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RESEARCH ARTICLE

Land use intensification results in abrupt transitions between extensively and intensively managed grasslands

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Abstract

1. Understanding whether land use intensification causes regime shifts (i.e. persistent, large changes in ecosystem states) is of key importance for management, particularly if these shifts occur abruptly as thresholds in land use intensity are crossed. Further, these threshold responses can show hysteretic dynamics, where the transition between states cannot simply be undone by reducing land use intensity to its initial level, and instead larger changes are required. However, quantitative evidence for threshold responses and their dynamics remain scarce.
2. Here we use a unique, long-term grassland database in Germany to identify threshold responses to land use intensity. We include data on the response of 16 ecosystem functions (including plant biomass, herbivory, litter decomposition, pathogen infection, water recharge, C and N fluxes and retention and enzymatic activity) and the diversity of 21 taxa (including above-ground and below-ground taxa such as vascular plants, lichens, bryophytes, arthropods, vertebrates, fungi, protists and bacteria). Then, we use increased variance as an early warning signal to evaluate if threshold responses are indicative of critical transitions between states. Finally, we use temporal data to identify hysteretic dynamics associated with those transitions.

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3. We show that 5 out of 10 above-ground taxa, fungal diversity, shoot biomass and soil N retention showed threshold responses to land use intensity, that is abrupt changes between extensively and intensively managed grasslands. Some of the thresholds were associated with increased variance in the response variables, suggesting a potential critical transition between ecosystem states. Time-series analysis indicated that ecosystem functions showed a hysteretic response to land use intensity, but diversity measures did not.
4. Our results suggest threshold responses to land use intensity are relatively common in the grasslands we studied. These thresholds show abrupt changes in the ecosystem when highly diverse extensively managed grasslands are managed slightly more intensively. Further, shifting back to the functioning seen in extensively managed grasslands may be challenging, as it requires larger reductions in land use intensity than those required to shift to the high intensity state. Identifying thresholds along land use gradients is critical to prevent ecosystem degradation and conserve biodiversity and ecosystem functions in semi-natural grasslands.

KEYWORDS
above- and below-ground diversity, ecosystem functions, grasslands, hysteresis, land use intensification, regime shifts, thresholds

1 | INTRODUCTION

Land use intensification is a major cause of biodiversity loss across trophic levels (Allan et al., 2015; Rounsevell et al., 2018) and can lead to a homogenization of community composition (Gámez-Virués et al., 2015; Gossner et al., 2016). In addition, increasing land use intensity can decrease ecosystem multifunctionality by increasing yield at the expense of other ecosystem functions, such as soil C storage and nutrient retention (Soussana & Lemaire, 2014) and of services like cultural and aesthetic value, pollination and pest control (Allan et al., 2015; Dainese et al., 2019). Land use intensity effects are frequently non-linear, meaning that abrupt changes in grassland biodiversity and functioning occur as land use intensity increases (Allan et al., 2014; Kleijn et al., 2009). However, few studies have tested how common these non-linear responses are across a range of different taxa and ecosystem functions. In addition, it is unclear whether these non-linear changes result in regime shifts, that is persistent, large changes in system-state variables, such as biodiversity or ecosystem functions (Scheffer & Carpenter, 2003). Identifying regime shifts is critical to determine the sustainability of different forms of ecosystem management, particularly when they affect human well-being (Crépin et al., 2012).

Large changes in ecosystem states, leading to regime shifts, can occur at different rates (Figure 1a). A regime shift can occur gradually when the state variable shows a linear response (Figure 1b). However, when the response is abrupt, the regime shift can be associated with a threshold response where a small change in the external driver, *for example* land use, leads to a sudden and large change in the system-state variable, which is further accelerated by internal feedbacks (Briske et al., 2006; Ratajczak et al., 2018; Suding et al., 2004). Theories propose two types of dynamics associated with thresholds (Suding & Hobbs, 2009): first, the system can revert to its previous state when the driver returns to its original level, that is the regime shift is reversible (Figure 1c). In the second case, however, the system may not easily revert to its previous state, resulting in a critical transition between distinct stable states (Figure 1d). In this case, the transition between states cannot simply be undone by restoring the driver to its initial level but it requires larger changes to recover the previous state (i.e. hysteresis, Dakos et al., 2019; Scheffer & Carpenter, 2003). Some studies have identified thresholds in grassland vegetation responses to grazing (Briske et al., 2005; Sasaki et al., 2008), but none have tested for thresholds in the response of multiple aspects of diversity, and ecosystem functioning, to several elements of land use, or whether thresholds are associated with hysteresis responses.

Although threshold responses have sometimes been observed (Sasaki et al., 2015), several studies have suggested that there is no quantitative evidence for them and that thresholds are rarely detectable (Hillebrand et al., 2020). Several factors may explain these mixed findings. First, different ecosystem functions, and the diversity of different taxa, are likely to vary in their response to external drivers (Allan et al., 2015; Newbold et al., 2015; Soliveres et al., 2016). Thus, the absence of a threshold for one function or

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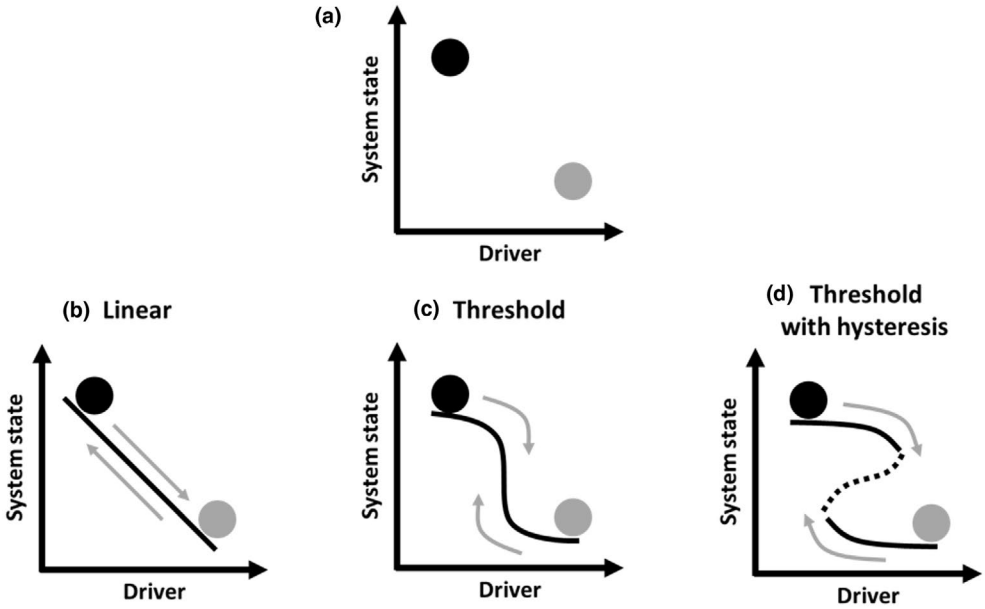


