LETTER

doi:10.1038/nature20575

Land–use intensification causes multitrophic homogenization of grassland communities

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Land-use intensification is a major driver of biodiversity loss[1,2]. Alongside reductions in local species diversity, biotic homogenization at larger spatial scales is of great concern for conservation. Biotic homogenization means a decrease in β-diversity (the compositional dissimilarity between sites). Most studies have investigated losses in local (α)-diversity[1,3] and neglected biodiversity loss at larger spatial scales. Studies addressing β-diversity have focused on single or a few organism groups (for example, ref. 4), and it is thus unknown whether land-use intensification homogenizes communities at different trophic levels, above- and belowground. Here we show that even moderate increases in local land-use intensity (LUI) cause biotic homogenization across microbial, plant and animal groups, both above- and belowground, and that this is largely independent of changes in α-diversity. We analysed a unique grassland biodiversity dataset, with abundances of more than 4,000 species belonging to 12 trophic groups. LUI, and, in particular, high mowing intensity, had consistent effects on β-diversity across groups, causing a homogenization of soil microbial, fungal pathogen, plant and arthropod communities. These effects were nonlinear and the strongest declines in β-diversity occurred in the transition from extensively managed to intermediate intensity grassland. LUI tended to reduce local α-diversity in aboveground groups, whereas the α-diversity increased in belowground groups. Correlations between the β-diversity of different groups, particularly between plants and their consumers, became weaker at high LUI. This suggests a loss of specialist species and is further evidence for biotic homogenization. The consistently negative effects of LUI on landscape-scale biodiversity underscore the high value of extensively managed grasslands for conserving multitrophic biodiversity and ecosystem service provision. Indeed, biotic homogenization rather than local diversity loss could prove to be the most substantial consequence of land-use intensification.

Land-use intensification threatens biodiversity[2,4] by reducing the α-diversity of many taxa[1,3]. Similarly, β-diversity[5] may decline strongly. This biotic homogenization[6–9] might occur through either a loss of rare or specialized species (reducing differences between communities), a gain of widespread, generalist species in intensively managed systems (increasing similarity), or most likely a combination of both. Most studies have investigated loss of species richness, but global change may have larger effects on community composition than on local diversity[10,11]. To separate biotic homogenization from loss of species richness requires measures of β-diversity that distinguish pure species turnover from changes in α-diversity[5]. To predict and manage the loss of β-diversity, we also need to understand whether biotic homogenization occurs at a constant rate as land use intensifies. Land-use intensification can affect α-diversity nonlinearly[1,12], but, although environmental gradients can have nonlinear effects on β-diversity[13,14], no such effects of land use have been investigated. Here we use data from several landscapes and regions to analyse land-use effects on species turnover (β-turnover)[15,16] and on total β-diversity (also including differences in species richness) across a wide range of trophic groups.

Different types of organisms probably respond differently to land use. In grasslands, α-diversity belowground may be less affected than aboveground[1]. However, land-use intensification may homogenize species composition belowground and reduce β-diversity without reducing

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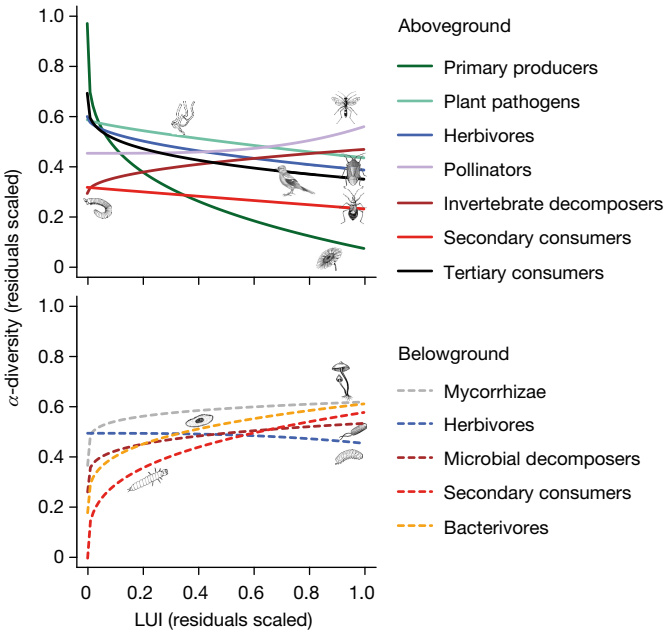

Figure 1 | The effect of LUI on α-diversity above- and belowground. The partial effect of local LUI was generated with a power law model fitted to the species richness of the seven aboveground (solid lines) and the five belowground trophic groups (dashed lines) ($n = 105$ plots; for details, see Methods). Species richness and LUI were corrected for differences due to region, pH, soil nutrients, sdLUI (standard deviation of LUI across five years) and isolation, by taking residuals, and were then scaled between 0 and 1.

α-diversity, as shown for tropical soil bacteria[17]. Biotic homogenization might therefore be widespread, but at present we lack a broader view of how land-use intensification alters α- and β-diversity of distinct functional or trophic groups. The loss of specialist species, which generally accompanies biotic homogenization, could also reduce correlations between the β-diversities of different groups[18], indicating changes in trophic structure.

We compiled a unique set of biodiversity data, including more than 4,000 species of plants, arthropods, foliar fungal pathogens, mycorrhizal fungi, bacteria, protists, bats and birds, measured on 105 grasslands varying in local LUI (a compound index of grazing, mowing and fertilization intensity)[19]. We divided the species into 12 groups on the basis of trophic level and whether they lived above- or belowground. We modelled the effect of LUI on α- and β-diversity of each group, accounting for potential environmental and spatial effects. We assessed biotic homogenization in three ways, by testing: (1) for an overall negative effect of land use on β-diversity; (2) where along the land-use gradient the greatest change in β-diversity occurred; and (3) whether correlations among β-diversity of different trophic groups were reduced, which would indicate a loss of specialist species.

High LUI reduced α-diversity for most aboveground groups, but had neutral or positive effects on belowground organisms (Fig. 1). These results were consistent regardless of the weight given to common species, that is, whether α-diversity was measured as species richness, Shannon or Simpson diversity (Extended Data Fig. 1). Land-use effects were not driven by co-varying environmental factors because we adjusted for soil pH, nutrients and geography (see Methods). Differences between above- and belowground communities may occur because they respond at different spatial scales[20] and belowground groups are better protected from disturbance[21]. Alternatively, a shift towards bacterial-dominated communities in more intensively managed grasslands[22] may have cascaded up to increase the diversity of higher trophic levels. Nevertheless, these opposing above- and belowground responses were unanticipated and have not previously been shown in a multitrophic dataset.

We then analysed the effects of land-use on β-diversity and found widespread evidence for biotic homogenization both above and below ground. We modelled β-diversity between all possible plot pairs using linear models, again correcting for other environmental and geographic drivers, and including two descriptors of LUI: the mean and the difference in LUI (ΔLUI) between them. The mean LUI represents overall intensity; any negative effects on β-diversity indicate biotic homogenization. The linear ΔLUI term represents land-use heterogeneity and positive effects indicate that mixing grasslands of low and high LUI increases β-diversity. Increasing land-use intensity (mean LUI) had strong negative effects on the β-turnover of many above- (4 out of 7) and belowground (2 out of 5) groups (Fig. 2a, Extended Data Figs 2 and 3), indicating biotic homogenization both above- and belowground, in contrast to the opposing responses of α-diversity. Belowground groups, especially mycorrhizae and bacterivores, were therefore homogenized at high LUI even though their α-diversity increased. These stronger effects of LUI on belowground β-turnover extend findings from Amazonian bacterial communities, responding to marked changes in land use[17], to a much larger number of groups. For many groups, increasing LUI had an even larger effect on total β-diversity, which includes changes in species richness and turnover (Extended Data Fig. 4). This was particularly evident for plants, which suffered substantial species loss. In general, ΔLUI effects were smaller than mean LUI effects, showing that increasing land-use heterogeneity has limited potential to offset negative effects of intensification. Land-use heterogeneity might be even less beneficial in cases where high LUI grasslands are dominated by exotic species of low conservation value. Our multitrophic results suggest that, despite their differences in dispersal rates and body sizes[23,24], large-scale spatial dynamics are similar in below- and aboveground groups.

We next investigated whether the rate of biotic homogenization was constant over the LUI gradient, and found that it peaked in the transition from low to intermediate LUI. Using generalized dissimilarity modelling (GDM) we fitted nonlinear effects of ΔLUI on β-diversity along the LUI gradient[13]. LUI was a major driver of β-turnover and total β-diversity, even compared to the large spatial and nutrient differences between the grasslands (deviance explained in Fig. 2b and relative effects in Extended Data Figs 5–7; Supplementary Information Section 5). There was a general trend for saturating responses in the β-diversity of aboveground (plants, herbivores and pollinators) and belowground groups (bacterivores and mycorrhizae) (Fig. 2b), which was parallel to the α-diversity response aboveground[1]. Differences in LUI between grasslands therefore drive turnover only at low overall LUI and increasing land-use heterogeneity beyond a certain point will not increase β-diversity, supporting the conclusion that minimizing LUI across the landscape most effectively enhances β-diversity. Some other groups, plant pathogens and secondary consumers, showed accelerating responses in β-diversity, which indicates strong homogenization in the most intensively managed grasslands. When we analysed the effects of the LUI components (grazing, mowing and fertilization) separately in the GDMs, mowing intensity was the main driver of biotic homogenization for most groups (Extended Data Fig. 8). Frequent mowing creates a homogenous sward, reduces flowering and seed set, causes high insect mortality and may lead to soil compaction, all of which may cause extinctions of rare species and favour a small set of disturbance-tolerant species both above- and belowground. In a global analysis, elevated nutrient input proved to be a main driver of soil microbial community composition[25]. In our study, fertilization had comparatively minor effects: increased homogeneity in soil nutrient levels at high LUI seemed to reduce β-diversity (see Supplementary Table 5 for LUI results without soil nutrients) less than homogenization of disturbance regimes.

