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Spatial scale dependence of plant functional diversity and its response to land-use intensity in grassland farming systems

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ABSTRACT

Land use effects on plant functional diversity have so far been primarily analysed at the local plot scale in semi-natural grassland fields. However, farms represent a focal spatial scale as farmer-specific management decisions across several fields shape the regional trait space. To better understand the scale dependency of plant functional diversity while accounting for regional context, we examined (i) its magnitude across the plot, farm and regional scale and the impact of land-use intensity (ii) at both the plot and farm scale as well as (iii) on farm-to-regional functional dissimilarity in three temperate regions of Central Europe. We quantified functional diversity based on three leaf traits, applying Carmona et al.'s trait probability density framework that incorporates intraspecific variability. Our results show that functional richness increased and divergence decreased from the plot to the farm scale, while evenness showed a unimodal trend across scales. Despite incorporating within-farm heterogeneity by aggregating plot data to the farm scale, hump-shaped effects of grazing and fertilisation on functional richness remained detectable in some regions, but effects were weak and similar to the plot scale. Furthermore, farm-to-regional functional dissimilarity was negatively correlated with farm-level functional richness and consequently increased if farms were grazed very little or not at all. Our findings highlight that farm-to-regional functional dissimilarity, when used in conjunction with farm-level functional richness, can help identify farms with a variety of complementary plant strategies contextualised for a region. This could support conservation planning and assessing the success of eco-schemes implemented within the Common Agricultural Policy.

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1. Introduction

Semi-natural grasslands in Europe, once rich in plant species (Diekmann et al., 2019; Hejcman et al., 2013; Widmer et al., 2025), have been particularly affected by land-use intensification in recent decades (Horka et al., 2025; Wesche et al., 2012). Intensified mowing, grazing and fertilisation aim to maximise fodder production in semi-natural grasslands, but lead to decreasing plant diversity (Andraczek et al., 2023; Balfour et al., 2025; Beckmann et al., 2019; Schulz et al., 2024). A decline in plant species diversity often comes along with a reduced variety of plant functional traits, and, in turn in plant functional diversity, which is predominantly analysed at small spatial scales, at the plot scale (Busch et al., 2018; Van Meerbeek et al., 2014), typically ranging from 1 to 100 m^2. However, changes in biodiversity patterns are scale-dependent (Chase et al., 2018; Pescador et al., 2021). Analyses confined to the plot scale risk overlooking the spatial scales at which management interventions are implemented (Lindborg et al., 2017). To capture land-use intensity effects more comprehensively, functional diversity needs to be analysed at both the plot scale and at the scale of management interventions, thereby reducing the spatial mismatch inherent in social-ecological systems like semi-natural grasslands (Cumming et al., 2006; Gabriel et al., 2010; Pelosi et al., 2010). In Europe, the farm scale represents a key spatial scale for biodiversity research in agricultural landscapes (Ejrnæs et al., 2024; Klaus et al., 2024; Meyer et al., 2025a; Napoleone et al., 2022) since farmers can apply for agricultural subsidies that are regulated in the European Union by the Common Agricultural Policy (CAP) and thus influence management decisions.

The species-area relationship is very well researched for taxonomic diversity (MacArthur and Wilson, 1967; Palmer and White, 1994; Tjørve, 2003) and scale-dependent effects of land-use practices on plant species richness in grasslands are increasingly documented (Bolliger et al., 2025; Buzhdygan et al., 2025; Lepš, 2014; Spiegelberger et al., 2006). A similar but less consistent pattern has been reported for functional diversity, depending on which functional diversity index is considered. For instance, functional richness, defined as the maximum trait space filled (Carmona et al., 2016), tends to increase with area, partly because of its positive correlation with species richness (Dias et al., 2025; Karadimou et al., 2016), although it may saturate more rapidly (Cumming and Child, 2009; Mazel et al., 2014). The evidence for spatial scale effects on functional evenness, representing how traits are distributed according to their abundance within the total trait space, and functional divergence, expressing how the trait abundances are distributed in relation to the centre of the trait space (Carmona et al., 2016), is mixed. A negative functional evenness-area relationship was found by Karadimou et al. (2016). They argue that functional evenness would decrease with scale because the abundance of rare species as well as dominant species increases with area (Karadimou et al., 2016). However, there are also arguments for the opposite direction of the relationship. As the sampling area increases, the relative abundances of species could become more balanced across the metacommunity, particularly when environmental heterogeneity increases, which ultimately can lead to higher functional evenness in the trait space (Passy et al., 2024). So far, the responses of functional evenness and divergence to increasing spatial scale remain poorly understood (Suárez-Castro et al., 2022), especially when accounting for intraspecific variation as is possible by using the trait probability density framework (Carmona et al., 2016). In recent years, it has been possible to analyse patterns in plant functional diversity across entire regions using remote sensing (Rossi et al., 2020; Schneider et al., 2017). However, it remains unclear how functional diversity indices change systematically from the plot to the farm scale and from the farm to the regional scale, highlighting the need for a multi-scale approach (see also Suárez-Castro et al., 2018).

Land-use intensity effects on plant functional traits and diversity have been primarily analysed at the local plot scale (Busch et al., 2018; Pakeman, 2011; Van Meerbeek et al., 2014; Zhang et al., 2023), while only few studies have focused on larger spatial scales (Biswas et al., 2016; de Bello et al., 2013c; Janeček et al., 2013; Laliberté et al., 2013), or even scaling up to whole bioregions (Rosa et al., 2025). Only very few empirical studies have examined the effects of farm-level land-use practices (Carmona et al., 2020; Napoleone et al., 2025) or of different farming regimes, such as organic farming (Goded et al., 2019; Rotchés-Ribalta et al., 2023), on plot-level or field-level functional diversity. However, farm-level land-use intensity effects on farm-level plant functional diversity have not been explicitly investigated to our knowledge.

As mowing and grazing are disturbances affecting plant community dynamics, effects on functional diversity could also be linked to the intermediate disturbance hypothesis, which predicts the highest plant diversity at the intermediate level of disturbance (Connell, 1978). The relationship has been documented for taxonomic diversity in grasslands at the plot (Fulbright et al., 2023), patch (Li et al., 2021), metacommunity (Yuan et al., 2016) and even global scale (Gao and Carmel, 2020). A similar pattern is assumed for functional richness. At the plot scale, extensively managed grasslands were found to harbour high functional evenness, although strong shifts in the community trait structure were found at high grazing intensities (Le Bagousse-Pinguet et al., 2025). Higher grazing disturbance regimes were also found to increase functional divergence (de Bello et al., 2013c), albeit calculated as the functional dissimilarity between co-occurring species in a plot. In contrast, no clear relationship has been found between disturbance and the functional divergence index (Pakeman, 2011). The variation in land-use intensity between grassland fields of the same farm may promote functional diversity, such as sought by diversified farming systems or crop rotation (Sánchez et al., 2022), but has rarely been addressed on farm-level functional richness, evenness and divergence.

