Land-use intensification causes homogenization of grassland communities across trophic levels

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Abstract

Land-use intensification is a major driver of biodiversity loss^{1,2}. Alongside reductions in local species diversity, the homogenisation of biodiversity at larger spatial scales, i.e. an increase in compositional similarity or a decrease in β -diversity, is of great concern for conservation. Most studies have investigated losses in local (α) diversity^{1,3} neglecting biodiversity loss at larger spatial scales, i.e. the degree of biotic homogenization. Studies addressing β -diversity have focussed on single or a few organism groups at a time, which means we lack a general understanding of whether land-use intensification reduces β -diversity at different trophic levels, above- and belowground.

Here we show that even moderate increases in local land-use intensity (LUI) cause biotic homogenization across many microbial, plant and animal groups, both above- and belowground, and that this is largely independent of changes in α -diversity.

We analyse a unique grassland biodiversity dataset, with abundances of more than 4000 species belonging to 12 trophic groups. Land-use intensification had consistent effects on β -diversity across the groups, causing a homogenisation of soil microbial, fungal pathogen, plant and arthropod communities. These effects were non-linear and the strongest declines in β -diversity occurred in the transition from extensively managed to intermediate intensity grassland. In contrast, LUI tended to reduce local α -diversity in aboveground groups, but increased it in belowground groups. Correlations between the β -diversity of different groups, particularly those between plants and their consumers, became weaker at high LUI. This suggests a loss of specialist species and is therefore further evidence for biotic homogenisation.

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. It may even suggest that biotic homogenisation rather than local diversity loss could be the most significant consequence of land-use intensification.

Text

Land-use intensification is a major driver of biodiversity loss^{2,4}, causing a reduction in the α -diversity of many taxa^{1,3}. Similarly, β -diversity, or the difference in species composition between communities⁵, may decline strongly following land-use intensification, for example when rare or specialised species are lost and intensively managed systems become dominated by generalist species; a process known as biotic homogenisation⁶⁻⁹. The loss of large-scale diversity, following biotic homogenisation, may also impair landscape scale ecosystem functioning¹⁰. Although most studies have focussed on loss of species richness, global change may in fact have larger effects on the composition of communities than on their local diversity^{11,12}. However to separate biotic homogenisation from loss of species richness it is important to use measures of β -diversity that separate pure species turnover from changes in α -diversity⁵. To predict and manage the loss of β -diversity, we need to understand whether biotic homogenisation occurs at a constant rate as land use is intensified. Land-use intensification can have non-linear effects on α -diversity^{1,13} but, although non-linear effects of environmental gradients on β -diversity have been found^{14,15}, no such effects of land use have been investigated to date. Here we use data from several landscapes and regions to analyse effects of land use on species turnover^{16,17} as well as on total β -diversity (which also includes differences in species richness) across a wide range of trophic groups.

Different types of organisms are likely to respond differently to land-use intensification. In grasslands, belowground α -diversity may be less affected than aboveground α -diversity¹. However, land-use intensification could homogenise species composition belowground and reduce β -diversity without reducing α -diversity, as shown for tropical soil bacteria¹⁸. Biotic homogenisation might therefore be widespread across different organisms but at this point, 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 that generally

111 accompanies biotic homogenisation could also reduce correlations between the β -diversities
112 of different groups¹⁹, leading to changes in trophic structure.

113 We compiled a unique set of biodiversity data including more than 4000 species of
114 plants, arthropods, foliar fungal pathogens, mycorrhizal fungi, bacteria, protists and birds,
115 measured on 105 grasslands that vary in local land-use intensity (LUI: a combination of
116 grazing, mowing and fertilisation intensity)²⁰. We divided the species into 12 functional
117 groups based on trophic level and whether they occur above- or belowground. For each of
118 those groups we calculated α - and β -diversity. We then modelled the effect of LUI on these
119 diversity measures, accounting for potential environmental and spatial effects. We tested for
120 biotic homogenisation in three ways: first by testing for an overall negative effect of land-use
121 on β -diversity, secondly by testing where along the land-use gradient the greatest change in β -
122 diversity occurred and how important land-use was as a driver of β -diversity and finally, by
123 testing for correlations among β -diversity of different functional groups to determine if land-
124 use reduces correlations, which would indicate a loss of specialist species.