Effects of LUI on total β-diversity were generally larger when measurements were weighted by species abundances (Extended Data Fig. 4). Intensively managed grasslands may be dominated by the same common species, even if they differ in their rare species. Indeed, a common

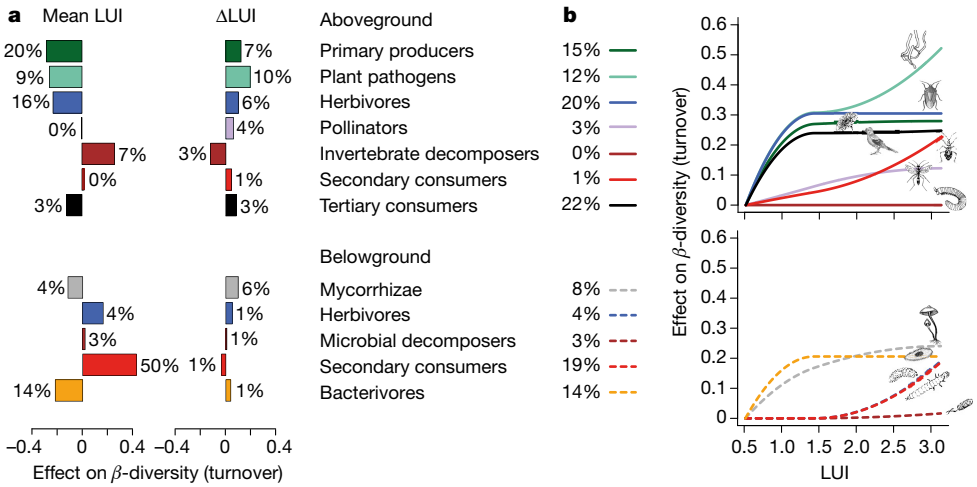

Figure 2 | Effects of LUI on β-diversity above- and belowground. **a**, Bars show partial effects of mean LUI and differences in LUI (ΔLUI) between plot pairs (105 plots), on species turnover (β_{sim}), from linear models. Numbers adjoining bars are the proportion of explained variance uniquely explained by mean LUI or ΔLUI. **b**, Results from the generalized dissimilarity models (GDMs) showing the effect of ΔLUI on β_{sim} along the LUI gradient, with percentages of deviance uniquely explained by LUI. Higher maximum curves indicate larger effects. All effects are corrected for environmental covariates and explanatory variables are scaled to allow comparisons across trophic levels.

practice in grassland management is to seed intensively used plots with a few fast-growing species of high nutritional value, which reinforces the homogenization of plant communities under high LUI. Increased abundance of common, generalist species might also drive biotic homogenization in other trophic groups. Under high LUI, dominance increased in most aboveground groups, although not in belowground groups (Extended Data Fig. 1). Increased dominance by a small set of common species, across a wide array of trophic groups, might threaten the delivery of critical ecosystem services in intensively managed landscapes[26].

Despite the overall consistency of land-use effects, some exceptions are worth noting. Bacteria responded weakly and had very low β-diversity, perhaps because their taxonomic resolution was coarser than for other groups (Methods). Responses of pollinators were also weak, possibly because their β-diversity responds more to land use at the landscape scale[27], as shown by the strong response to grassland isolation (Extended Data Fig. 5, Supplementary Information Section 5). In most other groups, isolation was a much less important driver of β-diversity. Only in three invertebrate groups did β-diversity increase with LUI; however, these groups were species-poor and had a lower sample coverage (see Supplementary Information Section 2 and Extended Data Fig. 9).The relative importance of LUI as a driver of β-diversity therefore varied between trophic groups (Extended Data Fig. 7), but it affected key ecosystem service providers such as plants and herbivores, as well as rare birds, which have a high conservation value.

High LUI also homogenized trophic structure and disrupted correlations between β-diversity of adjacent trophic levels. We calculated correlations between β-diversities for sets of plots with low, versus high,

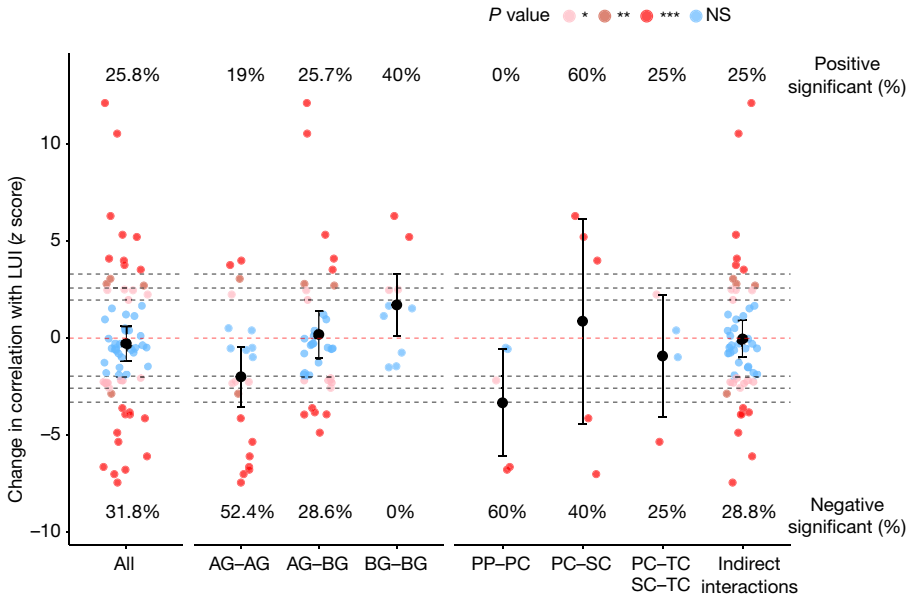

Figure 3 | Effect of LUI on correlations between the β-diversities (β_{sim}) of different trophic groups. *z* scores (positive *z* scores indicate that correlations are higher at high LUI, and negative *z* scores indicate that correlations are lower at high LUI) and *P* values (dashed lines separate *P* levels; $*P<0.05$, $**P<0.01$, $***P<0.001$, NS, not significant) show the change in correlation strength (R^2 values from matrix regressions, corrected for effects of differences in LUI) between low (52 plots) and high LUI (53), comparing observed values to random values (see Methods). All correlations were grouped into categories: AG, aboveground; BG, belowground; PP, primary producers; PC, primary consumers; SC, secondary consumers; TC, tertiary consumers. Each coloured dot represents one correlation, black dots represent the mean and black bars the 95% confidence intervals. For statistical details see Supplementary Information Section 5.

LUI and expected a drop in correlations at high LUI, which would indicate biotic homogenization. Correlation strength dropped by more than 50% on average (for $R^2 > 0.1$ at low LUI) at high LUI and correlations between aboveground groups and between producers and primary consumers (plants and herbivores or pathogens) declined substantially (Fig. 3 and Extended Data Fig. 10), potentially reflecting a loss of host specialists. Some correlations increased in strength but these mainly involved the species-poor invertebrate groups whose β-diversity increased with LUI (see Supplementary Table 6). A previous study[28] showed that land-use intensification disrupted correlations in α-diversity and we extend this finding to show spatial decoupling for a wider range of trophic groups.

By analysing a uniquely comprehensive biodiversity dataset, we showed that LUI substantially reduces β-diversity across many different trophic groups. This threatens biodiversity by homogenizing communities within and across agricultural landscapes. The consequences of biotic homogenization for landscape-scale ecosystem service provisioning remain uncertain, but are likely to be severe[26]. Moreover, our results show that measures to reduce management intensity should be most effective at intermediate LUI[12]; they also underscore the high value of extensively managed grassland for conserving multitrophic diversity by showing that reduced intensity across the landscape effectively promotes large-scale diversity. This could be achieved by increasing the area of extensively managed grasslands in general, and especially by reducing the intensity of mowing. Conservation strategies and agricultural policies will increase in effectiveness if they aim to maintain the heterogeneity of biotic communities at the landscape scale, for instance by coupling subsidies to landscape-scale measures of diversity.

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

Received 2 June; accepted 25 October 2016.
Published online 30 November 2016.

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Supplementary Information is available in the online version of the paper.

Acknowledgements We are grateful to J. Chase and M. Fitzpatrick for their comments and suggestions on a previous version of the manuscript; B. Büche, R. Achtziger, T. Wagner, F. Köhler, T. Blick and M.-A. Fritze for arthropod species identification and U. Kern for creating the small icons of the 12 trophic groups used in the figures. We thank the managers of the three Exploratories, K. Hartwich, S. Gockel, K. Wiesner and M. Gorke for their work in maintaining the plot and project infrastructure; C. Fischer and S. Pfeiffer for giving support through the central office, M. Owonibi for managing the central data base; and E. Linsenmair, D. Hessenmöller, J. Nieschulze, I. Schöning and the late E. Kalko for their role in setting up the Biodiversity Exploratories project. We are also grateful to E. Kalko for her invaluable inspiration and for launching the studies on bats and birds. The work has been funded by the DFG Priority Program 1374 'Infrastructure-Biodiversity-Exploratories'. Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen and Brandenburg (according to §72 BbgNatSchG).

Author Contributions M.M.G. and E.A. conceived the idea for the manuscript, and defined the final analysis, M.M.G., E.A., C.P., T.M.L. and T.K. analysed the data, M.M.G. and E.A. wrote the first manuscript draft and finalized the manuscript. A.M.K., C.B., C.N.W., C.W., D.J.P., D.P., E.P., F.B., H.A., I.S., J.K., J.M., J.S., J.O., K.J., K.B., M.Tü., M.Ts., M.F., M.L., M.M.G., M.W., N.B., P.C.V., S.Bl., S.Bo., S.A.S., S.C.R, S.K., S.W., T.D., T.W., V.B., V.W., and W.W.W. contributed data. T.M.L., F.G., S.Bo., D.P., L.R.J., K.B., S.C.R., A.C.K., O.P., P.S., T.T., W.W.W. and J.S. contributed substantially to revisions. All authors commented on the manuscript.

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Reviewer Information *Nature* thanks P. Barton, S. Prober and the other anonymous reviewer(s) for their contribution to the peer review of this work.

METHODS

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

Study system. The study was conducted as part of the Biodiversity Exploratories project (www.biodiversity-exploratories.de) in three German regions: (1) The UNESCO Biosphere area Schwäbische Alb in the low mountain range in south-western Germany (420 km^2, 460–860 m above sea level (a.s.l.)); (2) the Hainich National Park and its surrounding areas in the hilly lands of central Germany (1560 km^2, 285–550 m a.s.l.); and (3) the UNESCO Biosphere Reserve Schorfheide-Chorin in the glacially formed lowlands of northeastern Germany (1300 km^2 in size, 3–140 m a.s.l.). The three regions differ in climate, geology and topography, but each is characterized by a gradient of LUIs typical for large parts of temperate Europe[29]. Land-use gradients in this study range from semi-natural to intensively managed grasslands, because natural grasslands, that do not require management to prevent succession to forest, are almost absent from western and central Europe. In each region, 50 grassland plots were chosen from a total of 500 candidate plots, on which initial vegetation and land-use surveys were conducted, by stratified random sampling. This ensured that the plots covered the whole range of LUIs and management types, while minimizing confounding factors such as spatial position or soil type[29]. Thereby we avoided, for instance, sampling low-intensity grasslands only in the low productive parts of the landscape. All grasslands have a long history of broadly similar LUI (that is, low intensity grasslands have not been recently converted from high intensity grasslands and vice versa and all had been grasslands for at least 10 years before the start of project), although we are aware that temporal variation in land use is substantial[1]. In this study, we analysed a subset of 105 plots (Schwäbische Alb: 32, Hainich-Dün: 37, Schorfheide-Chorin: 36) for which data on all taxa (see below) were available.