FIGURE 1 Trajectories for regime shifts in ecosystems. Ecosystems experience a regime shift when they show a large change in an ecosystem state (i.e. variables describing the ecosystem) (a). This change can be due to one or more environmental drivers and can be gradual or fast, leading to multiple relationships (unbroken black line) between ecosystem state and environmental drivers. The regime shift can be gradual if the ecosystem state changes linearly with the driver (b) or abruptly (c). In that case, the abrupt change associates with a threshold response to the environmental driver. In addition, the regime shift can show hysteresis if the direction of the change (grey arrow) is associated with different thresholds (d). In this case, bringing the driver back across the original threshold will not return the ecosystem to its previous state (broken black lines).

diversity does not preclude the existence of thresholds for others. However, most studies looking for thresholds focus on a small number of ecosystem components; typically, diversity measures and more rarely ecosystem functions (Sasaki et al., 2015, but see Evans et al., 2017). Second, consistently detecting thresholds in response to external drivers can be challenging when ecosystem responses are highly variable (Hillebrand et al., 2020), meaning that extensive datasets are needed to robustly identify thresholds. Finally, extensive sampling needs to be combined with longitudinal data to identify critical transitions in ecosystem states, that is using early warning signals (indicators of a system approaching a critical transition, Scheffer et al., 2009), or to evaluate the dynamics associated with thresholds, that is to test for hysteresis (Sasaki et al., 2015), and such data are rarely available. Thus, testing for thresholds in ecosystem responses requires studies with continuous measures of external drivers and ecosystem responses across many sites and multiple years.

In this study, we use a large database from 150 semi-natural, temperate grasslands in central Europe to identify thresholds in the response of the diversity of 21 taxonomic groups (including plants, arthropods, birds, bats and soil microbes) and 16 ecosystem functions (including productivity, measures of nitrogen, carbon and phosphorus cycling and herbivory and pathogen attack), to a gradient of land use intensity. We considered effects of three land use components, grazing, mowing and fertilization, both individually and combined in a composite land use index (Blüthgen et al., 2012). We asked the following questions: (i) do diversity measures of multiple taxa (across multiple trophic levels) and ecosystem functions show threshold responses to the land use gradient? and if so, (ii) are these thresholds indicative of critical transitions and hysteresis? To answer these questions, we used a three-step analysis. First, we identified which variables showed a non-linear response to land use intensity and tested whether those responses were associated with specific thresholds. Second, we looked for early warning signals of critical transitions, by testing for increased spatial variation along the land use gradient just before the identified threshold. Finally, we used 12 years of land use data to identify hysteretic dynamics, based on whether observed thresholds changed depending on the land use history (i.e. if land use intensity had recently decreased or increased on a grassland).

2 | METHODS

2.1 | Study area

The studied grasslands are part of the Biodiversity Exploratories project (www.biodiversity-exploratories.de) (Fischer et al., 2010) and are located in three different regions of Germany: the Schwäbische Alb plateau, as a part of the UNESCO Biosphere Reserve Schwäbische Alb (south-west), Hainich-Dün region (central) and the UNESCO Biosphere Reserve Schorfheide-Chorin (north-east). The regions differ in geology, topography, climate and soils (Fischer et al., 2010). Detailed information about the studied

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regions can be found in Table S1. In 2007, 50 permanent grassland plots of 50 m × 50 m were established in each region (150 in total). Plots had been grasslands for at least 20 years before the start of the project. A detailed explanation of the research design can be found at https://www.biodiversity-exploratories.de/en/about-us/research-design/. Fieldwork was coordinated by the Local Management teams, which were responsible for obtaining required permits.

2.2 | Land use intensity

Plots in all three regions were selected to cover land use gradients typical for central Europe (Blüthgen et al., 2012). To assess land use intensity (LUI), annual questionnaires were sent to landowners asking them about the intensities of grazing, mowing and fertilization on each plot (Blüthgen et al., 2012; Vogt et al., 2019). For grazing intensity (G), farmers reported the type (cattle, horse and sheep), stocking density and the duration of grazing periods (standardized to livestock units·grazing days·ha^{-1}·year^{-1}, Vogt et al., 2019). For mowing frequency (M), farmers reported the number of annual cuts (number of cuts·year^{-1}), and for fertilization (F), they reported the total fertilizer addition from which we calculated the amount of nitrogen added (kg N·ha^{-1}·year^{-1}). The individual components (G, M, F) were then standardized to their means across regions, and a continuous compound index of LUI was calculated by summing the standardized components (LUI = G + M + F, Blüthgen et al., 2012). The combined index provides a simple measure of overall land use intensity, given that individual components, such as mowing and fertilization, are strongly correlated with each other (Table S2).

2.3 | Biodiversity

Taxonomic diversity data were collected for 21 above and below-ground taxa. Above-ground diversity was measured for vascular plants, lichens, bryophytes, arthropods (divided into herbivores, omnivores, predators, detritivores and pollinators) and vertebrates (granivores and insectivores, birds and bats). Below-ground diversity included arthropods (divided into predators and detritivores), bacteria, fungi (divided into decomposers, pathogens, symbionts and others) and protists (divided into bacterivores, eukaryvores, omnivores and parasites). Species diversity for vascular plants, bryophytes and lichens was collected in a 4 m × 4 m subplot located in the middle of each plot. Arthropod species diversity was collected above-ground, using sweep netting along 150-m transects, and below-ground, using soil core extractions. Bird species diversity was collected using standardized 5-min point-counts, recording all individuals seen and heard from the centre of the plot. Bat species diversity was measured using standardized acoustic monitoring. Diversity of bacteria, fungi and protists was assessed as the number of operational taxonomic units (OTU), based on metabarcoding approaches using DNA extracted from soil samples. We defined grassland taxonomic diversity for each group as the number of species/OTUs identified. All diversity data were measured in all plots and detailed information about the collection can be found in Table S3.

