser
Aves	Aves	Chordata	Animalia	Above	Observation: cumulative species list over 3 y	27	2008–2010: five times per plot per year	Böhm, Renner, Kalko
Chiroptera	Mammalia	Chordata	Animalia	Above	Monitoring of echolocation: cumulative species list over 3 y	27	2008–2010	Jung, Kalko
Lichens	Lichen	Lichen	Lichen	Above	% cover 4 × 4-m subplot	27	2009: once per plot	Boch, Prati, Fischer
Bryophyta	Bryophyta	Embryophyta	Plantae	Above	% cover 4 × 4-m subplot	27	2009: once per plot	Müller, Boch, Prati, Fischer
Asterids	Dicotyledons	Embryophyta	Plantae	Above	% cover 4 × 4-m subplot	25	2009: once per plot	Müller, Boch, Socher, Prati, Fischer
Ranunculales	Dicotyledons	Embryophyta	Plantae	Above	% cover 4 × 4-m subplot	25	2009: once per plot	Müller, Boch, Socher, Prati, Fischer
Rosids	Dicotyledons	Embryophyta	Plantae	Above	% cover 4 × 4-m subplot	25	2009: once per plot	Müller, Boch, Socher, Prati, Fischer
Monocotyledons	Monocotyledons	Embryophyta	Plantae	Above	% cover 4 × 4-m subplot	25	2009: once per plot	Müller, Boch, Socher, Prati, Fischer
Lumbricidae	Clitellata	Annelida	Animalia	Below	Hand sorting from soil cores 20 × 10 cm	26	2008: two soil cores per plot	Birkhofer, Diekötter, Wolters