Study design and land-use measures. All plots were continuously managed by farmers. Information on management practices, including the level of fertilization (kg N ha^{-1} yr^{-1}), grazing (number of livestock units ha^{-1} yr^{-1}) and mowing (number of cuts per year), was assessed annually by standardized interviews with the land owners. LUI at the local scale was then quantified as a compound index on the basis of summing the standardized intensities of these three components[19]. We decided to employ a compound index of LUI because the individual components are correlated with each other (fertilization and mowing are positively correlated, and grazing and mowing negatively correlated[19]) and the distribution of overall intensity is more even (each individual component has many 0 values). Each component was divided by the global mean value for each year to standardize the components[19]. We then calculated the mean LUI for each plot over five years (2006–2010) because this reflects the average LUI around the years when most of the data was assessed (2008, 2009 and 2011). At the low end of land-use intensity, with a LUI of 0.5, grasslands are typically unfertilized, not mown, and grazed by 40–50 sheep per hectare for about 10 days (or more rarely by 1–3 cattle per hectare for 20 days). At an intermediate LUI of 1.5, grasslands are usually unfertilized (or fertilized with less than 30 kg N ha^{-1} y^{-1}), and are either mown twice a year or grazed by four cattle per hectare for about 50 days. At the high end of land-use intensity with a LUI of 3, grasslands are typically fertilized at a rate of 60–120 kg N ha^{-1} y^{-1}, are mown 2–3 times a year or grazed by 5–10 cattle for 100–150 days, or are managed by a combination of grazing and mowing. In addition to using the LUI index (that is, where all three types of land use are given equal weight), we tested the individual standardized land-use components in our models to separate nutrient and disturbance effects.

Covariates. We corrected for a series of other variables that might affect diversity. In addition to the mean land use across time, we quantified two other measures of land use: (1) the temporal variation of LUI, as its standard deviation (sdLUI) across five years (2006–2010) because this has been shown to increase α-diversity[1]; and (2) to measure effects of land use at the landscape scale, which may also be important drivers of diversity[6], we calculated one minus the proportion of grasslands (including managed grasslands and semi-natural vegetation and thus all potential habitat for grassland species) within 500 m of each plot as a proxy for isolation. Plot neighbourhood cover was mapped in 2009 using high resolution (40 cm) aerial photographs from 2008, including the following land-cover types besides grasslands: arable land, forest, roads, trees (woodlots smaller than 1 ha), urban areas and water bodies.

We also corrected for soil nutrients and pH. We sampled the upper 10 cm of the mineral soil to assess soil variables. This was conducted in May 2011 with 14 locations per plot along two 18-m transects with distances of 3 m between sampling points, for details see ref. 30 and Supplementary Information Section 1. Soil nutrients were quantified by the first axis of a principal component analysis (PCA, ade4 package[31]) of nitrogen stock, total soil nitrogen, organic carbon stock, soil inorganic carbon, soil organic carbon, soil C:N ratio (Supplementary Table 1). Note that our measure of soil nutrients partly includes, in addition to natural variation among soils, the effect of fertilization, which in turn is also part of the LUI. Therefore, our estimates on the effects of LUI are on the conservative side and fitting models without the soil nutrient variable slightly increases the strength of the LUI effects in some cases, see Supplementary Information Sections 4, 5. Finally, in the analysis of β-diversity, we also corrected for spatial distance between all sites. To consider spatial effects on β-diversity, we calculated geographic distance between each pair of plots on the basis of geographic coordinates using Euclidean distances in the R package vegan[32].

Biodiversity assessment. We assessed biodiversity across a broad range of organisms from bacteria to vertebrates using molecular (bacteria, arbuscular mycorrhizal fungi and protists) as well as morphological (plants, arthropods and pathogenic fungi) or acoustic characteristics (bird and bat calls).

Vascular plants, bryophytes and lichens. We sampled vascular plants between mid-May and mid-June 2009, bryophytes (2007–2008) and lichens (2007–2008) in an area of 4 m × 4 m on each plot, and estimated the percentage cover of each occurring species. For details see refs 33, 34 for vascular plants, ref. 35 for lichens and ref. 36 for bryophytes).

Arthropods. All arthropods of the herb layer were sampled in 2008 by different methods. For sampling Araneae, Coleoptera, Hemiptera: Heteroptera and Auchenorrhyncha, Hymenoptera: Symphyta, Neuroptera, Orthoptera, Dermaptera and Dictyoptera we used biannual (June and August) sweep netting by conducting 60 double sweeps along three 50-m long plot border transects[37,38]. Additionally, Diptera and Hymenoptera were hand-collected during their visits on flowers, identified and individuals counted[39]. This survey involved a transect of 200 m × 3 m along the edge of the plot, for which three transect walks were performed on a single day (total, 6 h). In some cases, plots were measured several times; these were averaged in less than one month apart or, if repeated over one month later, the earlier measure was used[39]. We conducted surveys of butterflies and day-active moths (hereafter termed as Lepidoptera) from beginning of May to mid August[40,41]. We sampled Lepidoptera on fixed transects in the three regions repeating the sampling three times in a randomized sequence within each region. Each transect had a length of 300 m and we recorded all Lepidoptera within 30 min per site within a 5 m corridor.

Soil arthropods (Myriapoda, soil living larvae) were sampled in spring 2011 (within ten days in April) by collecting two soil cores (diameter, 20 cm, depth, 10 cm) from each plot. Soil fauna was extracted from the first core using a modified heat extraction system[42] over a period of eight days and the second soil core was hand-sorted for soil macrofauna.

All arthropod species were assigned to one of four trophic groups (herbivores, pollinators, predators and decomposers) on the basis of their known main food resource as adults.

Pathogenic fungi. From July to August 2011, we sampled pathogenic fungi including rust, powdery mildew, downy mildew and smut fungi in four transects of 25 m × 1 m per plot. We inspected all occurring vascular plant species for infested individuals, sampled them and later identified the pathogenic fungi to the species level.

Birds. Birds were sampled by audio-visual point counts[43] covering the area of the respective grassland plot (50 m × 50 m). We noted all individuals of each bird species during the five-minute interval. In each year, from 2008 to 2012, we visited each plot five times between 15 March and 15 June (1st surveying period, 15–30 March; 2nd, 15–30 April; 3rd, 1–15 May; 4th, 16–31 May; 5th, 1–15 June). A maximum of 15 plots was surveyed per day from sunrise to 11:00; occasionally the evening chorus was surveyed after 17:00 (<20 times out of 750 events per year). The sequence in which plots were visited was randomized. The maximum number of birds displaying per site per year (that is, the maximum number of record individuals per species over the five rounds within a surveying year) was used as a measure of the relative abundance of birds. We considered a species as present in the particular plot if it was recorded at least once during a survey within each year. Aerial species (swifts and swallows) were excluded from analysis, as they had only been surveyed irregularly and without standardization. For this study, we combined species richness and relative abundance data across the five sampling periods.

Bats. We surveyed bats from June to September during the years 2008, 2009 and 2010. Plot sampling was conducted along a 24 min point-stop transect of 200 m at the borders of each grassland plot. Sampling started 30 min after local sunset and was limited to the first half of the night (01:00) to account for the first peak in bat activity[44]. We randomly sampled 4–6 plots per night. Each plot was surveyed twice during each year with a minimum time interval between repeated sampling of five weeks. Acoustic recordings of bats were taken in real time (sample rate: 384 kHz, 16 bit) with a Pettersson-D1000x bat detector (Pettersson Electronic AG, Uppsala, Sweden) and triggered manually by an observer listening through headphones to the output of the heterodyne system while continuously scanning the frequency

range between 20 and 80 kHz. Bat species identification was conducted using Avisoft SAS Laboratory Pro, Version 5.0.24 (R. Specht, Avisoft Bioacoustics, Berlin, Germany, Hamming window, 1024 FFT, 96% overlap) following various references on echolocation call parameters, for example refs 45–47. For details on species identification see ref. 48. In addition, we evaluated the number of bat passes that were defined as a minimum of two consecutive echolocation calls[49]. Successive passes within one recording were discriminated if the time interval between calls was larger than three times the regular pulse interval of the particular species[48,50].

Belowground microorganisms. At each grassland plot fourteen soil cores (diameter, 8.3 cm) were taken from a 20 m × 20 m subarea and soil from the upper 10 cm of the A horizon was homogenized after removal of root material. The bulk sample was split into subsamples for the analyses of bacteria, protists and arbuscular mycorrhizal fungi.

For bacteria, 10 g of the homogenized soil was put immediately on liquid nitrogen and stored until RNA extraction[51]. Briefly, total RNA was isolated from soils and reverse transcribed into cDNA. Amplicons of the V3 region of the 16S rRNA gene were sequenced on an Illumina Hiseq platform using universal bacterial primers as described in ref. 52.

For the analysis of protists, 1 g of the bulk soil sample was used for DNA extraction and the analyses of the V4 region of the 18S rRNA gene amplified using eukaryotic specific primers. Sequences were filtered for (1) 100% forward primer match; (2) length ≥ 200–710 bp and (3) ambiguities (*N*). Traces were scanned for chimaeras, trimmed to 530 bp, dereplicated to group 100% identical amplicons, and singletons removed. Remaining sequences were treated as operational taxonomic units (OTUs) and aligned to the PR^2 database using BLASTn (default parameters). One hit per sequence was retained. Only OTUs with 100% coverage and protist taxa (excluding Metazoa, Fungi and Streptophyta) were retained for analysis.

For the study of arbuscular mycorrhizal fungi, total microbial DNA was isolated from the bulk soil sample using a MoBioPowerSoil DNA Isolation Kit. The NS31-a.m.1 fragment of the fungal 18S rDNA was amplified using arbuscular mycorrhizal fungal specific primers[53] and sequenced using a Genome Sequencer FLX+ 454 System. The reads were quality filtered using Mothur[54] and classified using the MaarjaM AMF reference database[55]. A total of 825 arbuscular mycorrhizal fungal OTUs were detected.

Detailed description of the data processing of bacteria, protists and arbuscular mycorrhizal fungi is presented in Supplementary Information Section 2.