2.4 | Ecosystem functions

A total of 16 ecosystem functions were measured on each plot. Function data included grassland productivity (above- and below-ground), proxies of energy transfer between trophic levels (herbivory, seed and dung depletion, litter decomposition, root decomposition, pathogen infection), biogeochemical cycling (carbon, nitrate and ammonia fluxes, phosphatase activity, potential nitrification, N and P retention) and hydrological processes (water recharge). Plant shoot biomass was measured in eight 0.5 m × 0.5 m squares and root biomass in 14 soil cores per plot. Herbivory was calculated by measuring the proportion of leaf area damaged by insects, on 100 random leaves selected from the biomass sample. Seed and dung depletion was calculated as the proportion of cattle dung or sunflower seeds removed after 48 h exposure. Litter and root decomposition was calculated as the mass loss from litterbags after 4 and 6 months, respectively. Pathogen infection was estimated by visual inspection and calculated as the cover weighted mean of pathogen prevalence and severity per plant species. Proxies of carbon, nitrate and ammonia fluxes were calculated using composite indices including several enzymatic activities (Carbon: β-Glucosidase, N-Acetyl-β-Glucosaminidase and Xylosidase; Nitrate: Denitrification enzyme; Ammonia: Urease) and functional genes (Nitrate: nitrogenase, nrxA gene for *nitrobacter*, 16S rRNA gene for *nitrospira*; Ammonia: ammonia oxidation genes for archaea and bacteria). C-cycling enzyme activities were analysed using fluorogenic substrate and fluorometric detection, N-cycling enzyme activities as well as potential nitrification were photometrically analysed and the abundance of functional genes was quantified via real-time qPCR analysis. Nutrient retention (N, P) was measured as the remaining anion content in resin bags buried 20 cm deep for 140 days. Water recharge was calculated using a water balance model using climatic and soil data. These functions are strongly connected to ecosystem services in the study area (Felipe-Lucia et al., 2020). All functions data were measured in all plots and detailed information about the collection is included in Table S4.

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Plot with different land use intensity (continuous variable)	50 × 50 m permanent grasslands plots	150 plots

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2.6 | Identification of thresholds in the response of diversity and function to land use

We first tested for the shape of response of each variable to land use intensity. As threshold responses are only possible for variables showing non-linear responses, we first checked whether any diversity and ecosystem functions variables showed non-linear responses to land use intensity and its three components. Although we focus on the effects of LUI, as they are more easily interpretable, we followed the recommendations of (Joint Research Centre, 2008), to also run analyses for its three individual components (grazing, mowing, fertilization). We compared linear regression models for each variable to quadratic regression models and generalized additive models (GAM, Hastie & Tibshirani, 1990). Quadratic models allow for non-linear effects, with one turning point in the relationship between the variables, while GAMs allow for complex non-linear responses, with several turning points. Both quadratic models and GAMs are often used to identify ecological thresholds (Berdugo et al., 2020). The best fitting model for each response was selected using the Akaike Information Criterion (AIC). Specifically, we considered that quadratic models or GAMs had better fits than the linear model when they had AIC values at least 2 units lower than the linear model ($\Delta AIC = AIC_{lin} - AIC_{qua,GAM} > 2$, Burnham & Anderson, 2003). Then, for variables that showed a non-linear response, we tested whether they also had a threshold (i.e. an abrupt shift) in their response to LUI, and its three components, using segmented regression (Muggeo, 2003). Segmented regressions were only applied to those variables that showed non-linear responses because they force break points in the explanatory variable, potentially leading to overfitting and spurious thresholds, if the response is in fact linear. In addition, if GAMs suggested the existence of several turning points, we fitted segmented regressions with more than one break point. When the segmented regression model was significant and indicated a better fit than the linear model (based on $\Delta AIC > 2$), we considered that the variable showed a threshold response. To control for the effect of region on biodiversity and functions, we used the residuals of each variable from a model including region as the explanatory variable. All variables were standardized by subtracting the mean and dividing by the standard deviation before running the models. We used the *gam* (Hastie, 2019) and *segmented* (Muggeo, 2008) packages in R.

As land use intensity varied over time in each plot, we always tested the response of each diversity and function to the land use intensity in the previous year (e.g. the response of plant diversity in 2013 to grazing in 2012). Similarly, when variables were measured in several years, the mean value for the time period of measurement was used for both explanatory and response variables (e.g. the response of average plant diversity during 2011–2013 to average grazing during 2010–2012). We decided to use the land use value from the previous year because the study area is continuously managed and the different taxa and ecosystem functions were measured before most land use practices in a given year have occurred. However, although LUI changes over time, the changes are not sufficient to dramatically alter the land use levels of the plots: both LUI and its components showed strong positive correlations between years (mean $r \pm$ standard error; LUI $r = 0.7 \pm 0.01$; grazing $r = 0.65 \pm 0.01$; mowing $r = 0.74 \pm 0.01$; fertilization $r = 0.71 \pm 0.01$) and all years were strongly related ($r > 0.74$) to the mean values over the total time period (Figure S1).

2.7 | Test of early warning signals at ecological thresholds

To identify early warning signals of critical transitions, we first evaluated changes in the spatial variability of the diversity and function measures along the land use gradients. An increase in variability of system-state variables between locations has been considered an early warning signal for regime shifts between alternative states (Scheffer et al., 2009). To test for this, we used a moving window approach along the land use gradients. All plots were sorted from lowest to highest LUI, or lowest to highest values of each LUI component, and then, the variance of each diversity and function measure was calculated across subsets of 15 plots along the gradient. That is if plots are ranked from 1 to 150, the first subset included plots 1–15, next subset plots 2–16, until the last subset included plots 136–150. Each subset accounts for 10% of the plots (Dakos et al., 2012) and covers a range of 0.2 ± 0.01 LUI units, 26 ± 1.3 livestock unit·grazing days·ha^{-1}·y^{-1}, 0.25 ± 0.01 cuts·y^{-1} and 6.4 ± 0.6 kg N·ha^{-1}·y^{-1}. Variance is a commonly used metric to anticipate critical transitions, and it provides qualitatively similar results to other indices, such as the coefficient of variation (Proverbio et al., 2023), but it is preferred when working on residuals (Dakos et al., 2012). We then tested if the variance in a given subset was significantly different from a random expectation. The expected variance for each subset was estimated by assembling 2000 subsets of 15 random plots and estimating the variance for each random subset. We then calculated the 95% confidence interval across these random subsets as the values at percentiles 2.5 and 97.5.

