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

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.

Ample 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

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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

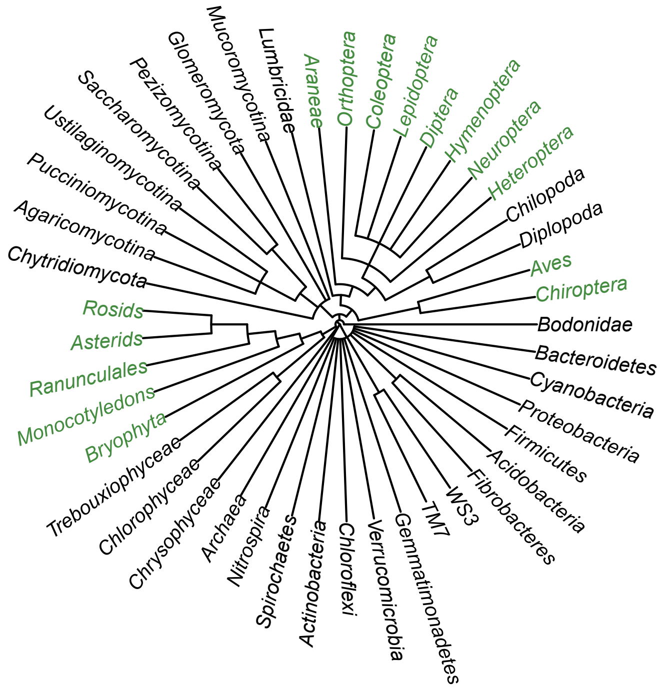

Fig. 1. Organism groups used to calculate multidiversity. Of 49 taxonomic groups surveyed on 27 grasslands, 45 are shown on the tree. Eighteen groups were measured on all 150 grasslands, and 16 of them are shown in green on the tree. The groups WS3 and TM7 are candidate bacterial phyla. In addition to 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/), 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. 2*A*). 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

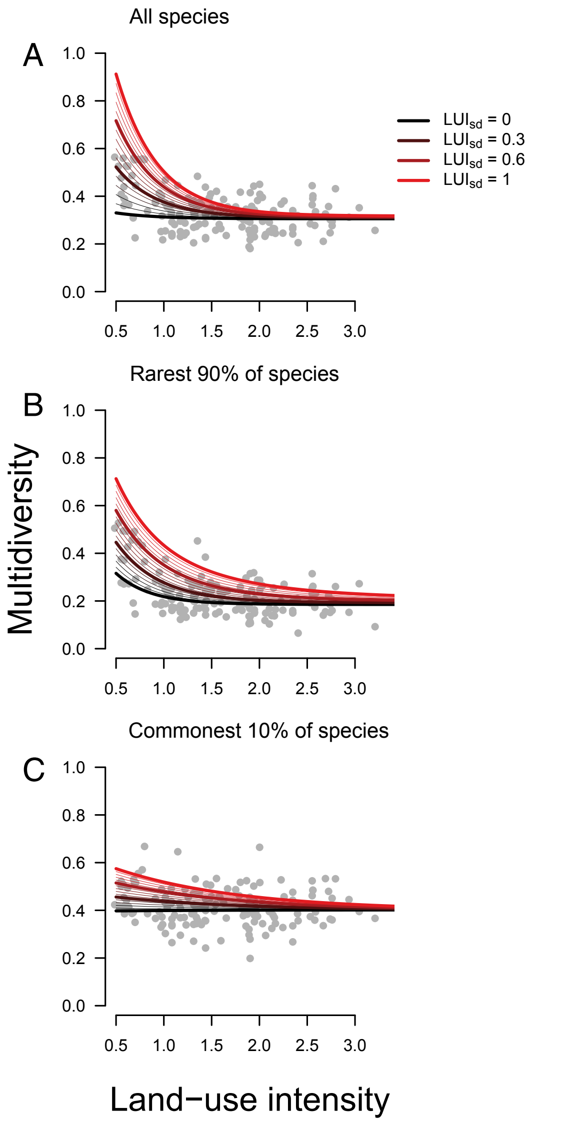

Fig. 2. Effect of LUI on multidiversity of 18 taxonomic groups of all species (*A*), relatively rare species (i.e., the 90% of species with the lowest total abundance) (*B*), and relatively common species (i.e., the 10% of species with the highest total abundance across plots) (*C*). Lines show model 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. S1*C* 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. 2*A*), supporting our land-use variation hypothesis. In the analysis of 18 groups of organisms in 150 grasslands, all of the