Statistical analyses. All analyses were conducted in R 3.0.2 (ref. 56).

Sample completeness. To test for sample completeness, we used a previously published approach of sample coverage[57,58]. Coverage is defined as the proportion of the total number of individuals in an assemblage that belong to species represented in the sample. We used two approaches to estimate sample coverage. First, we estimated sample coverage for low (52) and high (53) LUI plots on the basis of species incidences. Second, we estimated sample coverage for each plot on the basis of species abundances. Sample coverage did not differ significantly along the LUI gradient and was estimated to be higher than 90% in all trophic groups, except aboveground invertebrate decomposers and secondary consumers (Extended Data Fig. 10 and Supplementary Table 2-2). Therefore, the results for secondary consumers and invertebrate decomposers should be treated with caution but there is no evidence that any undersampling is biased along the LUI gradient. A further line of evidence for the robustness of our findings to issues of sample completeness is provided by the results for different *q*-levels. When increasing *q*-levels, rare species are less strongly weighted in the calculation of β-diversity. As we found similar or even stronger responses of β-diversity to LUI at higher *q*-levels (see below) this further indicates that undersampling of rare species is unlikely to affect the conclusions of our study. Analyses were conducted using the iNEXT function in the iNEXT library[59].

Diversity measures. We calculated several measures of α- and β-diversity for each of the 12 trophic groups (Fig. 1). We used previously published *q*-metrics[60,61] to incorporate different weightings for species abundance in α- and β-diversity. These are based on Hill numbers[62], and allow the calculation of diversity measures in which increasing weight is given to species abundances. At $q = 0$, rare and abundant species are weighted equally, which corresponds to species richness for α-diversity and the Sørensen index of dissimilarity for β-diversity. At $q = 1$, species are weighted in proportion to their frequency in the sampled community, which corresponds to the exponential of Shannon entropy (or effective number of species) for α-diversity and Horn's index of dissimilarity for β-diversity. Finally, at $q = 2$, abundant species receive more weight relative to their frequency and this corresponds to the inverse Simpson index for β-diversity and Morisita–Horn index for β-diversity[63,64]. Analyses were conducted using multipart function in the vegan library[65].

Spatial turnover in composition between locations involves two main processes: a replacement of species (pure turnover) and changes in species richness[15,16]. To test for effects on β-diversity that are independent of species richness differences, we used the Simpson dissimilarity β_{sim}, which is the turnover component of Sørensen dissimilarity, see also ref. 16. Details on β- (diversity across the three study regions) as well as β-diversity partitioning is given in Supplementary Information Section 3.

α-diversity analysis. To analyse the response of α-diversity to land use, we used power law models that allow different shapes of responses to be fitted. We modelled the response of α-diversity for each of the 12 trophic groups, calculated with $q = 0$, 1 or 2. The explanatory variable was LUI, the model formula was $y = a + (b \times \mathrm{LUI}^c)$, where *a* (intercept), *b* (slope) and *c* (degree of curvation) are parameters estimated by the model. In order to correct for confounding environmental effects we analysed residuals in the power law models. We calculated residuals from linear models with diversity or land use (LUI) as the response variable and region, soil nutrients, pH, variation in LUI (sdLUI) and isolation (1 – proportion of grasslands in the plot surrounding) as explanatory variables. We calculated residuals because incorporating many explanatory variables in the power law models would have led to extremely complex models. After taking residuals, we then scaled all explanatory and response variables between 0 and 1, to allow comparison of effects and responses. Models were fitted using the gnls function in the nlme library[66].

β-diversity analysis. *Linear models.* To analyse the response of β-diversity to land-use intensification, we first fitted linear models. These were fitted to values of turnover (β_{sim}), total β-diversity (Sørensen, $q = 0$) and abundance weighted β-diversity ($q = 1$ or 2) for each of the 12 trophic groups. Explanatory variables in these models were: the mean LUI, sdLUI, isolation, soil nutrients and pH between each pair of plots. The effects of mean LUI provide a test of biotic homogenization: a negative effect indicates that land-use intensification reduces turnover. In this case, reducing LUI across the landscape would promote β-diversity. However, as plot pairs with the same mean LUI can either be very similar in LUI or come from different ends of the gradient, we also fitted differences in LUI (ΔLUI) between all plot pairs. This term tests for the effect of land-use heterogeneity, that is, whether β-diversity is higher between plots of different intensities. A positive effect would suggest that maximizing land-use heterogeneity across the landscape would increase β-diversity. The terms mean LUI and ΔLUI are not correlated with each other although ΔLUI is constrained to zero at maximum and minimum mean LUI. We additionally fitted differences in all other variables (sdLUI, isolation, soil nutrients and pH) together with the spatial distance between all plot pairs in the models. To compare the effects of the different predictors, we scaled all predictors to between 0 and 1. We then calculated the variance explained uniquely by mean LUI or ΔLUI by comparing the variance explained by the full model with that explained by models containing all terms except mean LUI or ΔLUI. The unique variance is expressed as a proportion of the total explained variance. We calculated the significance of all terms in the linear models using a permutation procedure, implemented with the lmp function in the lmPerm library[67], using 100,000 iterations.

We also ran a second series of linear models in which we replaced mean LUI with the mean grazing, mowing and fertilization intensity between plot pairs (all scaled to the maximum across plots) and replaced ΔLUI with differences in grazing, mowing and fertilization between plots. Finally, we ran linear models without soil nutrient levels, to test whether effects of LUI were mediated by its effects on soil nutrients.

Generalized dissimilarity modelling. To analyse the nonlinear effects of differences in LUI, we used GDM[13]. This is a matrix regression technique for modelling turnover in species composition between sites as a function of the spatial and/or environmental distance between them. The advantages of GDM are that it can incorporate variation in the rate of compositional turnover along an environmental or spatial gradient (non-stationarity) and that it allows the relationships between dissimilarity and distance to be nonlinear. The only constraint is that compositional turnover is assumed to always increase with distance between sites (monotonicity). For more details on GDM see ref. 13. All GDMs were fitted using the gdm function in the gdm library[68]. We plot the partial effect of each predictor, that is, while holding all other predictors constant, against the level of a given predictors to visualize the results of the GDM (Extended Data Fig. 5 and Supplementary Table 5-1). The height of the line shows how large the effect of LUI is relative to all other predictors in the model. Variation in compositional turnover along an environmental or spatial gradient can be seen from the shape of the line, which shows how the effect of a given predictor on compositional turnover varies with the mean level of that predictor. For instance, for LUI, the shape of the line shows how the effect of heterogeneity in LUI varies with mean LUI. We also calculated a bootstrapped *P* value for each term in the full GDM, using the gdm.varImp function in the gdm library (Supplementary Table 5-2). Additionally we estimated uncertainty for the GDM plots by using 100 bootstraps for each model, each time removing 30% of the plot pairs and then fitting a GDM and extracting the predictions. We then calculated the s.d. of the predictions and added this (±) to the fitted line (Extended Data Fig. 6). This is based on the function plotUncertainty in the gdm library.

We fitted GDMs to four measures of β-diversity for each group: turnover (β_{sim}), total β-diversity (Sorensen, $q=0$) and abundance weighted β-diversity ($q=1$ and 2). In each case differences in LUI were fitted as an explanatory variable. To correct for spatial, environmental and other land-use distances, we additionally fitted the spatial distance between plots, differences in pH, differences in nutrients, differences in sdLUI and differences in isolation in the model. We also ran GDMs with individual land-use components, that is, with grazing, mowing and fertilization, instead of LUI. These models had the same covariates as the LUI models. For the linear models, we ran the LUI GDMs without soil nutrient levels to test whether some effects of LUI were driven by soil nutrients. In both cases, the effects of LUI were very similar regardless of whether soil nutrients were included or not; this indicates that LUI effects on β-diversity are mostly not caused by LUI homogenizing the soil abiotic environment.

Furthermore, it is possible to estimate the amount of deviance in compositional turnover explained by the GDM. Note that the GDM optimizes the fit between predictors and response variables, so different models can have different response spline shapes. We also determined the proportion of deviance uniquely attributable to land use. We did this by comparing the deviance explained by a GDM containing all of the variables and a GDM with all variables except the difference in LUI between plots. We calculated the unique deviance explained by LUI as the difference in deviance explained between these models. We then converted this to a percentage by dividing by the deviance explained by the full GDM.

Correlation in β-diversity between trophic groups. To test for possible effects of land use on the correlation of β-diversities between trophic groups, we used partial multivariate correlograms and multiple regressions (pmgram and MRM functions in the ecodist library[69]). We correlated β-diversity of different groups (β_{sim}, $q=0$, $q=1$, and $q=2$; see above), and corrected for LUI distances between plots. We corrected for LUI to account for potential shared responses to common environmental drivers. We did this by using the residuals for the matrix correlations between trophic levels. The multiple regressions use permutation tests (999 permutations) of significance for the regression coefficients and for the R^2 values.

To test whether the strength of correlations differed between low and high LUIs, we divided the 105 plots into 52 low (less than median LUI) and 53 high (greater than median LUI) intensity plots and calculated the R^2-value differences between high and low LUI ($R^2_{high}-R^2_{low}$). We then compared these values to a distribution of simulated R^2-values differences ($n=1{,}899$) where we randomized the LUI differences between plots. On the basis of this random distribution, we calculated Z scores (standardized effect sizes (SES)) and P values. Significant values thus indicate stronger trophic interactions at lower (or higher) LUI than expected by chance.

Data availability. The data will become publicly available according to the Rules of Procedure of the German Science Foundation (DFG)-funded Biodiversity Exploratories, that is, five years after completion of the datasets.