Although early warning signals were originally developed for temporal data, spatial gradients are frequently used as proxies when appropriate temporal series are not available (Blois et al., 2013; Eby et al., 2017; Kéfi et al., 2014). Nevertheless, interpreting changes in spatial variance is more challenging as confounding factors can cause high variability related to local environmental conditions (Huston, 1999). We therefore tested for increasing variability through time for those variables with temporal data available. Specifically, we calculated the variance through time of the functions or diversity data for each plot. We then related the temporal variance in diversity or functioning to the average LUI of the plot.

2.8 | Evaluation of hysteretic responses in the ecosystem

Finally, we evaluated whether ecosystem thresholds indicated hysteretic responses to land use by examining whether responses differed when LUI and its components increased or decreased over time. If hysteresis occurs, we would expect diversity and functions

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to respond differently to LUI, depending on whether LUI increases (intensification) or decreases (extensification). This should result in higher thresholds during land use intensification, that is land use needs to be reduced to a lower level to recover the pre intensification levels of diversity and function. For each plot in each year we determined whether LUI had increased or decreased compared to the previous year. All cases where land use remained unchanged between years were excluded, and mowing was omitted from the analysis due to insufficient data to test for hysteresis. We analysed all variables that exhibited a threshold response to LUI and repeated the threshold detection analysis to identify potential differences in thresholds in plot × year combinations which had experienced recent increases or decreases in LUI. We ran individual analyses for each combination of variable and year to account for plots experiencing increases or decreases in land use at different times (on average across years; LUI: intensification = 71.9 ± 3.3 plots, extensification = 71.5 ± 3.2; Grazing: intensification = 55 ± 2.9 plots, extensification = 54 ± 3; Fertilization: intensification = 30.6 ± 1.5 plots, extensification = 33.6 ± 1.4). In total, we ran 78 threshold models for LUI, 78 for grazing and 52 for fertilization. We then tested whether thresholds for variables on plots undergoing intensification differed from those on plots undergoing extensification. First, we tested if there were differences between intensification and extensification thresholds for each variable, using a two sample *t*-test. For those variables measured in only 1 year, we used the Welch modified two sample test using the error for the estimate of the threshold. The models were fitted using the *lme4* package in R (Bates et al., 2015). All statistical analysis were performed with R 3.6.2 (R Development Core Team, 2014).

3 | RESULTS

3.1 | Identification of ecological thresholds

We found that almost a third (29.3%) of the different taxa diversity measures and ecosystem functions responded non-linearly to land use intensification (Table S5.1). We found 9 non-linear responses for diversity (43% of taxa) and 2 for functions (13% of functions). In general, above-ground taxa showed more non-linear responses to LUI (6 of the 10 taxa, 60%) than below-ground taxa (3 fungal guilds out of the 11 taxa, 27%). For the 11 variables which showed non-linear responses to land use intensification, we identified 9 (diversity of 7 taxa and 2 functions, Figure 2) with a threshold response. In general, above-ground diversity showed a steep decline before the threshold and a more modest decline after the threshold. However, below-ground diversity increased until the threshold, after which diversity stabilized similar to a saturating response (Figure 2). For functions, plant shoot biomass showed a saturating response while N retention started to decline only after the threshold. Thresholds were remarkably consistent between variables and occurred around a land use intensity (LUI) value of 1 (most above-ground diversity metrics) and 1.5–2 (fungal diversity, plant shoot biomass and N retention). To better understand what this threshold means, we calculated the mean value of individual LUI components across the plots, within the estimated standard error around the LUI threshold value (24 plots with LUI = 1.42 ± 0.12). We found grazing values of 130.9 ± 24.5 livestock units·grazing days·ha^{-1}·year^{-1}; mowing of 1 ± 0.2 cuts·year^{-1}; and fertilization of 4.9 ± 1.6 kg N·ha^{-1}·year^{-1}. The transition threshold seems therefore associated with a switch from unfertilized grasslands (39 of 41 plots, 95%, have no fertilization below LUI threshold) to fertilized grasslands (70 of 85 plots, 82%, are fertilized above the LUI threshold).

We also found that the diversity of several trophic levels and functions had threshold responses to each land use component (grazing: 4 taxa and 3 functions; mowing: 3 taxa; fertilization: 1 taxon and 3 functions. Figure S2.1–3 and Table S5.2–4). Most of these thresholds occurred at very low levels, which probably represent a threshold between the presence or absence of the land use component (31% of grasslands considered were not grazed, 35% were not mown and 60% were unfertilized). Precise threshold values are presented in Table S6.

3.2 | Early warning signals at ecological thresholds

Using a moving window approach, we found that 3 variables showing a threshold response to LUI (33% of the total) also showed a significant increase in variance, relative to random expectations, within the LUI threshold. The three groups were vascular plants, lichens and vertebrate granivores (Figure 3). However, we also observed significant increases in variance at a similar LUI value for three below-ground variables that did not show a threshold response to land use intensity (e.g. Symbiotic fungi, Bacteria, Root biomass, Figure S3.1). In addition, N retention and bryophyte diversity showed increased variance at either very high or low LUI, which was unrelated to the threshold. This same pattern was observed for individual land use components (Figure S3.2–4). Finally, results using temporal variation showed higher variance at LUI values within the threshold for all variables, but also at LUI values unrelated to the threshold (Figure S4).