125 Land-use intensification strongly reduced α -diversity for most aboveground groups, but had
126 neutral or positive effects on belowground organisms (Fig. 1). These results were consistent if
127 alpha diversity was measured as species richness or as Shannon and Simpson diversity, which
128 give more weight to common species (see methods). Land-use effects were not driven by
129 covarying environmental factors because we analysed the effect of LUI, after adjusting for
130 soil pH, nutrients and geography (see methods for details). Differences in the effect of land-
131 use intensity on the species richness of above- vs. belowground communities may occur
132 because they respond at different spatial scales²¹ and belowground groups are better protected
133 from disturbance²². Alternatively a shift towards bacterial-dominated microbial communities
134 in more intensively managed grasslands²³ may have cascaded up to increase the diversity of
135 higher trophic levels. Nevertheless, these opposing responses above and belowground are
136 surprising and have not been shown before in an extensive multitrophic data set.

We then tested for land-use effects on β -diversity and found widespread evidence for biotic homogenisation both above- and belowground. We modelled β -turnover between all possible plot pairs using linear models, again correcting for other environmental and geographic drivers, and including two descriptors of LUI: the minimum (min-LUI) and the difference in LUI (Δ -LUI) between each pair of plots. Min-LUI represents the overall level of intensification; and negative effects of min-LUI on β -turnover show biotic homogenisation. The linear Δ -LUI term can increase β -turnover if plots at low and high LUI harbour different species. These linear models showed that increasing land-use intensity (min-LUI) had a negative effect on the β -diversity of many above and belowground groups (Fig. 2A), indicating consistent biotic homogenisation, in contrast to the more inconsistent response of α -diversity. For many groups, increasing LUI had an even larger effect on total β -diversity because this includes changes both in species richness and turnover (Extended Data Fig. 2). This was particularly evident in plants, which suffered substantial local species loss. Importantly, belowground groups, especially mycorrhizae and bacterivores, were homogenised at high LUI even though their α -diversity increased. These stronger effects of land-use intensity on β -diversity belowground extend the results for bacterial communities responding to more drastic land-use changes in the Amazon¹⁸. Our general result based on a wide range of trophic levels suggests that despite the differences in dispersal rates and body sizes^{24,25} belowground groups seem to show similar large scale spatial dynamics to aboveground groups.

We next tested whether biotic homogenisation occurs non-linearly and found pronounced biotic homogenisation in the transition from low to intermediate land-use intensity. We used generalised dissimilarity modelling (GDM) to allow the effect of Δ -LUI on β -diversity to vary non-linearly along the LUI gradient¹⁴. The GDMs also test the importance of LUI as a driver of β -diversity in comparison to other environmental and geographic factors. Differences in LUI between grasslands explained a significant proportion of the deviance in

β -diversity for most groups (Fig. 2B) and were one of the most important drivers of β -diversity, even in comparison with the large differences in space or nutrients between the grasslands (Extended Data Fig. 3 and 5; Supplement S4). We also found strong non-linear responses of β -diversity to land-use intensity. There was a general trend for saturating responses in aboveground groups such as plants, herbivores and pollinators together with belowground groups, bacterivores and mycorrhizae (Fig. 2B). These results indicate that differences in LUI between grasslands drive turnover at low overall LUI, with further intensification having no effect on turnover. Combined with the overall negative effects of LUI on β -diversity (linear models; Fig. 2A), this indicates biotic homogenisation in the transition from low to intermediate land-use intensity, paralleling the response of α -diversity aboveground¹. Some other groups, i.e. plant pathogens and secondary consumers, showed accelerating responses in β -diversity, which indicates strong homogenisation in the most intensively managed grasslands. Our results therefore indicate a strong and non-linear homogenisation of communities, both above- and belowground, following land-use intensification and highlight the importance of conserving extensively managed grasslands to preserve landscape scale diversity.

Effects of LUI on β -diversity were generally larger when measures were abundance weighted (Extended Data Fig. 4). This suggests that intensively-managed grasslands tend to be dominated by the same species even if they differed in their rare species, which would be expected if locally dominant species are also widespread²⁶. Indeed, intensification increased dominance in most aboveground groups; although not in belowground groups (Extended Figure 1). The strong effects of land-use intensity on abundance weighted β -diversity indicate that intensively managed grasslands become dominated by a small set of common species across a wide array of trophic groups. This may reduce a range of ecosystem functions¹⁰ and threaten the delivery of critical ecosystem services in intensively managed landscapes.