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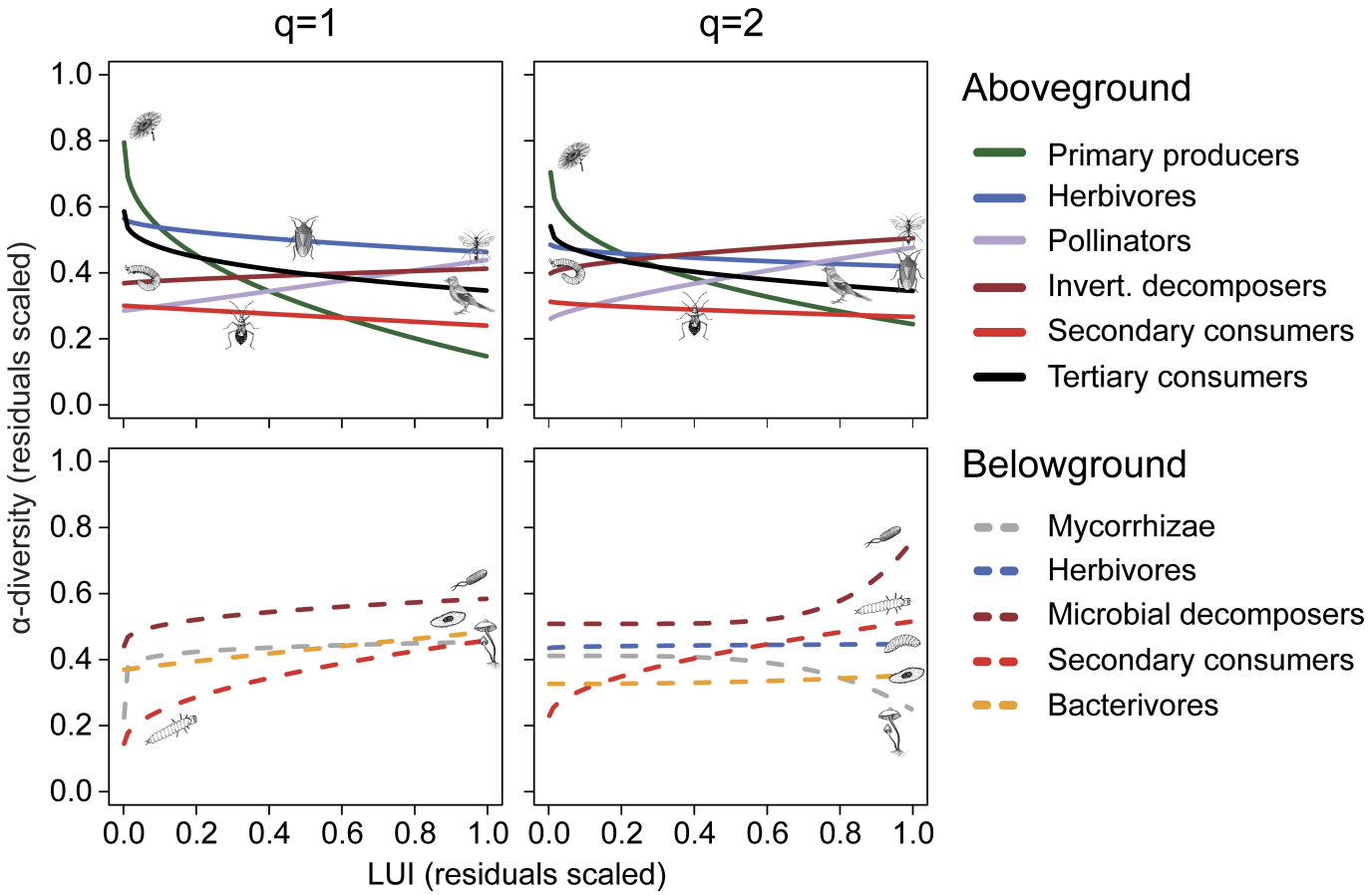
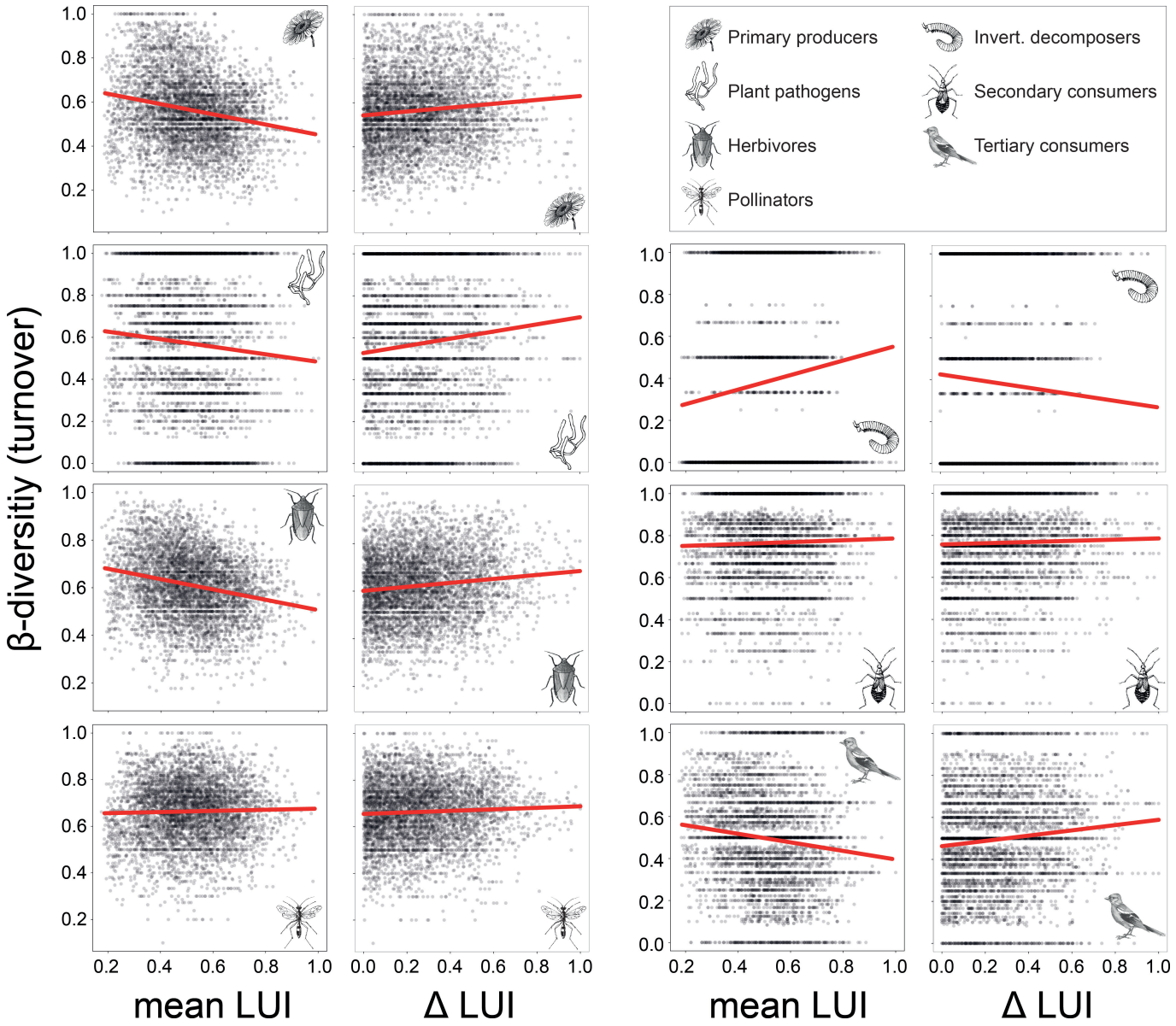
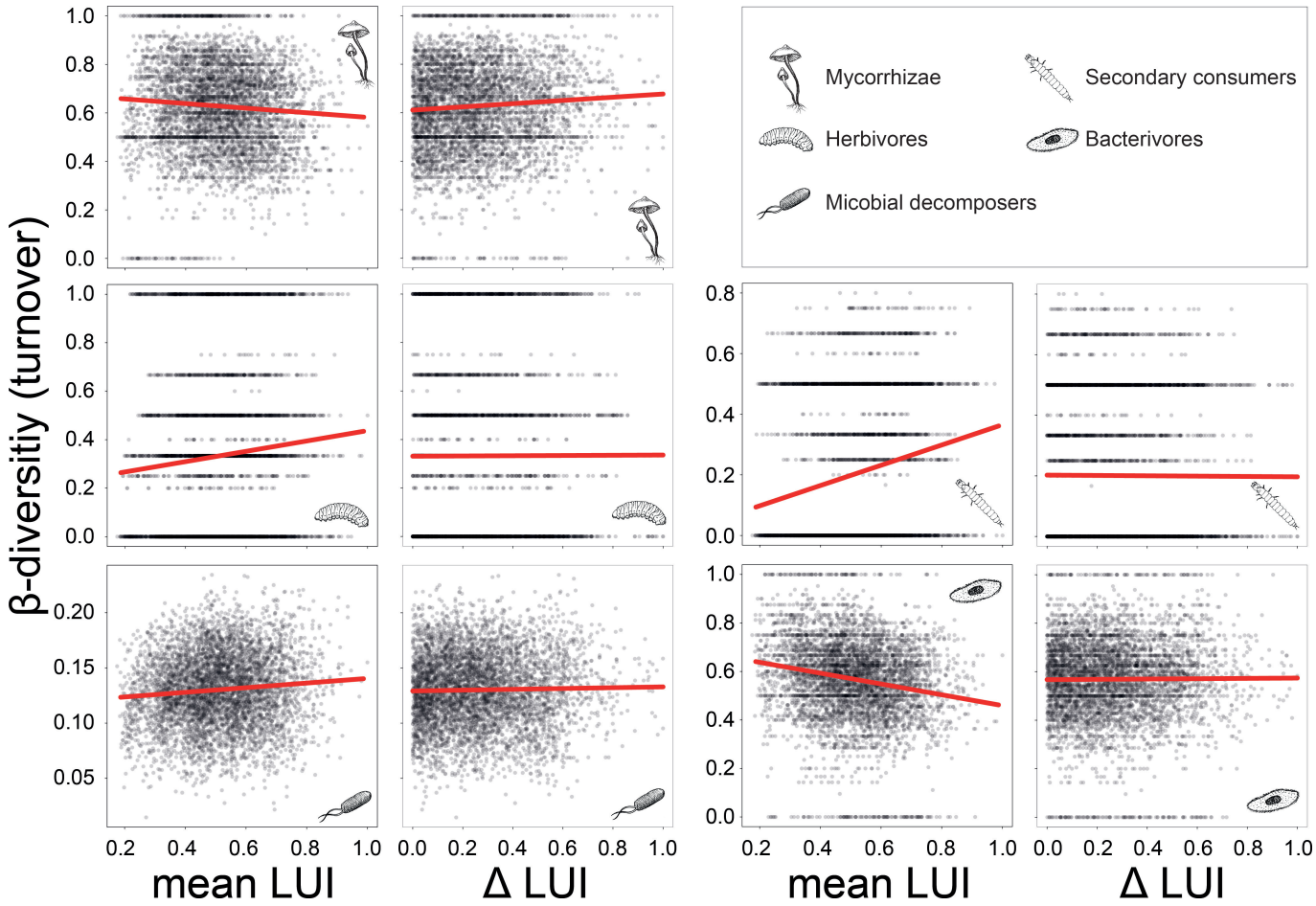