Functional diversity can also be conceptualised within the framework of alpha, beta and gamma diversity (Whittaker, 1972), similarly as differentiated for taxonomic diversity. Alpha diversity refers to local scales (diversity within a single habitat), gamma diversity to regional scales (diversity within all habitats) and beta diversity to turnover between communities (dissimilarity between habitats) (Whittaker, 1972). Land-use intensification is known to homogenise plant species composition and thus reduce beta diversity at a given spatial scale (Gossner et al., 2016), but its effects on beta functional diversity across scales remain poorly understood. Functional dissimilarity, quantified by analysing the overlap of traits in a multidimensional space, can be considered as a facet of beta diversity without considering the identities of species and with less context dependence (Carmona et al., 2016; de Bello et al., 2013a). It thus offers a suitable metric to compare the differences in trait spaces between two spatial scales. Comparing farm-level and regional-level trait spaces through functional dissimilarity can therefore provide novel insights into how farm management contributes to the functional diversity of a region.

In this study, we aim to address the spatial scale mismatch between vegetation surveys and farmer-specific management interventions by analysing the effects of land-use practices on plant functional diversity focussing on the management- and socioeconomic-relevant farm scale, while comparing it to the plot and regional scale. Accounting for intraspecific trait variation using the trait probability density framework (Carmona et al., 2016) in combination with a bootstrapping approach (Maitner et al., 2023) to spatially aggregate vegetation data, we first quantify functional richness, evenness and divergence across the plot, farm and regional scale. We then test how mowing, grazing and fertilisation intensity, as well as their spatial variation between plots of the same farm influence functional diversity indices and farm-to-regional functional dissimilarity. Specifically, we test three hypotheses:

H1. Plant functional richness, evenness and divergence vary systematically with spatial scale, differing between the plot, farm and regional scale.

H2. (i) Extensively managed grasslands at the plot and farm scale and

(ii) a greater spatial variation in land-use intensity between plots of a farm are associated with higher functional diversity.

H3. Farms managed less intensively than the regional average exhibit higher functional dissimilarity between farm-level and regional-level trait spaces.

2. Materials and methods

2.1. Study area and design

Our study was conducted in semi-natural grasslands within three German regions belonging to the Biodiversity Exploratories, a large-scale and long-term research platform for functional biodiversity research (Fischer et al., 2010). The regions Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb are located along a north-east to south-west gradient across Germany (Fig. 1a) and differ in climatic, geomorphological and soil conditions. The mean annual temperature across all regions is 6–8.5 °C (Fischer et al., 2010). The elevation (approximately 80 m, 400 m and 700 m) and the mean annual precipitation (approximately 550 mm, 650 mm and 850 mm) increase from north to south (Fischer et al., 2010). The main soil types and the geology of the grasslands are: Histosol in a young glacial landscape in Schorfheide-Chorin; Cambisol on calcareous bedrock in Hainich-Dün; and Leptosol on calcareous bedrock with Karst in Schwäbische Alb (Fischer et al., 2010). Within and across regions, grasslands are subjected to contrasting intensity levels of mowing, grazing and fertilisation (Blüthgen et al., 2012). Although crop fields or meadow margins might also be part of farms in these regions, only grassland fields classified as meadows, pastures or mown pastures were investigated in this study.

We analysed plant functional diversity for seven years at three nested spatial scales, with plots nested in farms and farms nested in regions (Fig. 1a). The smallest unit represented grassland plots (50 $\times$50 m^2). Plots managed by the same farmers were grouped into farms (8–13 farms per year), together building the farm scale (see Franke et al., 2025, for the assignment of plots to farms). Each of the three regions comprised 45–50 plots per year, together representing the regional scale.

2.2. Field data sampling

In each region, vegetation inventories and leaf trait sampling were conducted in 50 permanent grassland plots. Species inventories were recorded annually from 2017 to 2023 in spring (May-June) within 16 m^2 subplots, estimating percentage coverage of all vascular plant species (Hinderling and Keller, 2025). Leaf traits were sampled in spring 2017 and 2018 in these 16 m^2 subplots (Prati et al., 2021) and again in spring and autumn 2020, 2021 and 2023 in three 1 m^2 subplots of selected plots (Meyer et al., 2025b; Fig. 1a). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg. We focused on three leaf traits central to the leaf economics spectrum (Wright et al., 2004): specific leaf area [mm^2 mg^{-1}], leaf area [mm^2] and leaf dry matter content [%]. Trait sampling followed standard protocols (Pérez-Harguindeguy et al., 2013). In 2017–2018, eight plant individuals per species were sampled for the ten most frequent species in each 16 m^2 subplot. In 2020–2023, one individual was sampled for each species with a cover $\geq$ 1% in the 1 m^2 subplots, resulting in up to three individuals per species and plot. After removing species with fewer than six trait measurements, the median of trait measurements per species was 33 and trait measurements of a total of 146 species were included across all regions and years (11719 individuals sampled in 2017–18 and 2111 individuals in 2020–23). The species composition of the most frequent species per plot differed most strongly between Schwäbische Alb and the other two regions, while Schorfheide-Chorin and Hainich-Dün showed more similar dominant species (Fig. S11).

2.3. Land-use practices

Land-use practices were recorded annually through interviews with farmers who owned the grassland fields, where research plots were installed (dataset see Franke et al., 2025; Vogt et al., 2019). The land-use practices applied in grasslands of our study site were mowing, grazing and fertilisation. Mowing was measured as the number of cuts per year. Grazing was measured in livestock units (LSU) multiplied by the number of days that the livestock grazed per hectare and year. Livestock units take the size and age of the cattle, sheep, goats and horses into account (Fischer et al., 2010). The fertilisation intensity was measured as the nitrogen input in kilograms of nitrogen per hectare and year.

Data on these land-use practices were obtained from the LUI calculation tool (see Ostrowski et al., 2020). We calculated the average intensity of the land-use practices for each of the seven observation years (2017–2023) at each of the three spatial scales based on the observation year and the two respective previous years. This temporal averaging led to decimal numbers for the three land-use practices, including mowing which is usually expressed as discrete number of mowing cuts. Land-use intensity was averaged as land-use practices changed between years and because a mean over years is more robust (Blüthgen et al., 2012). Furthermore, to quantify the impact of the spatial variation of land-use intensity within farms, we calculated the coefficient of variation (CV) with the same procedure as for the calculation of the mean. At the plot and farm scale, the mean and spatial variation of land-use practices differed between the regions (Fig. S12). Land-use practices across plots of the same farm were either similar (e.g. only mown fields) or different (e.g. a combination of mown and grazed fields) and the relative proportion of these farm types varied between the regions (Fig. S13).