Despite the overall consistency of land-use effects, some exceptions are worth noting. Microbial decomposers (bacteria) responded weakly and had very low β -diversity. This may be because bacterial taxa were resolved to family level, a coarser taxonomic resolution than most other groups. Responses of pollinators were also weak, possibly because β -diversity of pollinators responds more to land use at the landscape scale (as shown by the strong effect of grassland isolation on β -diversity, Extended Data Fig. 3). Landscape structure is a key determinant of pollinator diversity²⁷ and fragmentation is detrimental to many pollinators^{28,29}. However, in most other groups, isolation was a much less important driver of β -diversity than local land-use intensity (Extended Data Fig. 3). The relative importance of LUI as a driver of β -diversity therefore varied between functional groups (Extended Data Fig. 5), but it affected key ecosystem service providers such as plants and herbivores, as well as rare birds, which have high conservation value.

Land-use intensification also homogenised trophic structure and disrupted correlations between β -diversity at adjacent trophic levels. We analysed correlations between the β -diversities of different functional groups by contrasting sets of plots with low versus high land-use intensity. We expected a drop in correlations at higher levels of LUI, which would be a further signal of biotic homogenisation and would imply that communities suffer functional decoupling at these levels. Correlation strength dropped by >50% on average (for $R^2 > 0.1$ at low LUI) following land-use intensification. While correlations between aboveground groups were markedly reduced by land-use intensification, belowground correlations were weak at any level of LUI. The correlations between producers and primary consumers (plants and herbivores or plants and pathogens) were strongly reduced by land use (Fig. 3, Extended Data Fig. 6), which may reflect a loss of host specialists in intensively managed grasslands. Since correlations were corrected for differences in LUI, effects are not driven by shared responses to common environmental drivers. Manning et al.³⁰ showed that land-use intensification disrupted correlations in α -diversity and we extend this analysis to additionally show spatial

214 decoupling for a wider range of functional groups, which provides further evidence for biotic
215 homogenisation across trophic levels.

216 Our results clearly show that land-use intensification substantially reduces the β -
217 diversity of many functional groups. This threatens biodiversity by homogenizing
218 communities within and across agricultural landscapes. These responses indicate that
219 measures to reduce management intensity are likely to be most effective at intermediate land-
220 use intensity¹³ and they underscore the high value of extensively managed grassland for
221 conserving multitrophic diversity at larger spatial scales. The consequences of biotic
222 homogenisation for landscape-scale ecosystem service provisioning remain uncertain, but are
223 likely to be severe. To counter these developments, conservation strategies and agricultural
224 policies should focus their attention on maintaining the heterogeneity of biotic communities at
225 the landscape scale, e.g. by coupling subsidies to landscape-scale measures of diversity.

228 **Figure 1 | Effect of land-use intensity (LUI) on α -diversity above- and belowground.** The
229 partial effect of local LUI comes from a power law model fitted to the species richness of the
230 seven aboveground (solid lines) and the five belowground trophic levels (dashed lines) (for
231 more details see methods). Species richness and LUI were corrected for differences due to
232 region, pH, soil nutrients, sdLUI and isolation, by taking residuals, and were then scaled
233 between 0 and 1.

234
235

237 **Figure 2 | Effects of land-use intensity (LUI) on β -diversity above- and belowground.**

238 (A) Partial effects of minimum LUI (min LUI) and differences in LUI (Δ LUI), between plot
239 pairs, on the species turnover component of β -diversity (β_{sim}) for seven aboveground and five
240 belowground groups, from linear models. Negative effects of minimum LUI indicate that land
241 use intensification reduces β -diversity. The bars show coefficients from the models. Numbers
242 adjoining bars are the proportion of the total explained variance that is uniquely explained by
243 minimum LUI or differences in LUI among plot pairs, based on hierarchical partitioning. (B)
244 Results from Generalised Dissimilarity Models (GDMs) are shown for the turnover
245 component β_{sim} for the same trophic groups. The figures show the effect of differences in LUI
246 on β -diversity (calculated between all plot pairs). Effects of differences in LUI can vary non-
247 linearly along the gradient of LUI. Higher maximum curves indicate larger effects of
248 differences in LUI on β -diversity. The values in the legend are the percent deviance explained
249 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).