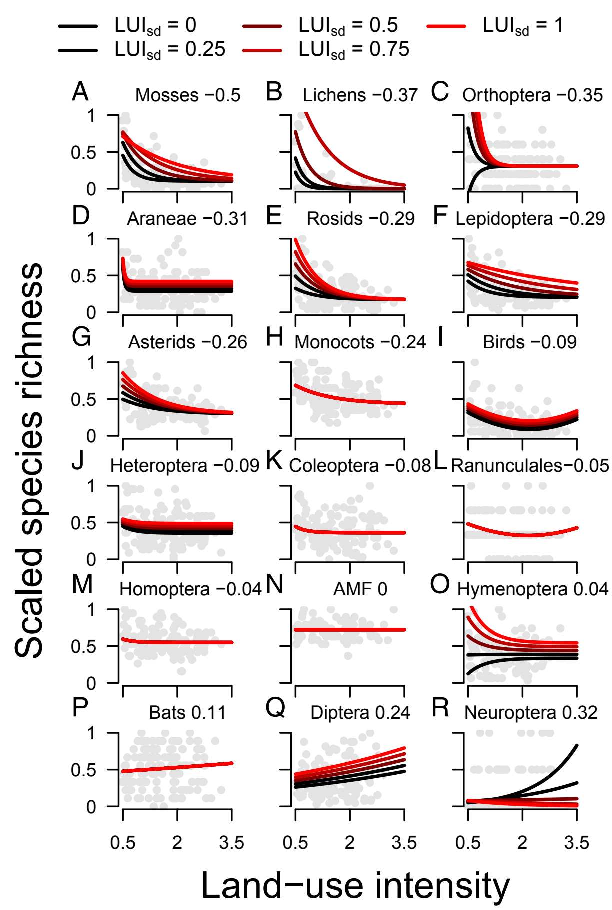

Fig. 3. Response to LUI of scaled species richness for the 18 taxonomic groups measured on 150 plots. For each group, the predictions from the best-fit model are shown (*Methods* and Table S2). Where temporal variation in LUI (LUI_{sd}) appeared in the model, model fits are shown for different values 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. 2*A*). 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. 3*R*). 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. 2*B* 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. 2*B*). 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

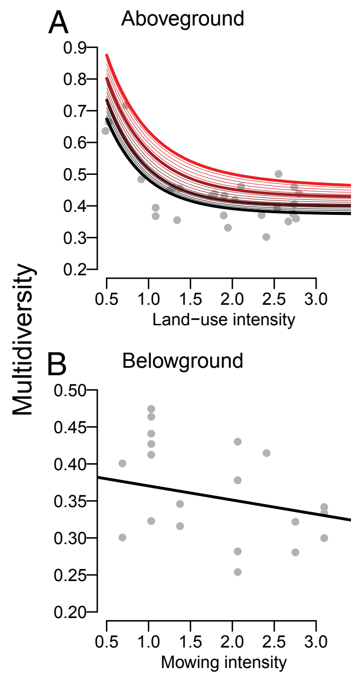

Fig. 4. Response of the multidiversity of all 49 groups across 27 grasslands differed between the aboveground (*A*, 17 taxonomic groups) and belowground (*B*, 32 taxonomic groups) compartments. (*A*) Model predictions were calculated using multimodel averaging across all models in the 95% confidence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

common species multidiversity (Fig. 2*C* 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. S1*C* 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. 4*A*). Belowground multidiversity, however, was much less affected by land-use intensification or by interannual variation in LUI (Fig. 4*B*): 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 β-diversity but without reducing α-diversity (27). Thus, belowground α-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

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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). 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 $N \cdot ha^{-1} \cdot y^{-1}$, 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 $N \cdot ha^{-1} \cdot y^{-1}$, 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 $N \cdot ha^{-1} \cdot y^{-1}$ or by cutting three times and fertilizing with 130 kg of $N \cdot ha^{-1} \cdot y^{-1}$. 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. S6*A*). 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 aboveground groups and the 33 belowground 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_{sd}. For the linear regressions (linear, quadratic, or cubic), we either fitted a main effect only for LUI_{sd} or an interaction between LUI_{sd} 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_{sd}. 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_{sd} and LUI or nonlinear models with more than one parameter modeled as a function of LUI_{sd} (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 4*A* 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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