3.3 | Hysteretic responses in the ecosystem

We estimated thresholds for each variable and each year, for all the plots that experienced intensification or extensification in each year. Individual analyses per response variable showed that LUI thresholds for diversity did not differ between plots undergoing intensification vs. extensification, while there were significant differences for functions (Figure 4). Specifically, the LUI threshold for N retention occurred at lower land use levels in plots where LUI had decreased from the previous year (extensification threshold at LUI = 1.06 ± 0.2 kg N·ha^{-1}·year^{-1}) compared to plots where LUI had increased (intensification threshold at LUI = 2.23 ± 0.4 kg N·ha^{-1}·year^{-1}, Figure 4). The same response for N retention was found when considering only fertilization (intensification threshold at

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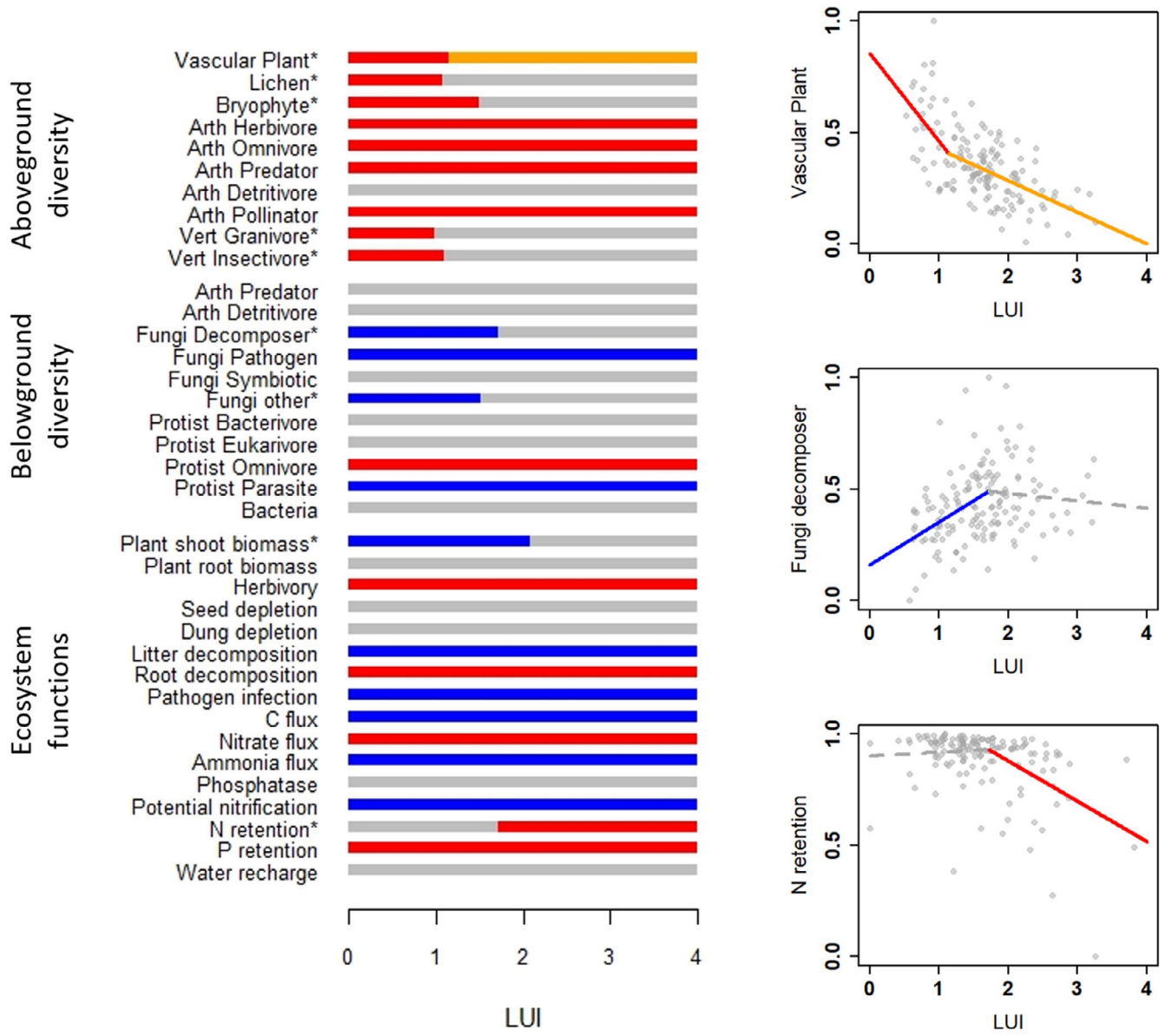


FIGURE 2 Threshold responses along LUI gradient for different taxa diversity and ecosystem functions. On the left, response to land use intensity (LUI) of all variables considered, including above- and below-ground diversity, and ecosystem functions. Different colours indicate different responses to LUI (red/orange = negative response; blue = positive response; grey = no response; vascular plant diversity always decreased with land use intensity but the strength of that decline was lower after the threshold, which is indicated as a shift from red to orange). *Indicates a variable showing a threshold response. On the right, one example of threshold response for above- (plants) and below-ground diversity (fungal decomposers) and ecosystem function (N retention).

fertilization = 225.8 ± 56.4 kg N·ha^{-1}·year^{-1}, extensification threshold at fertilization = 106.7 ± 5.5 kg N·ha^{-1}·year^{-1}; Table S7).

4 | DISCUSSION

4.1 | Identification of ecological thresholds

We found that threshold responses to land use intensity were only relatively common for above-ground taxa, with 50% showing threshold responses. In contrast, below-ground diversity and ecosystem functions showed mostly linear responses. This agrees with findings that above-ground biodiversity often declines non-linearly with land use intensification (Allan et al., 2014; Kleijn et al., 2009), while below-ground diversity may even increase with land use intensity (Le Provost et al., 2021; Gossner et al., 2016). Land use intensification can reduce above-ground diversity by homogenizing environmental conditions, by increasing arthropod mortality (grazing and mowing) or by favouring particular species (fertilization); however, below-ground diversity may be increased by nutrient inputs to the soil (Chen & Wise, 1999). In addition, the long management history of the studied grasslands may have reduced below-ground