Figure 3 | Effect of LUI on correlations between the β -diversities of different trophic groups. Correlations are R^2 values from matrix regressions between β_{sim} values of different groups (corrected for effects of differences in LUI on β -diversity). They are shown at low LUI (the 52 plots where $LUI < \text{median } LUI$) and at high LUI (53 plots). All correlations were grouped into categories according to whether they compared above- and belowground groups or compared between different trophic levels (AG = Aboveground, BG = Belowground, PP = primary producers, PC = primary consumers, SC = secondary consumers, TC = tertiary

260 consumers). Each dot represents the mean and standard error for the correlations in each
261 category.

Methods

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 South-western Germany, 2) the National Park Hainich and its surrounding areas in Central Germany, and 3) the UNESCO Biosphere Reserve Schorfheide-Chorin in North-eastern Germany. The three regions differ in climate, geology, and topography but each is characterized by a gradient of land use intensities (LUI) typical for large parts of temperate Europe³¹. In each region, 50 grassland plots were selected to cover the whole range of LUIs and management types, whilst minimizing confounding factors such as spatial position or soil type³¹. In this study, we sampled a subset of 105 plots (Schwäbische Alb: 32, Hainich-Dün: 37, Schorfheide-Chorin: 36) from which data for 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 ($\text{kg N ha}^{-1} \text{ yr}^{-1}$), grazing (number of livestock units $\text{ha}^{-1} \text{ y}^{-1}$) and mowing (number of cuts per year), was assessed annually by standardized interviews with the land owners. Land-use intensity at the local scale was then quantified as a compound index based on summing the standardized intensities of these three components. Each was divided by the global mean value for each year to standardize the components²⁰. We then calculated the mean LUI for each plot over five years (2006-2010) because this reflects the average land-use intensity around the years when most of the data was assessed (2008, 2009 and 2011).

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 that might affect diversity. We quantified the temporal variation of LUI, as its standard deviation (sd LUI) across five years (2006-2010) because this has been shown to increase α -diversity¹. To measure effects of land use at the landscape scale, which may also be important drivers of diversity⁶, we calculated one minus the proportion of grasslands within 500 m of each plot as a proxy for isolation. Plot surrounding data was mapped in 2009 using high resolution (40 cm) aerial photographs from 2008.

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,³² & Supplement 1.

We used pH and the first axis of a Principle Component Analysis (PCA) including soil nutrient variables (nitrogen stock, total soil nitrogen, organic carbon stock, soil inorganic carbon, soil organic carbon, soil C/N ratio). The PCA was conducted using the ade4 package³³ (Table S1). Note that our measure of soil nutrients includes, in addition to natural variation among soils, partly the effect of fertilization which in turn is also part of the LUI. Therefore our estimates on the effects of land-use intensity are on the conservative side. 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 based on geographic coordinates using Euclidian distances in the R package vegan³⁴.

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, pathogenic fungi) or acoustic (bird calls) taxonomy (vertebrates).

313 *Aboveground organisms*

314 *Vascular plants, bryophytes and lichens*

315 We sampled vascular plants between mid-May and mid-June 2009, bryophytes (2007 to 2008)
316 and lichens (2007 to 2008) in an area of 4 m × 4 m on each plot, and estimated the percentage
317 cover of each occurring species. For details see Socher et al.^{35,36} for vascular plants, Boch et
318 al.³⁷ for lichens, and Müller et al.³⁸ for bryophytes).

319

320 *Arthropods*

321 In 2008, we sampled aboveground arthropods of the herb layer either by biannual
322 (June/August) sweep netting (Araneae, Coleoptera, Heteroptera, Homoptera, Hymenoptera,
323 Neuroptera, Orthoptera) using 60 double sweeps along three 50 m long plot border
324 transects^{39,40}, triannual flower visitor observation (Diptera, Hymenoptera)⁴¹, or triannual
325 lepidopteran netting along a transect (Lepidoptera)^{42,43}. All arthropod species were assigned to
326 one of three trophic guilds (herbivores, predators and decomposers) based on their known
327 main food resource as adults.

328 Soil arthropods (Myriapoda, soil living larvae) were sampled in spring 2011 (within ten days
329 in April) by collecting two soil cores (diameter 20 cm, depth 10 cm) from each plot. Soil
330 fauna was extracted from the first core using a modified heat extraction system⁴⁴ over a period
331 of eight days and the second soil core was hand-sorted for soil macrofauna.