2.4. Data preparation

The data preparation and main analyses were carried out with the statistical software R version 4.5.1 (R Core Team, 2025) and are described in the following (see also flow chart on procedure in Fig. S10). At first, we anonymised the identification number of farms due to data protection regulations. Plants identified at the species level in the species inventories and leaf trait data were taxonomically harmonised based on the Leipzig catalogue of vascular plants using the 'lcvp' R package (Freiberg et al., 2020). We merged all trait data from the different years to create a comprehensive trait dataset. The merged trait data was then combined with the species abundance data for each year.

We defined the ranges for filtering leaf trait measurements more strictly than the trait ranges described in the protocol of Pérez-Harguindeguy et al. (2013): specific leaf area 1–100 [mm^2 mg^{-1}]; leaf area 1–124,740 [mm^2] (within the size of two A4 sheets); and leaf dry matter content 5–70 [%]. Traits were filtered in these ranges to eliminate measurement errors, e.g. caused by the incomplete rehydration of leaf samples. We standardised the trait values by applying a min-max scaling to the range of 0–1 to give each of the three leaf traits an equal influence in the calculation of the functional diversity indices.

We applied a hierarchical gap filling of the leaf trait data separately at the plot, farm and regional scale using the 'traitstrap' R package (Telford et al., 2023; see also Maitner et al., 2023) to maximise the availability of trait measurements for species following the nested study design, which ensures a similar trait coverage for the spatial units. This approach follows the partial pooling sampling strategy with an extensive sampling effort according to Botta-Dukát and Lukács (2021), providing a realistic and spatially explicit representation of the local vegetation. Leaf trait data of plant species with fewer than six measurements in all regions were removed prior to analysis. If there were fewer than five trait measurements available for the focal spatial scale of a plant species, trait data were added iteratively from higher spatial scales until at least five trait measurements per species were available (for concept see Fig. 1c). We chose the number of five measurements to keep a balance of representing intraspecific trait variation but not to use too many trait

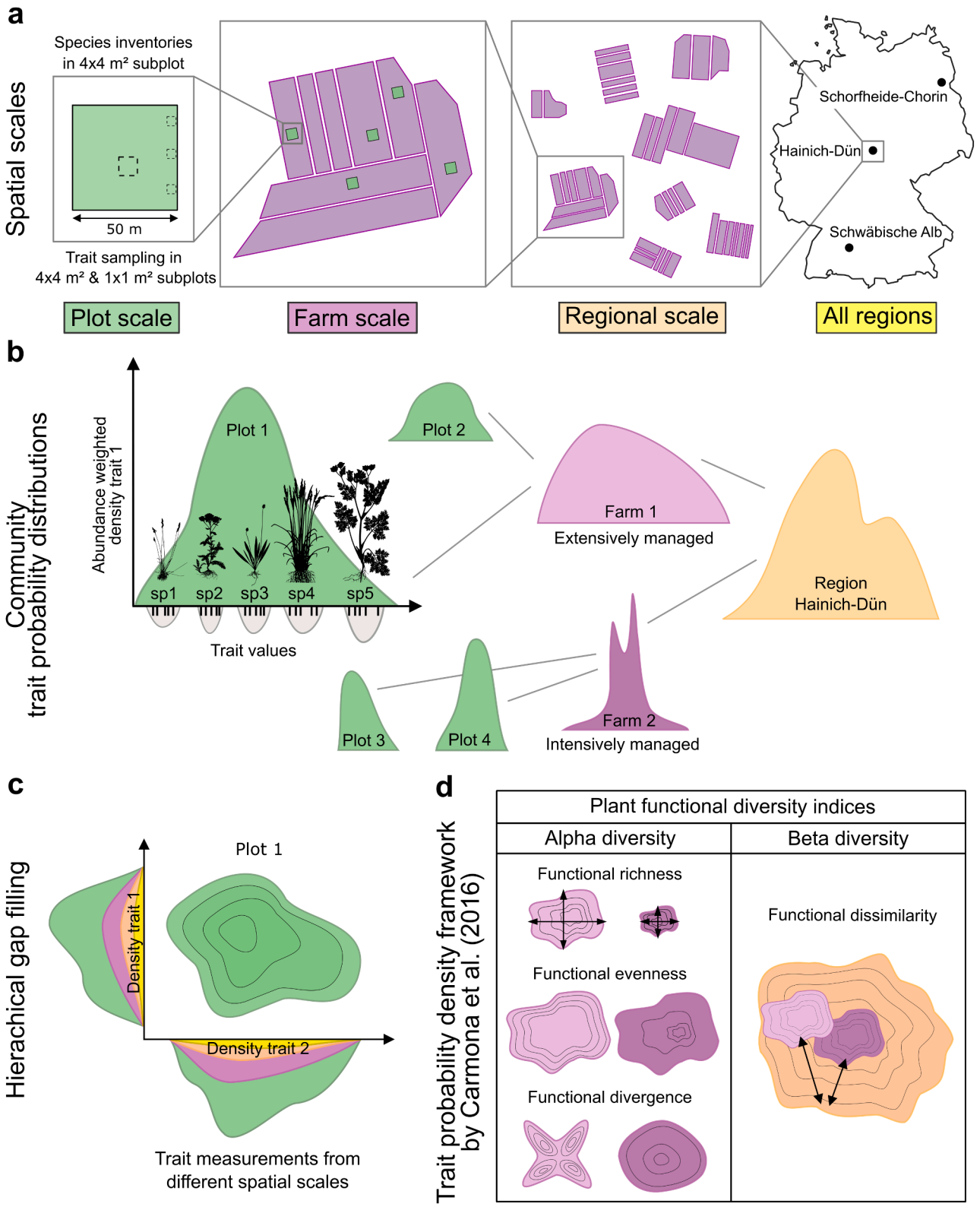

Fig. 1. Conceptual overview for analysing land use effects on functional diversity and functional dissimilarity across spatial scales, using the trait probability density framework (Carmona et al., 2016) in combination with a bootstrapping approach (Maitner et al., 2023). (a) Three nested spatial scales are addressed in this study: the plot, farm and regional scale. (b) Community trait probability distributions are based on a resampling of 200 trait measurements for a respective spatial unit. For example, five trait measurements of five species (sp) make up the distribution for Plot 1. (c) A two-dimensional trait space illustrates how distributions were built based on the trait sampling from different spatial hierarchies using the approach by Maitner et al. (2023) (colours indicate scales). (d) Functional diversity indices and farm-to-regional functional dissimilarity are illustrated from high (left) to low (right) values for an extensively and intensively managed farm, respectively. Source of polygon shape of Germany: © EuroGeographics for the administrative boundaries.

measurements from other than the focal plot, farm or region. To ensure that plant communities were well represented in the trait distribution, we removed plots and farms with less than 75% vegetation coverage with trait measurements for the respective year. This resulted in a high average vegetation coverage with trait measurements of 98% at both the plot and farm scale after the gap filling (for trait coverage after the hierarchical gap filling see Fig. S14). Farms with at least two plots were used. The number of plots per farm as well as the farms per region can vary between years when landowners of plots changed (see Table S10).