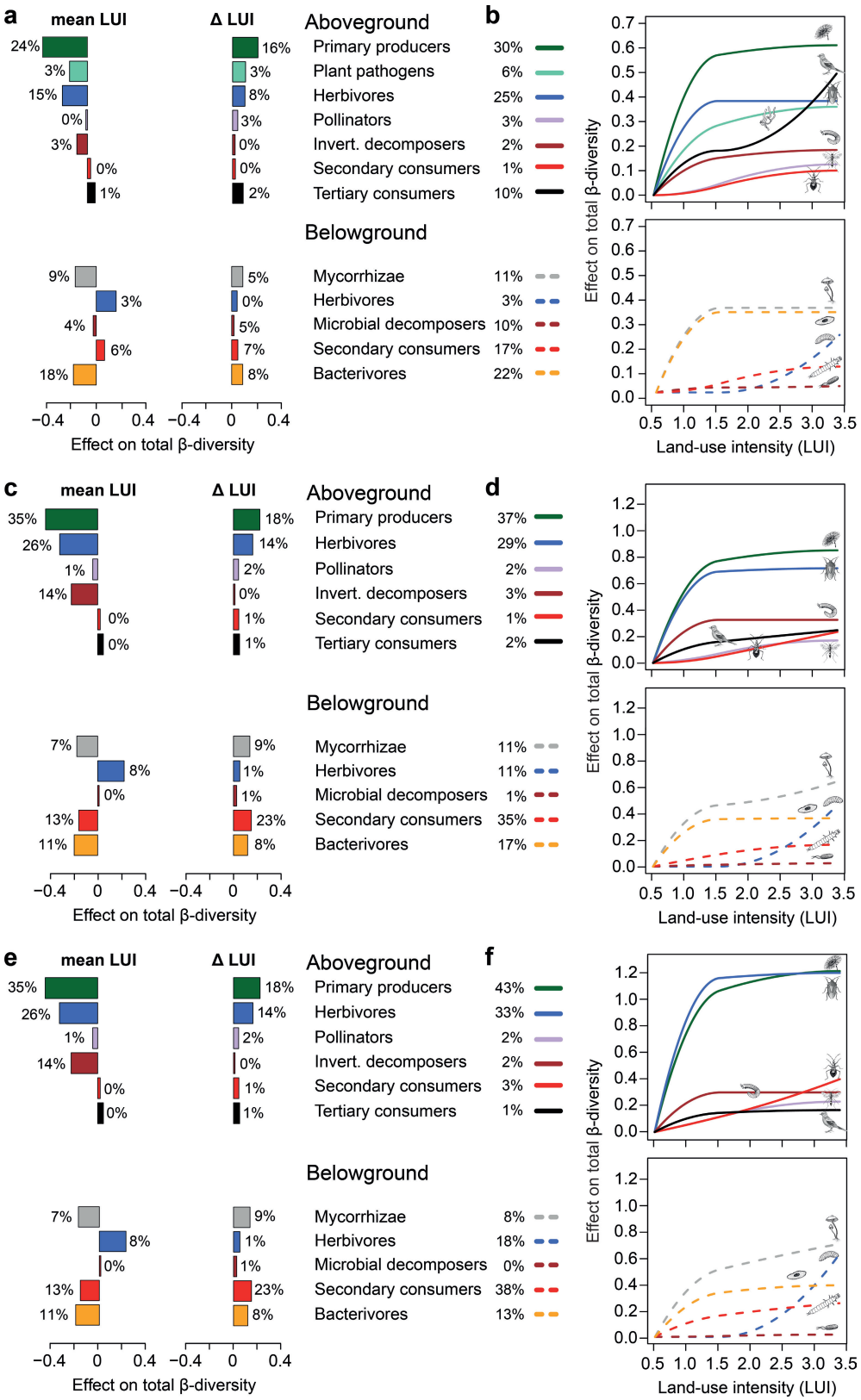
Extended Data Figure 1 | The effect of LUI on higher q-level α-diversity above- and belowground. The partial effect of local LUI comes from a power law model fitted to the exponential Shannon diversity ($q = 1$) and reciprocal Simpson index ($q = 2$) of the seven aboveground (solid lines) and the five belowground trophic groups (dashed lines) ($n = 105$ plots; for more details see Methods). In the model, all parameters of the power law function depended on temporal variation in LUI (sdLUI) and isolation. LUI effects are plotted at the mean values of these two variables. α-diversity and land-use variables were corrected for differences due to region, pH and soil nutrients, by taking residuals, and were then scaled between 0 and 1. The models for protists ($q = 1$ and $q = 2$) and mycorrhizae ($q = 2$) failed to converge and are therefore not shown. Note that plant pathogens are missing because, for this group, no data on abundance was available.



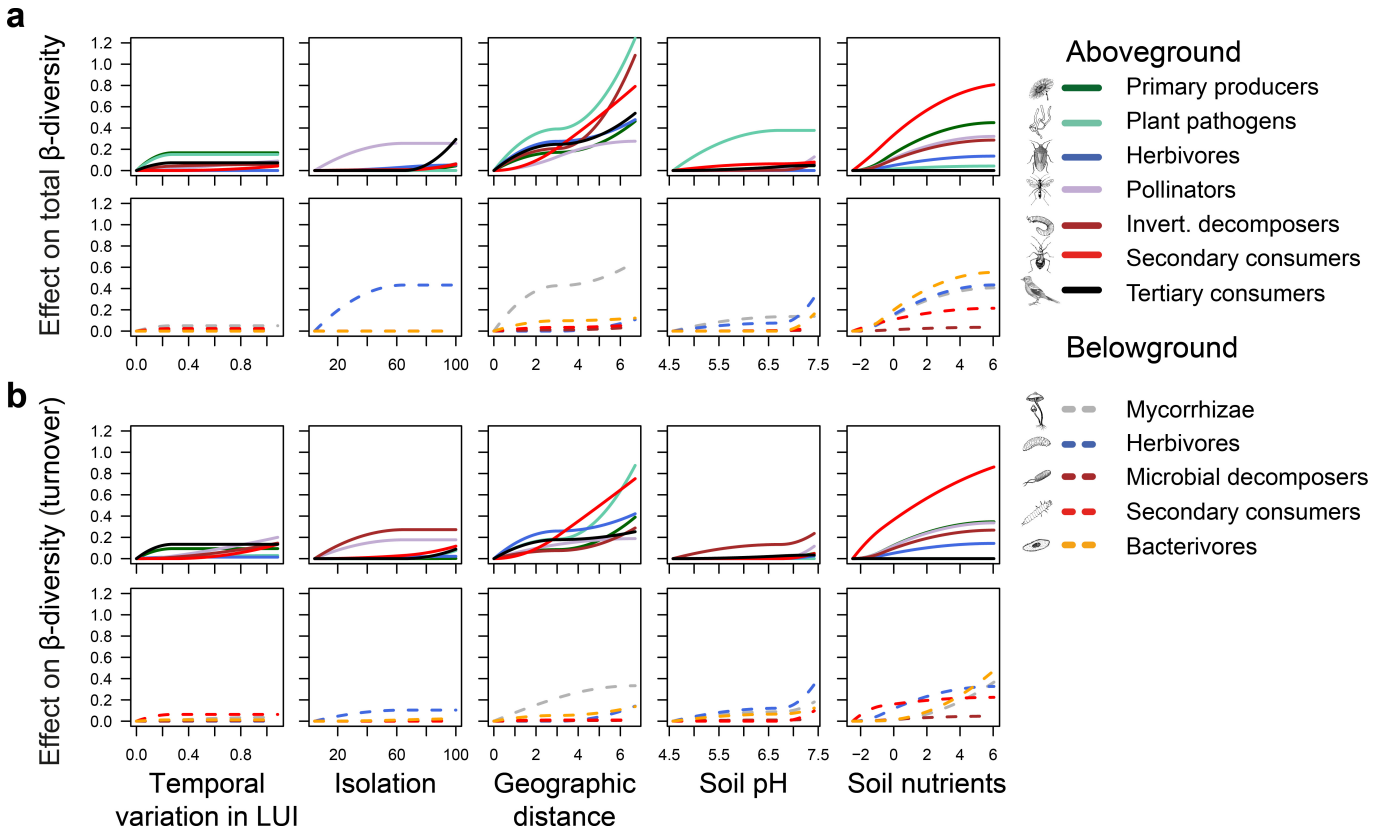
Extended Data Figure 2 | Effects of LUI on turnover of aboveground species. Scatter plots showing the effects of mean LUI and ΔLUI, between plot pairs ($n = 105$ plots), on the species turnover component of β-diversity for seven aboveground groups. Regression lines show predictions from linear models.



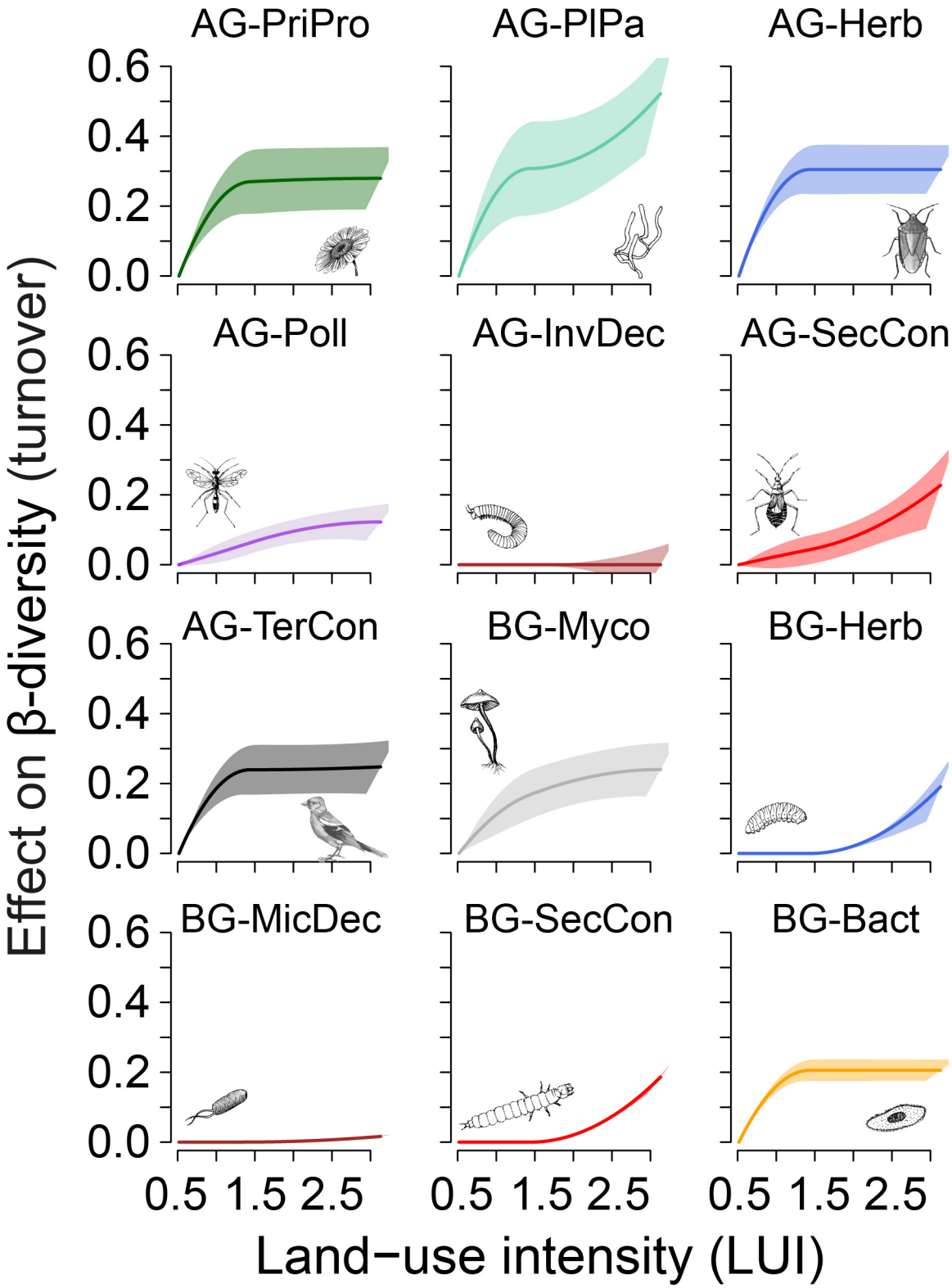
Extended Data Figure 3 | Effects of LUI on turnover of belowground species. Scatter plots showing the effects of mean LUI and ΔLUI, between plot pairs ($n = 105$ plots), on the species turnover component of β-diversity for five belowground groups. Regression lines show predictions from linear models.