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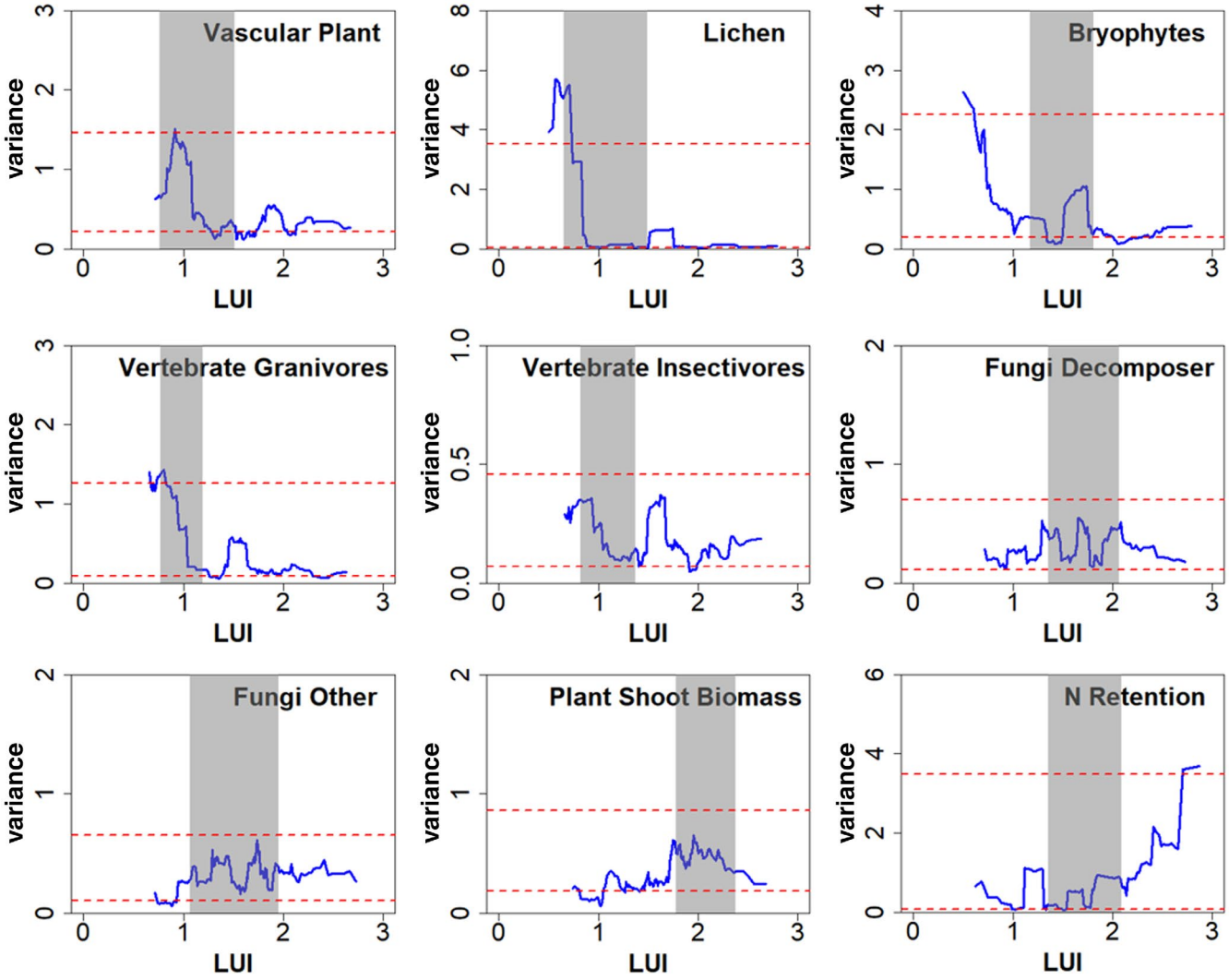


FIGURE 3 Variance for the considered taxa diversity and ecosystem functions showing a threshold response along the Land Use Intensity (LUI) gradient. The grey area represents the values along the gradient where a threshold was detected. Red dashed lines represent the confidence interval for the expected variance calculated based on bootstrapping the plots. Variance values higher than expected can be considered as indicative of a critical transition between ecosystem states.

responses to land use intensity, as below-ground communities may be affected more by soil history than recent changes in above-ground composition (Elgersma et al., 2011). Regarding functions, the lack of non-linear responses could be explained by ecological redundancy (Walker, 1992). It is possible that the loss of functionally important species with land use intensification can be partially compensated for by the remaining species, thus reducing abrupt responses (Muradian, 2001). These contrasting responses of biodiversity (above- and below-ground) and ecosystem functioning highlight the importance of simultaneously considering multiple ecosystem components to fully comprehend the overall impacts of land use intensification.

Remarkably, observed thresholds occurred at similar land use intensity (LUI) values. This might suggest that plant communities undergo a regime shift due to land use intensification that cascades to other taxa and functions. Looking at thresholds for LUI, together with those for grazing, mowing and fertilization, we observed two types of grasslands: extensively managed (LUI < 1) grasslands, which are unfertilized and lightly grazed, showing high above-ground diversity (especially of primary producers and vertebrates) and high nutrient retention; and intensively managed (LUI > 1.5) productive grasslands with high below-ground fungal diversity (Figure 2), which are fertilized and mown or intensively grazed. Low grazing intensities promote plant diversity by limiting dominant species (Boch et al., 2016; Busch et al., 2019; Maurer et al., 2006) and arthropod herbivore diversity by increasing spatial heterogeneity (van Klink et al., 2015). In contrast, the fertilizer addition associated with higher mowing frequencies selects for more competitive, taller and faster-growing plants, at the expense of smaller and slower-growing ones (Busch et al., 2019; DeMalach et al., 2017; Dickson et al., 2014; Gough et al., 2001). In the case of vertebrates, intensification in grasslands reduces diversity by limiting nesting options and increasing the risk of nest discovery by predators (Verhulst et al., 2004). In addition, biodiversity losses can cascade between different taxa. For example, a reduction