For each spatial unit (plot, farm or region at a specific year), the relative cover of each species was divided by the number of trait measurements of a plant species to obtain the probability of a trait value. These probabilities were used to randomly choose 200 trait measurements with replacement to construct trait probability distributions with the same sample size, which were then utilised to calculate functional diversity indices and functional dissimilarity. The sampling of 200 trait measurements was repeated five times with the 'traitstrap' R package (Telford et al., 2023) to account for a random sampling. For each repetition, a trait probability density distribution was constructed and functional diversity as well as functional dissimilarity were calculated. The five repetitions were summarised by calculating the average functional diversity indices and functional dissimilarity.

2.5. Construction of trait probability distributions

The construction of trait probability distributions was based on the 200 sampled trait values and was done with the 'TPD' R package (Carmona et al., 2019) according to the framework developed by Carmona et al. (2016), which can take into account intraspecific trait variation. This approach fitted three-dimensional kernel density estimates to the trait data (each leaf trait representing one dimension; R package 'ks'; Duong, 2007). These kernel density estimates were then transformed into discrete community trait probability distributions. This means that each standardised trait was divided into 50 equal parts, resulting in 50^3 cells of the three-dimensional distribution. As a result, trait probability distributions were constructed for each of the five repetitions, for each spatial unit (plots, farms and regions) and for each year (see Fig. 1b and flowchart Fig. S10).

2.6. Functional diversity indices and functional dissimilarity

We calculated the three functional diversity indices functional richness, evenness and divergence as well as functional dissimilarity based on the trait probability density framework by Carmona et al. (2016) using the 'TPD' R package (Carmona et al., 2019). According to Carmona et al. (2019), functional richness can be interpreted as the width of a one-dimensional trait space or the hypervolume of a multidimensional trait space, functional evenness as how evenly the trait space is distributed and functional divergence as how much mass of the distribution is far away from the centre of the distribution (see also Fig. 1d). More specifically, functional richness was calculated as the sum of the volumes of the cells of the trait probability density distribution that had a probability larger than zero. Functional evenness was calculated for cells with a probability greater than zero and is defined as the sum of the minimum values between the actual probability and an absolute even probability. Functional divergence is derived by multiplying the distance of grid cells from the centre of gravity in the trait space by their probability density and then adding up the results. As all three leaf traits have been standardised to the range [0, 1], the values of all three functional diversity indices lie between 0 and 1, representing low and high diversity, respectively. Functional dissimilarity, as a facet of cross-scale beta diversity, was calculated between farms and the respective region to quantify how dissimilar the trait spaces of farms are compared to the regional trait spaces. The functional dissimilarity is defined as the difference between one and the sum of the minimum probabilities of each grid cells of the two multidimensional trait probability density distributions which are compared (Carmona et al., 2019). Hence, identical distributions have a functional dissimilarity of zero.

2.7. Statistical analysis

For all statistical analyses, we z-transformed all predictors by subtracting the mean and dividing by the standard deviation. We fitted (generalised) linear mixed-effects models using the 'lme4' R package (Bates et al., 2015) with a normal error distribution and an identity link function or a gamma error distribution and a log link function (for model details see below and the repository Meyer and Nößler, 2026). We selected the most appropriate error distribution and link function by visually examining a plot of the actual versus the theoretical quantiles of the residuals (Q-Q plot).

There was one observation for each unit of the respective spatial scale in each of the seven years (2017–2023). Accordingly, our study handles the pseudo replicates by incorporating the unit identity and the year as random intercepts in the mixed-effects models (Table 1).

2.7.1. Spatial scale effects on functional diversity

For testing spatial scale effects on functional diversity (hypothesis 1), we used the spatial scale (plot, farm and region; denoted by β_{scale}) as categorical predictor and the functional richness, functional evenness and functional divergence as response variables in mixed-effects models. We accounted for the repeated sampling by incorporating the unit identity of plots, farms or regions ($u_{ID} \sim Normal(0, \sigma_{ID})$) and year ($v_{year} \sim Normal(0, \sigma_{year})$) as random intercepts. We chose to use generalised linear mixed-effects models with Gamma error distribution and log-link function for functional richness (*FRich*), as the response variable consisted of strictly positive values, many of which were close to zero:

$$FRich_{ID,year} \sim Gamma\left(\exp\left(\beta_{scale} + u_{ID} + v_{year}\right),\ \phi\right) \quad (1)$$

For functional evenness (*FEve*) and functional divergence (*FDiv*) we used instead a normal error distribution with identity link function:

$$FEve_{ID,year}, FDiv_{ID,year} \sim Normal\left(\beta_{scale} + u_{ID} + v_{year},\ \sigma\right) \quad (2)$$

For analysing the region-specific effect of the spatial scale on functional diversity, we additionally used separate models with region-specific coefficients for each spatial scale. We repeated the analysis with generalised additive models to check whether the number of plots, as a continuous variable for the spatial scale, had a similar influence on the functional diversity indices.

We used the 'emmeans' R package (Lenth, 2025) to obtain estimated marginal means of functional diversity estimates for all spatial scales and for all regions. We also calculated pairwise differences in functional diversity indices from plot to farm, from plot to regional and from farm to regional scale, across all regions and for each region separately. Pairwise *t*-tests with Bonferroni correction were performed to assess the significance of the change in functional diversity between scales.

Table 1
Sample size for the statistical analysis at each spatial scale.

Spatial scale	Sample size
Plot scale	N = 45–50 [median: 48] × 3 × 7 (number of plots per region × number of regions × number of years) = 1009
Farm scale	N = 8–13 [median: 9] × 3 × 7 (number of farms per region × number of regions × number of years) = 204
Regional scale	N = 3 × 7 (number of regions × number of years) = 21

2.7.2. Land-use intensity effects on functional diversity from plots to farms

For analysing the effect of land-use practices on functional diversity at the plot and farm scale (hypothesis 2), we fitted generalised linear mixed models with functional richness as response variable (for details on functional evenness and divergence see Appendix S2). We used linear and quadratic predictors of the mean land-use practices based on the assumption that the land-use intensity could have a unimodal influence on functional richness according to the intermediate disturbance hypothesis (Connell, 1978).