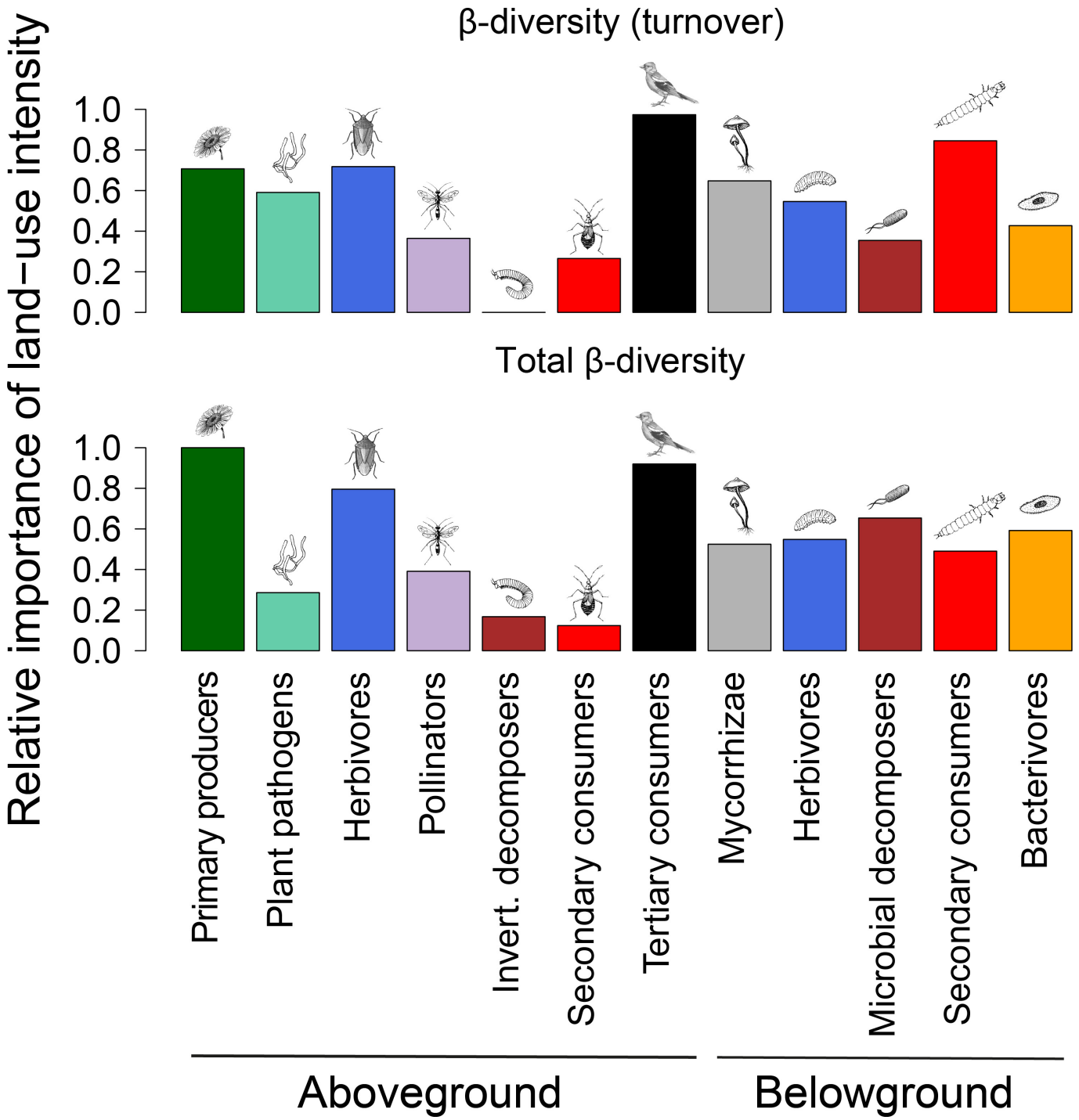
Extended Data Figure 4 | Effects of LUI on total β-diversity above- and belowground. **a**, **c**, **e**, Partial effects of mean LUI and ΔLUI, between plot pairs, on total β-diversity (**a**, Sørensen $q = 0$; **c**, Morisita $q = 1$; **e**, Morisita–Horn $q = 2$) for seven aboveground and five belowground groups from linear models. Negative effects of mean LUI indicate that land-use intensification reduces β-diversity. The bars show coefficients from the models. Numbers adjoining bars are the proportion of explained variance uniquely explained by mean LUI or ΔLUI. **b**, **d**, **f**, Results from the GDMs are shown for total β-diversity (**b**, Sørensen $q = 0$; **d**, Morisita $q = 1$; **f**, Morisita–Horn $q = 2$) for the same trophic groups. The figures show the effect of differences in LUI on β-diversity (calculated between all plot pairs). Effects of differences in LUI can vary nonlinearly along the gradient of LUI. Higher maximum curves indicate larger effects of differences in LUI on β-diversity. The values in the legend are the percentage of deviance that is explained uniquely by LUI. Effects of both linear models and GDMs are corrected for other drivers of β-diversity, and response and explanatory variables are scaled to allow comparisons across trophic groups ($n = 105$ plots; for details see Methods).



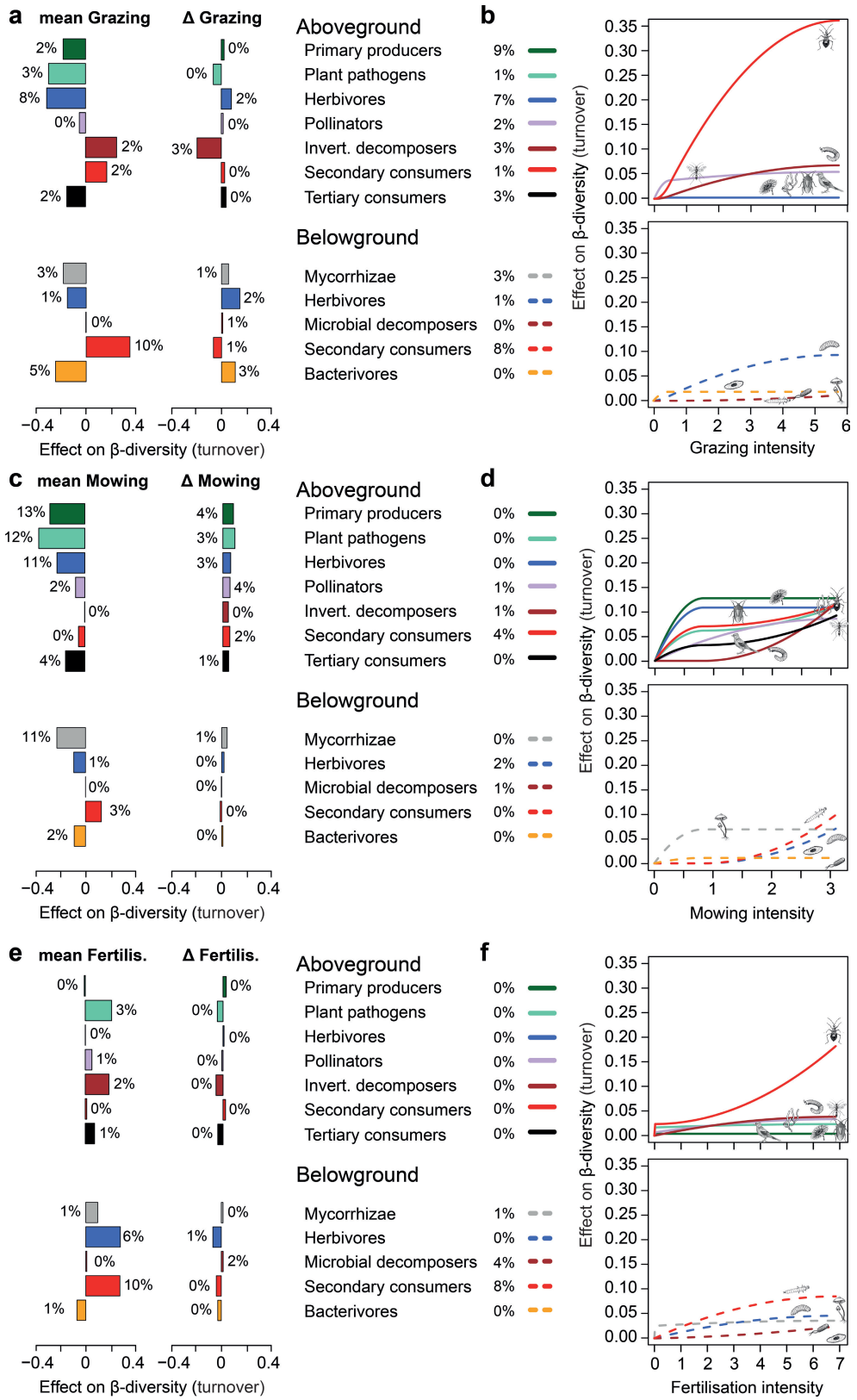
Extended Data Figure 5 | Partial effects of geographic and environmental distances and temporal variation in LUI on β-diversity above- and belowground. a, **b**, Results from GDMs are shown for seven aboveground and five belowground groups, with total β-diversity measured as the Sørensen index β_{sor} (**a**) or as the species turnover component β_{sim} (**b**). The figures show the effect of differences in each of the five variables on β-diversity (calculated between all plot pairs; $n = 105$ plots). Effects of differences in each explanatory variable can vary nonlinearly along the gradient of that variable and each is corrected for all other variables in the model. Higher maximum curves indicate larger effects of differences in a given variable on β-diversity. Soil nutrients refer to the scores of the first PCA axis. Temporal variation in LUI is shown as s.d. Geographic distance has to be multiplied by 100 km.