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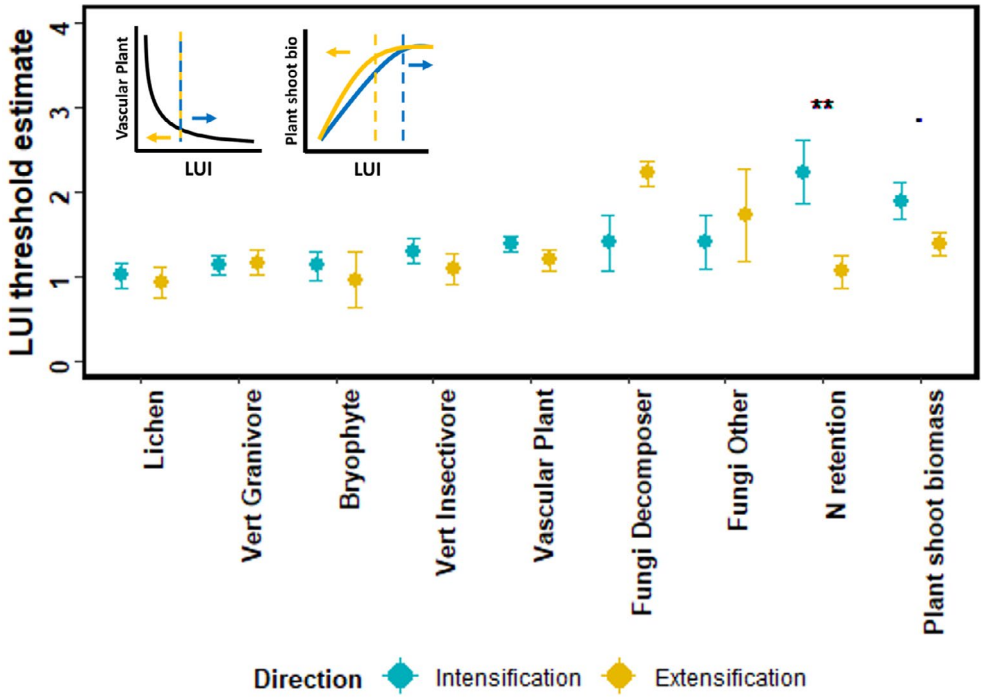


FIGURE 4 Variation in the Land Use Intensity (LUI) threshold depending on temporal changes in land use. Land use thresholds for each diversity and ecosystem function on plots where LUI had recently increased (intensification, blue line and dots) or decreased (extensification, orange line and dots). For diversity metrics, no threshold was affected by the direction of recent changes in LUI but ecosystem functions had different thresholds depending on whether LUI had recently increased or decreased, suggesting hysteresis and the presence of a critical transition between two ecosystem states. Inner subplots show (left) the threshold response of plant diversity to LUI, which is the same for plots where LUI had increased or decreased compared to the previous year; and (right) hysteresis for the threshold response of plant shoot biomass, where the threshold is different on plots where LUI had increased compared to the previous year (blue) or where it had decreased (yellow). '.' $p < 0.1$, $^{**}p < 0.01$.

in primary-producer diversity affects herbivores by reducing the diversity of resources available to them (Uchida & Ushimaru, 2014), or increased dominance of fast-growing species can lead to competitive exclusion of bryophytes (van der Wal et al., 2005). Fertilization, and increased dominance of fast-growing species in intensive grasslands, affect ecosystem functioning by increasing above-ground plant biomass (Allan et al., 2015; Lavorel & Grigulis, 2012). However, this increase may be non-linear. Environmental factors (e.g. soil water levels and light) limit further increases in biomass (Kleinebecker et al., 2014), and diversity loss associated with high fertilizer inputs results in a reduced increase in biomass at the highest levels of fertilization (Isbell, Reich, et al., 2013). The increase in above-ground plant biomass can also affect fungal communities (Voříšková & Baldrian, 2013), as more organic matter may increase fungal decomposer diversity (Cline et al., 2018). In turn, N retention decreases in highly intensified grassland soils as a result of decreased N uptake efficiency associated with high fertilizer inputs (Keuter et al., 2013). Our findings show that these well-known changes due to land use intensification may occur abruptly once a key threshold is crossed, which highlights the need to maintain low levels of land use to prevent rapid declines in diversity.

Thresholds associated with anthropogenic disturbance have been described for some ecosystems, such as eutrophicated lakes, and overgrazed drylands (Suding et al., 2004), but there had been little evidence for their importance in temperate grasslands (Sasaki et al., 2015). Some previous studies have found abrupt changes in certain ecosystem-state variables in response to particular land use components (e.g. increasing grazing intensity changed vegetation composition; fertilization changed vegetation composition and soil properties, Ramirez et al., 2010; Sasaki et al., 2008; Suding et al., 2005). In our analysis, most changes in response to individual components were associated with the presence or absence of the component (e.g. presence or absence of grazing). It is well known that grazed and ungrazed or fertilized and unfertilized grasslands differ dramatically (Bai et al., 2010, 2012). However, our results also show thresholds in response to an integrated measure of land use intensity. This suggests that changes in multiple land use components combine to cause an abrupt change in the overall ecosystem state. Global change drivers often occur together, which could result in ecosystem feedbacks and trigger regime shifts that would not occur if these drivers operated independently (Briske et al., 2005; Rillig et al., 2019; Suding et al., 2004). Finally, we identified few thresholds for those functions measured in only 1 year (N retention with LUI, root biomass and potential nitrification with grazing). It is possible that higher sampling effort could led to the identification of more thresholds and provide a more realistic picture of regime shifts in semi-natural grasslands. Altogether, our results confirm the large impact of land use intensification on ecosystems (Newbold et al., 2015, 2016; Thébault et al., 2014), while suggesting the existence of abrupt

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shifts in the diversity of above-ground primary producers and vertebrates, biomass production and nutrient retention in managed temperate grasslands.

4.2 | Early warning signals at ecological thresholds

Early warning signals, such as increasing variability near a threshold, have been suggested as indicators of a system being about to switch between stable states (Kéfi et al., 2014; Scheffer et al., 2009; Scheffer & Carpenter, 2003). Finding evidence for an increase in variance would therefore provide an indication that the thresholds we detected are associated with critical transitions. We found significant increases in spatial variance between plots within the LUI threshold for plants and granivorous birds, suggesting they may experience a critical transition associated with the threshold change in diversity. The same pattern was observed for plants in response to grazing. In addition, temporal variance in plant diversity also increased in the plots within the LUI threshold, providing more support for a critical transition in the plant community. However, several below-ground variables also showed significant increases in variance but not a threshold response, which suggests that an increase in variance may not be a reliable early warning signal. In grasslands, nutrient addition can cause a shift from slow growing, conservative, to fast-growing acquisitive plant species, which is associated with increased productivity and faster soil nutrient cycling (Eskelinen et al., 2020). At the transition between these two states, there may be greater variability in plant functional composition between grasslands, which results in greater variability in various below-ground processes. The existence of a critical transition between plant communities in managed grasslands could have important consequences. Extensively and intensively managed grasslands provide different ecosystem services, and a critical transition between these states would suggest that land use intensity needs to be kept well below the threshold in order to preserve the extensively managed, high-diversity state.