At the plot scale, we tested linear mixed-effects models, separately for all regions and within each region:

$$\begin{aligned} FRich_{ID,year} \sim\ & Normal(\beta_0 + \beta_1 \cdot mowing_{linear} + \beta_2 \cdot mowing_{quad} \\ & + \beta_3 \cdot grazing_{linear} + \beta_4 \cdot grazing_{quad} \\ & + \beta_5 \cdot fertilisation_{linear} + \beta_6 \cdot fertilisation_{quad} \\ & + u_{ID} + v_{year},\ \sigma) \end{aligned} \quad (3)$$

At the farm scale, we used generalised linear mixed-effects models with Gamma distributed residuals and a log-link function, including the mean intensity of farm-level land-use practices as well as their variation within farms as predictor variables. The variation of the intensity of each land-use practice within farms is calculated as the coefficient of variation (CV). As the number of plots per farm can influence farm-level functional diversity, we included it as confounding covariate. We fitted separate models across all regions and within each region:

$$\begin{aligned} FRich_{ID,year} \sim\ & Gamma(\exp(\beta_0 + \beta_1 \cdot mowing_{linear} + \beta_2 \cdot mowing_{quad} \\ & + \beta_3 \cdot grazing_{linear} + \beta_4 \cdot grazing_{quad} \\ & + \beta_5 \cdot fertilisation_{linear} + \beta_6 \cdot fertilisation_{quad} \\ & + \beta_7 \cdot mowing_{cv} + \beta_8 \cdot grazing_{cv} + \beta_9 \cdot fertilisation_{cv} \\ & + \beta_{10} \cdot plots\_per\_farm + u_{ID} + v_{year}),\ \phi) \end{aligned} \quad (4)$$

In addition, we tested all models at the farm scale with the same structure, but also included a variable summarising the spatial variation of the abiotic factors elevation, northness (derived from aspect), slope (Nieschulze and Ostrowski, 2023), soil carbon and nitrogen content in the top ten centimetres (Schöning and Klötzing, 2023) as well as a variable for the average geographical distance between grassland experimental plots (Nieschulze and Schulze, 2010) of a farm as a fixed effect. In addition, we tested Spearman's correlations between the abiotic variation variables and the functional diversity indices as well as for the variable distance between plots of a farm.

We used the standard deviations of the three-dimensional leaf trait space as an alternative approach for measuring the filled part of the full potential leaf trait space. For that, we calculated multivariate regressions, analysing the farm-level leaf trait space in response to farm-level land-use intensities (for methodological details see Appendix S3).

2.7.3. Land-use intensity effects on farm-to-regional functional dissimilarity

For analysing the influence of the relative farm-to-regional land-use intensity in response to the functional dissimilarity between farm-level and regional-level trait spaces (hypothesis 3), we constructed generalised linear mixed-effects models. For each of the three land-use practices, we calculated the squared difference between the mean land-use intensity of farms and the mean regional land-use intensity. For standardisation, we divided the squared differences by their standard deviation instead of the z-transformation. For each land-use practice, we split the land-use predictor variables into two by setting farm-level land-use intensities below and above the regional average to zero. This enabled the fitting of two quadratic coefficients for each land-use practice. Additionally, we used the z-transformed number of plots per farm as a covariate in the linear model, as functional richness increased and functional dissimilarity decreased with the number of plots per farm (see Fig. S18). We accounted for the repeated sampling by including farm identities and year as random intercepts. We used generalised linear models with Gamma error distributions and log link functions, fitting separate models across all regions and within each region:

$$\begin{aligned} FDiss_{ID,year} \sim\ & Gamma(\exp(\beta_0 + \beta_1 \cdot mowing_{low}^2 + \beta_2 \cdot mowing_{high}^2 \\ & + \beta_3 \cdot grazing_{low}^2 + \beta_4 \cdot grazing_{high}^2 \\ & + \beta_5 \cdot fertilisation_{low}^2 + \beta_6 \cdot fertilisation_{high}^2 \\ & + \beta_{10} \cdot plots\_per\_farm + u_{ID} + v_{year}),\ \phi) \end{aligned} \quad (5)$$

As a robustness check of the generalised linear models with quadratic coefficients, we repeated the analysis with generalised additive models, which are more flexible in the shape of the response curve (for methodological details see Appendix S4).

3. Results

3.1. Spatial scale effects on functional diversity

We detected increasing functional richness across all three scales as well as increasing functional evenness and decreasing functional divergence from the plot to farm scale. There was a tendency towards decreasing functional evenness from the farm to regional scale and a tendency towards decreasing functional divergence from the plot to regional scale (Fig. 2). The same trends of the functional diversity indices were observed when considering all regions together and separately. Furthermore, the pattern was similar when the spatial scale was represented by the number of plots as a continuous variable in the generalised additive models (Fig. S17).

We found that functional richness increased twofold from the plot to the farm scale across all regions (Fig. 2; Table S11). Furthermore, functional richness increased fourfold from the plot to regional scale. However, no significant difference was detected from the farm to the regional scale. When additionally including regional effects, we found that functional richness increased threefold from the plot to the farm scale in Schorfheide-Chorin and twofold in Hainich-Dün, albeit not in Schwäbische Alb (Table S12). Only in Schorfheide-Chorin there was additionally a sixfold increase of functional richness from the plot to regional scale. Functional richness was positively correlated with species richness (rho 0.39***) and Pielou's evenness (rho 0.58***) across scales, regions and years (Fig. S15).

Functional evenness was predicted to slightly increase by 4% from the plot to the farm scale (Fig. 2; Table S11). This slight increase in functional evenness from the plot to the farm scale was detectable only in Schorfheide-Chorin and Hainich-Dün (Table S12). Functional evenness was positively correlated with species richness (rho 0.53***) and Pielou's evenness (rho 0.42***) across scales, regions and years (Fig. S15). In contrast, functional divergence decreased by 5% from the plot to farm scale across all regions (Fig. 2; Table S11). This pattern was only detected in Schorfheide-Chorin, where functional divergence decreased by 4% (Table S12). Functional divergence was not correlated with species richness or Pielou's evenness (Fig. S15).

3.2. Land-use intensity effects on functional diversity from plots to farms

Functional richness varied along the grazing and fertilisation intensity gradients as well as with the spatial variation of fertilisation intensity at the farm scale in the regions Hainich-Dün and Schwäbische Alb (Fig. 3b; estimates and model fit statistics in Table S1). However, the models that included all three regions did not reveal a change in functional richness. At the plot scale, we additionally found effects of the mowing intensity on functional richness in Schorfheide-Chorin and Schwäbische Alb, although the regions showed opposite directions (Fig. 3a; estimates and model fit statistics in Table S2). We found a trend of a hump-shaped relationship between farm-level grazing intensity and functional richness in the model that included all regions. However, the quadratic estimate was only statistically different from zero in Schwäbische Alb. This hump-shaped pattern was also evident in the leaf trait space regression across all regions, where specific leaf area and leaf dry matter content responded nonlinearly to farm-level grazing intensity