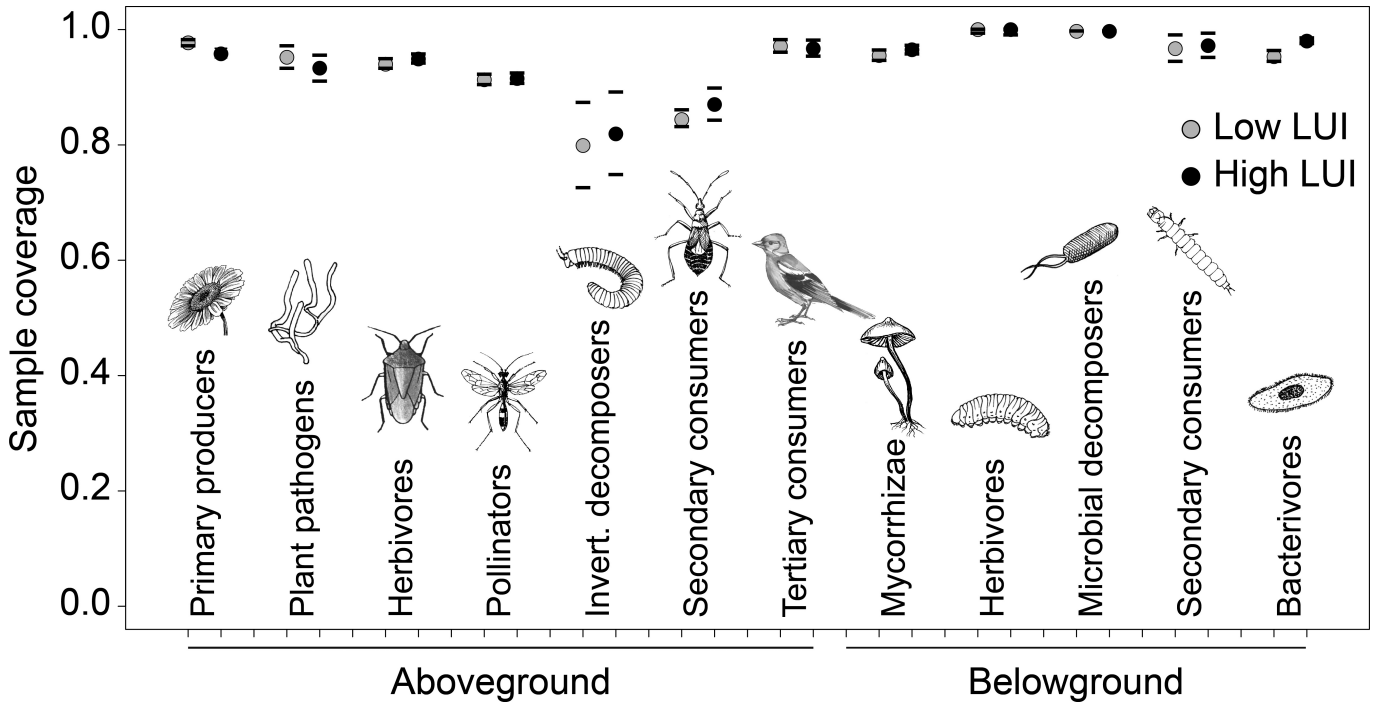
Extended Data Figure 6 | Uncertainty of effects of LUI on β-diversity above (AG) and belowground (BG). The uncertainty is calculated on the basis of 100 bootstraps for each model, each time removing 30% of the plot pairs, then fitting a GDM and extracting the predictions. Predictions are shown as fitted lines and s.d. Uncertainty is shown for all seven above- and five belowground trophic groups based on species turnover β_{sim} ($n = 105$ plots). PriPro, primary producers; PlPa, plant pathogens; Herb, herbivores; Poll, pollinators; InvDec, invertebrate decomposers; SecCon, secondary consumers; TerCon, tertiary consumers; Myco, Mycorrhizae; MicDec, microbial decomposers; Bact, bacterivores.



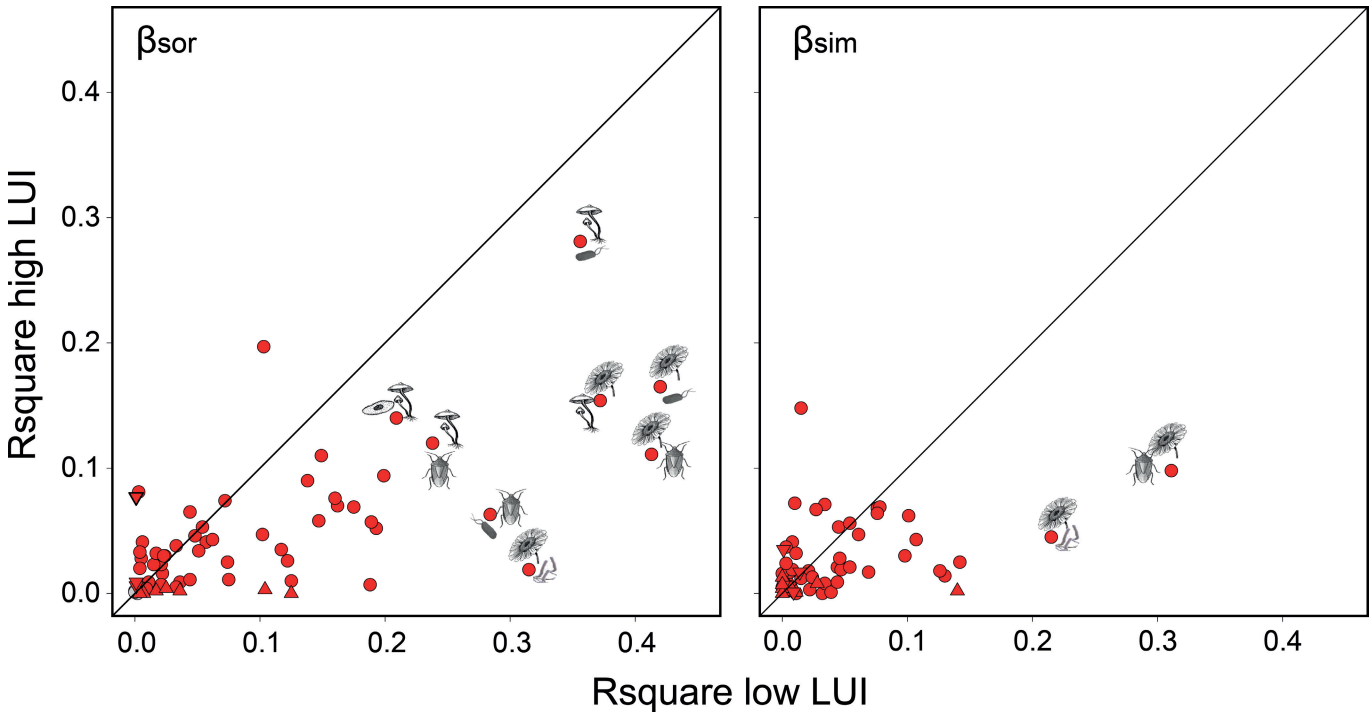
Extended Data Figure 7 | The relative importance of LUI as a driver of β-diversity. The bar plot shows the importance of LUI (in terms of total effect size) relative to the most important variable in the GDM. Results are shown for each trophic group, for the species turnover component (β_{sim}) and total β-diversity (Sørensen index) ($n = 105$ plots).



Extended Data Figure 8 | Effects of single land-use components on β-diversity above- and belowground. a, **c**, **e**, Partial effects of minimum LUI (min LUI) and ΔLUI between plot pairs ($n = 105$ plots), on the species turnover component of β-diversity (β_{sim}) for seven aboveground and five belowground groups based on linear models. Negative effects of minimum LUI indicate that land-use intensification reduces β-diversity. The bars show coefficients from the models. Numbers adjoining bars are the proportion of the total explained variance that is uniquely explained by minimum LUI or ΔLUI among plot pairs, on the basis of hierarchical partitioning. **b**, **d**, **f**, Results from GDMs are shown for the turnover component β_{sim} for the same trophic groups. The figures show the effect of ΔLUI on β-diversity (calculated between all plot pairs). Effects of ΔLUI can vary nonlinearly along the gradient of LUI. Higher maximum curves indicate larger effects of ΔLUI on β-diversity. The values in the legend are the percentage of deviance that is explained uniquely by LUI. Effects of both linear models and GDMs are corrected for other drivers of β-diversity, and response and explanatory variables are scaled to allow comparisons across trophic levels (see Methods).



Extended Data Figure 9 | Sample coverage of above- and belowground trophic groups based on species incidences. Sample coverage was calculated for low (52 plots) and high (53) LUI plots based on refs 57, 58. Coverage is defined as the proportion of the total number of individuals in an assemblage that belong to species represented in the sample, and is therefore a measure of sampling completeness. Means and 95% confidence intervals based on 200 bootstraps are shown.



Extended Data Figure 10 | The effect of LUI on the correlation between the β-diversities of different trophic groups. Each dot represents the correlation (R^2) between two trophic groups. Correlations are R^2 values from matrix regressions between β-diversity values of different groups (corrected for effects of differences in LUI on β-diversity). Significant correlations ($P < 0.05$) are marked in red. Upward and downward triangles indicate significance under low or high LUI only. Interactions with R^2 values higher than 0.2 in one of the LUI-categories are illustrated by icons. β-diversity was calculated as the Sørensen index (β_{sor}, total β-diversity) and as the species turnover component (β_{sim}) ($n = 105$ plots). For statistical details see Supplementary Information Section 5.