332

333 *Pathogenic fungi*

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

338

Birds

Birds were sampled by audio-visual point counts⁴⁵. We used fixed-radius point counts and noted all individuals of each bird species during the five-minute interval per point count locality and time period. In each year, from 2008 to 2012, we visited each site 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 were surveyed per day by one observer from sunrise to 11:00 h; occasionally the evening chorus was surveyed after 17:00 h (< 20 times out of 750 events per year). The sequence in which plots were visited was randomized. The maximum number of birds displaying site⁻¹ year⁻¹ (i.e. 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, since 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 assessed bat species richness parallel in all three regions from June to September during the years 2008, 2009 and 2010. Surveys were conducted along a 24 minute point-stop transect of 200 m around each grassland plot. The acoustic recordings in the grassland started a minimum of 30 minutes after local sunset and continued until 1:00 AM to account for the main activity peak of the bats during the first half of the night⁴⁶. We randomly sampled 4 to 6 plots per night. Each plot was surveyed twice during each year while keeping a minimum time interval between repeated sampling of five weeks. We recorded bats in real time (sample rate: 384 kHz, 16 bit) with a Petterson-D1000x bat detector (Pettersson Electronic AG, Uppsala, Sweden). We triggered individual recordings manually by listening through

headphones to the output of the heterodyne system while continuously scanning the frequency range between 20 and 80 kHz. For acoustic data analysis we used Avisoft SAS Lab Pro, Version 5.0.24 (R. Specht, Avisoft Bioacoustics, Berlin, Germany) and generated spectrograms with a Hamming window (1024 FFT, 96% overlap). We evaluated the number of bat passes which were defined as a minimum of two consecutive echolocation calls⁴⁷. Successive passes within the one minute recordings were discriminated if the time interval between calls was larger than three times the regular pulse interval of the particular species^{48,49}. In addition we identified species or sonotypes, based on a custom-made identification key and various references on echolocation call parameters e.g.^{50,51,52}. For additional details on species identification see Jung et al.⁴⁹.

Bacteria

At each grassland plot fourteen soil cores (diameter, 8.3 cm) were taken from a 20 m x 20 m subarea and soil from the upper 10 cm of the A horizon was homogenized after removal of root material. 10 g of the homogenized soil were put immediately on liquid nitrogen and stored until RNA extraction⁵³.

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 by Bartram et al.⁵⁴. Forward and reverse reads from V3 Illumina Amplicon sequencing longer than 100 bp were trimmed and dimers filtered out based on detection methods implemented in FastQC (<http://www.bioinformatics.babraham.ac.uk/projects/fastqc/>). FASTQ-files were synchronized for those rare cases where only one of both reads has been filtered out. Reads were joined using fastq-join⁵⁵ allowing 20 percent mismatch and a minimum overlap of 6. Converted FASTA files were checked for chimeras by Uchime integrated in Usearch 5.2.32⁵⁶ applying

the GOLD database from ChimeraSlayer (<http://drive5.com/otupipe/gold.tz>) as reference. Ca. 1 million reads of approximately 200 bp were obtained per soil sample.

The sequence reads were classified into hierarchical taxonomic levels using the RDP classifier^{57,58}. The total number of 1323 bacterial genera was detected in 106 plots (Extended Data Table 1). The abundance data are given as relative abundance: proportion of reads that can be assigned to a specific bacterial genus among all reads obtained from a given plot. Presence/Absence is given as presence (reads could be assigned to a bacterial genus) versus absence (no reads could be assigned to a bacterial genus). The full details are currently under preparation for another manuscript (Sikorski et al. in prep.).

Protists

One gram of soil from 150 grassland samples were collected^{59,60}, DNA extracted and 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's and (3.) ambiguities (N's). Traces were scanned for chimeras, trimmed to 530 bp's, dereplicated to group 100% identical amplicons and singletons removed. Remaining sequences were treated as OTUs and aligned to the PR² 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.

Arbuscular mycorrhizal fungi

Total microbial DNA was isolated from soils using a MoBioPowerSoil DNA Isolation Kit. The NS31-AM1 fragment of the fungal 18S rDNA was amplified using arbuscular mycorrhizal (AM) fungal specific primers⁶¹ and sequenced using a Genome Sequencer FLX+ 454 System. The reads were quality filtered using Mothur⁶² and classified using the

MaarjaM AMF reference database⁶³. A total of 825 AM fungal OTUs were detected. Detailed description of the data processing is presented in Supplement S2.

Statistical analyses

All analyses were conducted in R 3.0.2⁶⁴.