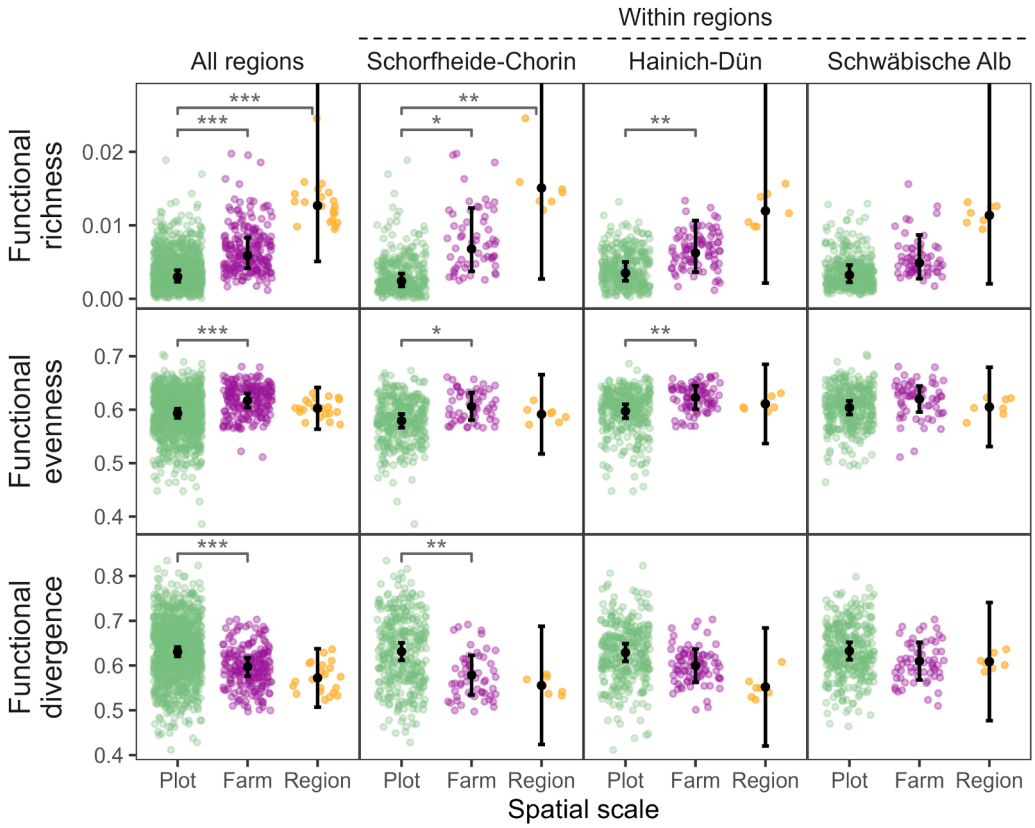

Fig. 2. Functional diversity indices based on the three leaf traits specific leaf area, leaf area and leaf dry matter content across the plot, farm and regional scale. For each index, separate models were fitted across all regions and for each region. One point refers to an observation year. Significant marginal pairwise differences of functional diversity indices between scales are indicated according to the significance levels $p < 0.05$*, $p < 0.01$** and $p < 0.001$*** and all results are reported in Tables S11 and S12. Changes in variance of functional diversity indices across scales and regions are visible with kernel density estimations shown in Fig. S16.

(Fig. 4; see more detailed results in Appendix S3). The plot-level grazing intensity had only a positive linear effect in Schwäbische Alb. Farm-level fertilisation showed a hump-shaped relationship with functional richness in Hainich-Dün, while there was only a positive linear effect in Schwäbische Alb. In Hainich-Dün, plot-level fertilisation had a negative linear effect on functional richness. However, in Schorfheide-Chorin we found a hump-shaped relationship between plot-level fertilisation and functional richness, as also detected in Hainich-Dün at the farm scale. Furthermore, we identified that a higher variation of fertilisation between plots of the same farm led to a higher functional richness in Hainich-Dün and Schwäbische Alb.

Models that additionally tested the effects of both abiotic variation and distance between plots at the farm scale showed collinearity between the number of plots per farm and the distance between plots. The main models were therefore compared with models that only included abiotic variation as additional fixed effect. However, abiotic variation had no significant influence on the functional diversity indices and its inclusion did not substantially improve model quality based on AIC comparisons (Tables S3, S6 and S9). Furthermore, neither the distance between plots nor the within-farm spatial variation of abiotic factors was significantly correlated with any functional diversity index (Fig. S3).

We detected no influence of plot-level and farm-level land-use practices on functional evenness as well as no effects of the spatial variation of land-use practices within farms (see more detailed results in Appendix S2: Fig. S1; Tables S4 and S5). However, functional divergence showed a negative linear response to fertilisation in Schorfheide-Chorin at the plot scale, while there were no land use effects detectable at the farm scale (see more detailed results in Appendix S2: Fig. S2; Tables S7 and S8).

3.3. *Land-use intensity effects on farm-to-regional functional dissimilarity*

A higher difference between the farm-level and regional-level intensity of land-use practices was associated with an increased farm-to-regional functional dissimilarity in the leaf trait space (Fig. 5). The quadratic estimates for the three land-use practices were predominantly positive in the statistical models, albeit not always statistically significant, and even some quadratic estimates were negative (Table S13).

A trend can be detected that one unit decrease in the relative land-use intensity was associated with a stronger increase in the farm-to-regional functional dissimilarity compared to one unit increase in the relative land-use intensity. In three of the four models tested, it was most evident that farms not grazed at all or with very few livestock units were linked to a greater increase of farm-to-regional functional dissimilarity than farms that were grazed more intensively compared to the regional average (Fig. 5). The analysis with generalised additive models led to similar results (Fig. S9; see more detailed results in Appendix S4). Regarding farms with a relatively higher land-use intensity compared to the regional average, we found lower farm-to-regional functional dissimilarity. This was most visible for the mowing and fertilisation intensity in the region Schwäbische Alb and as a trend for mowing across all regions (Fig. 5).

Farm-to-regional functional dissimilarities were largely consistent across regions, with median differences below 7% (Fig. S18a). The farm-to-regional functional dissimilarity decreased as the number of plots per farm increased (rho −0.57*** across regions; Fig. S18b), but was not negatively correlated with an increasing distance between plots of a farm (Fig. S18c). Farm-level functional richness was strongly negatively correlated with farm-to-regional functional dissimilarity (rho −0.69***; Fig. S18d). Moreover, farm-to-regional functional dissimilarity was