4.3 | Hysteretic responses in the ecosystem

Our results show that LUI thresholds for N retention can depend on whether land use recently increased or decreased. The fact that we found a lower LUI threshold when plots had recently experienced extensification is suggestive of hysteretic dynamics. A lower threshold under extensification indicates that returning to previous functioning levels requires lower land use intensity than that which is needed to change functioning as land use intensifies. Previous studies have suggested hysteretic dynamics in grasslands due to nutrient enrichment after fertilization (Isbell, Tilman, et al., 2013), as nutrients can persist in the soil for many years (Hrevušová et al., 2009; Spohn et al., 2016). This key role of nutrient enrichment aligns with the hysteretic response of N retention to the fertilization gradient. Thus, the slower recovery of nutrient retention, and slower decline in plant productivity, may occur because fast-growing plants can maintain high dominance and productivity for some years after land use is reduced (Baeten et al., 2011). On the other hand, diversity thresholds were not affected by the direction of change in land use, suggesting absence of hysteresis for biodiversity (Figure 4). This may be because diversity responds more slowly than functioning to land use changes (Bommarco et al., 2014; Löffler et al., 2020). We only looked at whether land use intensity had increased or decreased relative to the previous year, which does not test for long-term hysteresis. If diversity needs more time to respond, then land use might need to be reduced for several years before diversity increases again. We were not able to look at longer-term changes in land use as only 4% of plots experienced decreased, and 2% of plots increased, LUI for more than 5 consecutive years. Some studies have suggested that limited intensification can produce optimal biodiversity and functioning in grasslands, where yield is high without a loss of biodiversity (Yang et al., 2018); however, we do not find evidence for this. In our study area, land use extensification (i.e. reducing fertilization while keeping high grazing or mowing levels) will not immediately reduce yield but it will also not support a rapid recovery of diversity. Our results therefore suggest that LUI needs to drop below 1, that is no fertilization and low grazing or mowing, before high-diversity grasslands could be promoted. Finally, as abandonment of grassland management will lead to natural succession and the replacement of these semi-natural grasslands by shrubland and forests, extensive land practices are essential to preserve diverse grasslands (Queiroz et al., 2014). The existence of hysteresis associated with land use reinforces the idea that land use intensity needs to remain well below the threshold to attain successful conservation strategies.

5 | CONCLUSIONS

We found evidence for thresholds in how land use intensification affects above-ground diversity and for a transition from extensively managed grasslands with high above-ground diversity and high soil nutrient retention, to intensively managed grasslands with high biomass production and below-ground fungal diversity, but low above-ground diversity. Identifying these thresholds is key to prevent abrupt declines of biodiversity (LUI should not increase above 1) and to find the optimal, efficient management level allowing high productivity with lowest inputs (a LUI close to 2). In addition, extensively managed grasslands with land use levels below the threshold are priority targets for nature conservation, as it may be more difficult to restore grasslands functioning once the threshold is crossed. Our results highlight the importance of testing for effects of several global change drivers on multiple ecosystem components across many sites and multiple years to account for the high variability in responses that limit our capacity to identify thresholds. As global change drivers can lead to critical transitions, it is important to anticipate them in order to avoid undesirable changes in both diversity and ecosystem functioning.

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AUTHOR CONTRIBUTIONS

Hugo Saiz, Lena Neuenkamp, Caterina Penone and Eric Allan designed the project. Klaus Birkhofer, Nico Blüthgen, Steffen Boch, Michael Bonkowski, Francois Buscot, Anna Maria Fiore-Donno, Markus Fischer, Martin Freitag, Kezia Goldmann, Martin Gossner, Ute Hamer, Norbert Hölzel, Kirsten Jung, Ellen Kandeler, Valentin Klaus, Till Kleinebecker, Sophia Leimer, Sven Marham, Yvonne Oelmann, Jörg Overmann, Daniel Prati, Swen Renner, Sebastian Seibold, Michael Schloter, Ingo Schoening, Johannes Sikorski, Stephanie Socher, Emily Solly, Ingolf Steffan-Dewenter, Barbara Stempfhuber, Catrin Westphal, Wolfgang Wilcke, Tesfaye Wubet and Susanne Wurst collected the data. Hugo Saiz and Caterina Penone assembled the dataset. Hugo Saiz analysed the data; Hugo Saiz, Lena Neuenkamp, Caterina Penone and Eric Allan interpreted the results and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Hugo Saiz is a blog editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

All data is currently available under request in https://www.bexis.uni-jena.de/, within the dataset with id 27087 and 31207. This data will be publicly available following the embargo period. All information regarding data availability is explained in the Data Management Plan document (BE-DMP 2024-Core Project 10—Biodiversity Synthesis), Sections 6 and 7 (see Supporting Information).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Climatic and geomorphological information for the study area.

Table S2. Spearman rank correlation between LUI and individual land use components.

Table S3. Extended information on field surveys used to calculate taxonomic diversity.

Table S4. Extended information on field surveys used to calculate ecosystem functions.

Table S5. Model selection for the effect of LUI and individual land use components on the diversity of multiple taxa and ecosystem functions.

Table S6. Threshold values identified for the diversity of multiple taxa and ecosystem functions.

Table S7. Threshold values considering those plots increasing (intensification) or decreasing (extensification) land use value from the previous year.

Figure S1. Between-year correlation for land use intensity and its individual components.

Figure S2. Threshold responses along individual land use components gradient for different taxa and ecosystem functions.

Figure S3. Variance for the diversities and ecosystem functions along the LUI and its individual components gradients.

Figure S4. Variance in time for diversities and ecosystem functions along the LUI gradient.

Appendix S1. Biodiversity exploratories data management plan.

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