Diversity measures

We calculated several measures of α and β -diversity for each of the 12 trophic groups (Fig. 1). We used q-metrics proposed by Jost^{65,66} to incorporate different weightings for species abundance in α and β -diversity. These are based on Hill numbers⁶⁷, 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, this 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, this 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 α -diversity and Morisita-Horn index for β -diversity^{68,69}. Analyses were conducted using multipart function in vegan package⁷⁰.

Spatial turnover in composition between locations involves two main processes: a replacement of species (pure turnover) and changes in species richness total β -diversity measured as^{16,17}. To test for effects on β -diversity independent of species richness differences, we used the Simpson dissimilarity β_{sim} , which is the turnover component of Sørensen dissimilarity, as suggested by Baselga and Leprieur¹⁷. Details on γ - as well as β -diversity partitioning is given in the Supplement S3.

441 *Alpha diversity analysis*

442 In order to analyse the response of α -diversity to land use we used power law models which
443 allow different shapes of responses to be fitted. We modelled the response of α -diversity for
444 each of the 12 functional groups, calculated with $q = 0, 1$, and 2 . The explanatory variable was
445 LUI, the model formula was $y = a + b \cdot \text{LUI}^c$. In order to correct for confounding
446 environmental effects we analysed residuals in the power law models. We calculated residuals
447 from linear models with diversity or land use (LUI) as the response variable and region, soil
448 nutrients, pH, variation in LUI (sd LUI) and isolation (1-proportion of grasslands in the plot
449 surrounding) as explanatory variables. We calculated residuals because incorporating so many
450 explanatory variables in the power law models would have led to extremely complex models.
451 After taking residuals, we then scaled all explanatory and response variables between 0 and 1,
452 to allow comparison of effects and responses. Models were fitted using the `gnls` function in
453 the `nlme` library⁷¹.

454

455 *Beta diversity analysis*

456 Linear models

457 To analyse the response of β -diversity to land use intensification we first fitted linear models.
458 These were fitted to values of turnover (β_{sim}), total β -diversity (Sørensen, $q=0$) and
459 abundance weighted β -diversity ($q = 1$ and 2) for each of the 12 trophic groups. Explanatory
460 variables in these models were the same as for the α -diversity analysis: minimum LUI, sdLUI,
461 isolation, soil nutrients and pH between each pair of plots. The effects of minimum LUI
462 provide a test of biotic homogenization: a negative effect of minimum LUI indicates that
463 land-use intensification reduces turnover. However as plots with the same minimum LUI can
464 either be very similar in LUI or come from different ends of the gradient we also fitted
465 differences in LUI between all plot pairs. We additionally fitted the spatial distance between

all plot pairs, together with differences in pH, nutrients, sdLUI and isolation in the model to correct for spatial distance, and distance in environmental and other land use variables. In order to compare the effects of the different predictors we scaled all of them between 0 and 1. We then conducted variance partitioning, using the hier.part library in R, to determine the unique variance explained by each predictor. These models cannot be used for significance testing (due to pseudoreplication) but the parameter estimates and percentage explained variance are robust.

Generalized dissimilarity modelling

In order to analyse the non-linear effects of spatial differences in land-use intensity (LUI), we used generalised dissimilarity modelling (GDM)¹⁴. 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 great 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 non-linear. The only constraint is that compositional turnover is assumed to always increase with distance between sites (monotonicity). For more details on GDM see Ferrier et al.¹⁴. All GDMs were fitted using the "gdm" function in the gdm package⁷². We plot the partial effect of each predictor, i.e. whilst holding all other predictors constant, against the level of a given predictor to visualize the results of the GDM. The height of the line shows how large the effect of each predictor 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.

We fitted GDMs to four measures of β -diversity for each group: turnover (β_{sim}), total β -diversity (Sorenson, $q=0$) 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.

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

In order 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 library⁷³). We correlated β -diversity of different groups (β_{sim} , $q = 0$, $q = 1$, and $q = 2$ (see above)), whilst correcting for geographic and 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. To test whether the strength of correlations differed between low and high land-use intensities we divided the 105 plots into 52 low ($<$ median LUI) and 53 high ($>$ median LUI) intensity plots and compared the R^2 -values of the matrix correlations between low and high LUI. The multiple regressions use permutation tests (999 permutations) of significance for the regression coefficients and for the R-squared values. A change in interaction strength indicates a decoupling of trophic interactions.