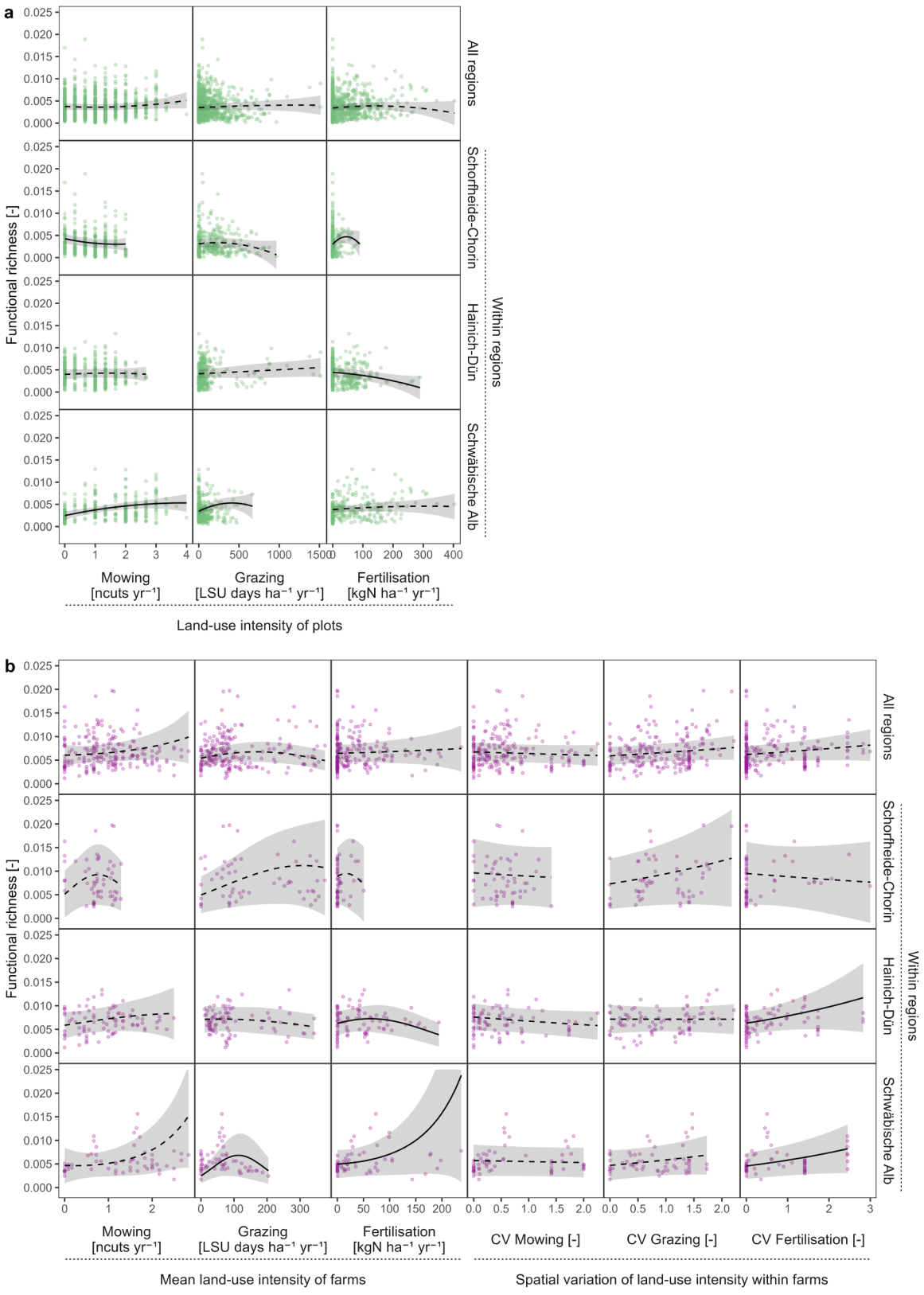

Fig. 3. Effects of the three-years average intensity of mowing, grazing and fertilisation on functional richness in (a) plots and (b) farms, as well as the effects of the spatial variation of land-use intensity within farms quantified as coefficient of variation (CV). Rows represent separate mixed-effects models based on all regions together (top row) and regional subsets, with standardised predictors that were back transformed to the original scale for interpretability. Solid regression lines indicate significant linear or quadratic coefficients ($p < 0.05$) and shaded areas represent 95% confidence intervals. Model fit statistics of the standardised predictors are reported in Table S1 (farm scale) and Table S2 (plot scale).