End notes

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543 **Author Information.** The data will become publicly available according to the Rules of
544 Procedure of the German Science Foundation (DFG)-funded Biodiversity Exploratories, i.e.
545 five years after completion of the data sets. Reprints and permissions information is available
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548

551 **Extended Data Figure 1 | Effect of land-use intensity (LUI) on higher q-level α-diversity**

552 **above- and belowground.** The partial effect of local LUI comes from a power law model
553 fitted to the exponential Shannon diversity (q=1) and reciprocal Simpson index (q=2) of the
554 seven aboveground (solid lines) and the five belowground trophic levels (dashed lines) (for
555 more details see methods). In the model all parameters of the power law function could
556 depend on temporal variation in LUI (sd LUI) and isolation and LUI effects are here plotted at
557 the mean values of these two variables. α-diversity and land-use variables were corrected for
558 differences due to region, pH and soil nutrients, by taking residuals, and were then scaled
559 between 0 and 1. The models for protists (q=1 and q=2) and mycorrhizae (q=2) failed to
560 converge and are therefore not shown. Note that plant pathogens are missing because for this
561 group no abundance data was available.

562

563

Extended Data Figure 2 | Effects of land-use intensity (LUI) on total β -diversity above and belowground. (A) Partial effects of minimum LUI (min LUI) and differences in LUI (Δ LUI), between plot pairs, on total β -diversity for seven aboveground and five belowground groups from linear models. Negative effects of minimum LUI indicate that land use intensification reduces β -diversity. The bars show coefficients from the models. (B) Results from Generalised Dissimilarity Models (GDMs) are shown for on total β -diversity 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 non-linearly 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 percent deviance 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 3 | Partial effects of temporal variation in LUI (sd LUI), isolation, geographic distance [x100km], soil pH, and soil nutrients on β -diversity above and belowground. Results from Generalised Dissimilarity Models (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). Effects of differences in each explanatory variable can vary non-linearly 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. In the graph showing geographic distance, solid lines indicate lower and dashed lines upper limit of distances within regions (left), between Schwäbische Alb/Hainich-Dün and Hainich-Dün/Schorfheide-Chorin (middle), and between Schwäbische Alb and Schorfheide-Chorin (right). Soil nutrients refer to the scores of the first PCA axis.

Extended Data Figure 4 | Effects of land-use intensity (LUI) on higher q-level β -diversity

above and belowground. (A, C) Partial effects of minimum LUI (min LUI) and differences in LUI (Δ LUI), between plot pairs, on total β -diversity (A: Morisita $q=1$; C: Morisita-Horn $q=2$) for six aboveground and five belowground groups from linear models. Negative effects of minimum LUI indicate that land use intensification reduces β -diversity. The bars show coefficients from the models. (B, D) Results from Generalised Dissimilarity Models (GDMs) are shown for on total β -diversity for the same trophic groups (B: Morisita $q=1$; D: Morisita-

603 Horn $q=2$). The figures show the effect of differences in LUI on β -diversity (calculated
604 between all plot pairs). Effects of differences in LUI can vary non-linearly along the gradient
605 of LUI. Higher maximum curves indicate larger effects of differences in LUI on β -diversity.
606 The values in the legend are the percent deviance explained uniquely by LUI. Effects of both,
607 linear models and GDMs, are corrected for other drivers of β -diversity and response and
608 explanatory variables are scaled to allow comparisons across trophic levels (see Methods).
609 Plant pathogens are missing because for this group no abundance data were available.

610

611

Extended Data Figure 5 | The relative importance of land-use intensity (LUI) as a driver of β -diversity. The barplot shows how important LUI is (in terms of total effect size) relative to the most important variable in the GDM. Results are shown for each trophic group and for total β -diversity (Soerensen Index, β_{sor}) and as the species turnover component (β_{sim}).

621 **Extended Data Figure 6 | Effect of land-use intensity (LUI) on the correlation between**
 622 **the β -diversities of different trophic groups.** Each dot represents the correlation (R^2)
 623 between two trophic levels. Correlations are R^2 values from matrix regressions between β_{sim}
 624 values of different groups (corrected for effects of differences in LUI on β -diversity).
 625 Significant correlations ($p < 0.05$) are marked in red. Upward and downward triangles
 626 indicate significance under low or high LUI only. Interactions with R^2 -values higher than 0.2
 627 in one of the LUI-categories are illustrated by icons. β -diversity was calculated as the
 628 Soerensen Index (β_{sor}) and as the species turnover component (β_{sim}).

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