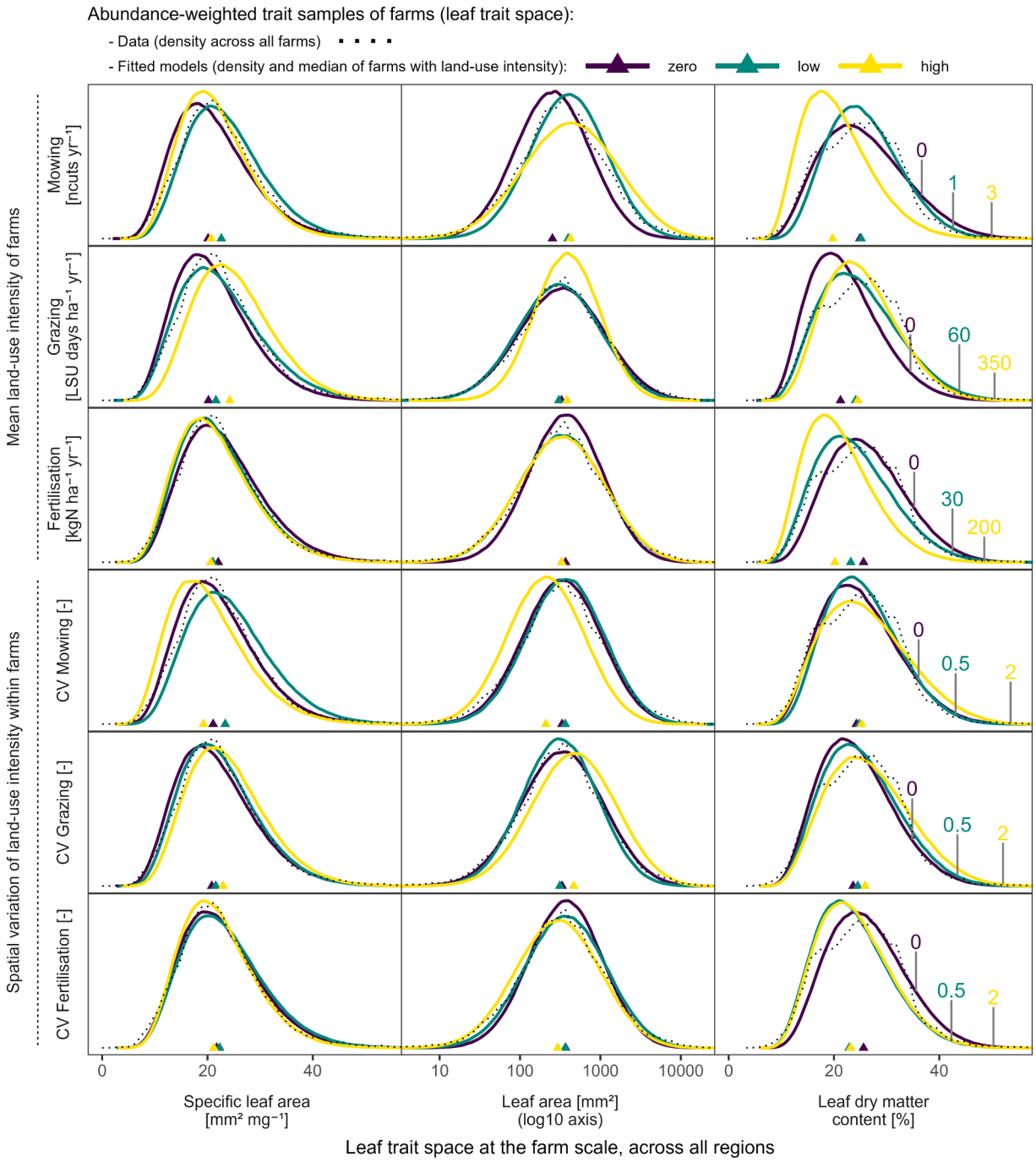

Fig. 4. Marginal (one-dimensional) density distributions of leaf trait spaces, derived from the trait space regressions, show responses to the mean intensity of mowing, grazing and fertilisation as well as their spatial variation at the farm scale across all regions. The width of the distributions can be interpreted similarly to functional richness. Separate models were fitted for the mean and coefficient of variation (CV) of each land-use practice (in rows). The predictor values used to create the marginal distributions show zero, low and high intensities in the subpanels on the right, each in a different colour and with the respective value. Methodological details on the trait space regression and two-dimensional density plots are reported in Appendix S3.

negatively associated with the average difference between farm-level and regional-level specific leaf area and leaf area, whereas positively correlated with the average difference of leaf dry matter content (Fig. S18e).

4. Discussion

Our study demonstrates that plant functional diversity varies across spatial scales. However, our multi-scale analysis of the effects of land-use intensity on plant functional diversity showed weak and similar effects at both the plot and farm scale, partly due to region-specific responses. Importantly, by using a cross-scale approach that compares trait spaces between the farm and regional scale, which has not yet been implemented in empirical studies to our knowledge, we revealed stronger and more consistent land-use intensity effects across regions. In this regard, we identified a trend of increasing farm-to-regional functional dissimilarity when farms were grazed less intensively compared to the regional average intensity.

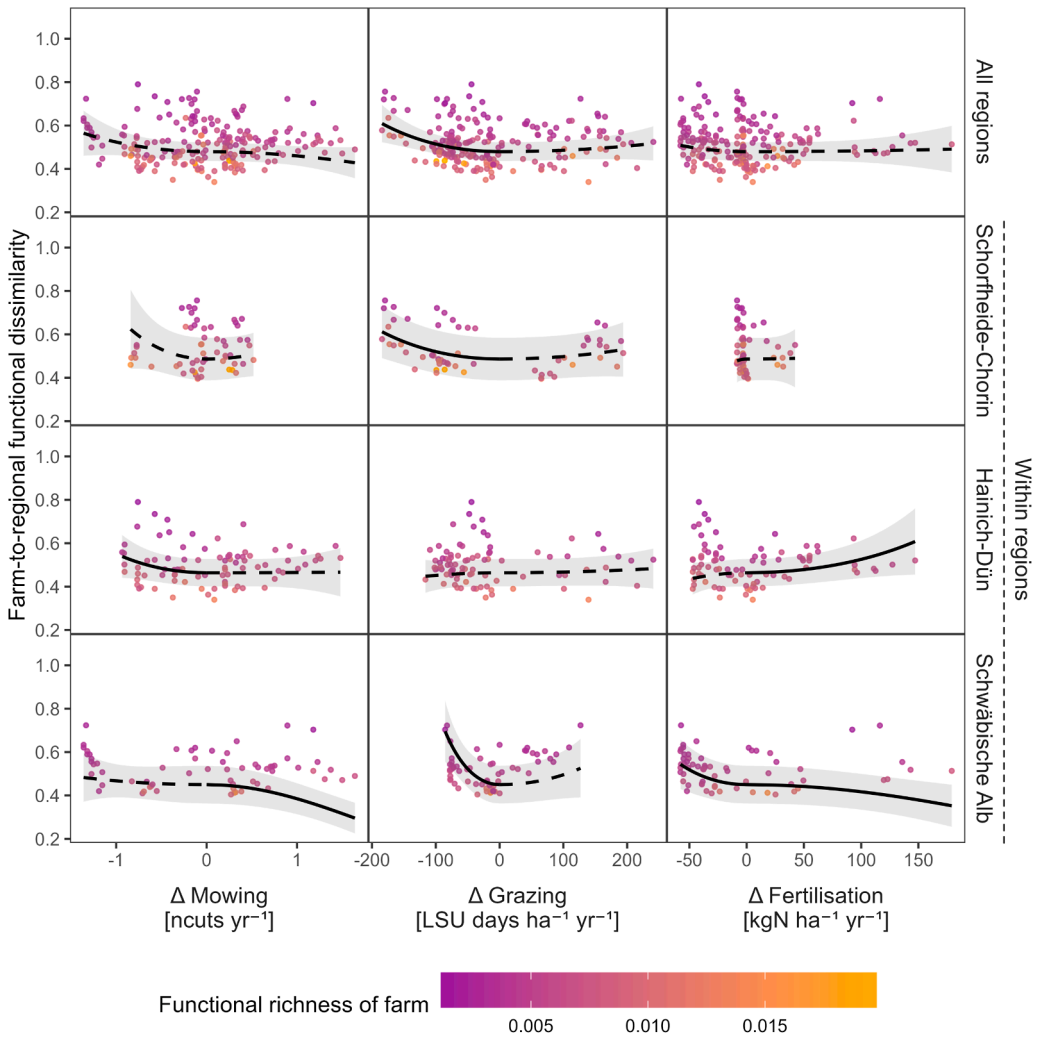

Fig. 5. Farm-to-regional functional dissimilarity in response to the difference between the farm-level and regional-level average of mowing, grazing and fertilisation intensity. Each land-use practice was split into two predictors, i.e. below and above the regional average intensity, to distinguish between farms that are managed more extensively than the regional average and farms that are managed more intensively. Four models were fitted, one across all regions (top row) and one for each region. Partial regression lines above or below the regional average intensity are solid if the quadratic coefficient of the land use predictor is significant ($p < 0.05$). Model fit statistics are reported in Table S13.

4.1. Spatial scale effects on functional diversity

We found that the functional diversity indices richness, evenness and divergence altered from the plot to the farm scale, confirming our first hypothesis that functional diversity is scale-dependent. However, no significant differences were observed between the farm and the regional scale, likely due to the limited number of aggregated values at the regional scale, where aggregation may also have led to information loss (Clark et al., 2011) and greater statistical uncertainty.

We provide evidence for a twofold increase of functional richness from the plot to the farm scale (2–13 plots aggregated) and a fourfold increase from the plot to the regional scale (50 plots aggregated) across all regions. This represents a substantial increase from the plot to farm scale compared with regional-level functional richness and indicates that farms contribute substantially to the hypervolume of the regional trait space. Aggregating a higher number of plots, which increases the spatial extent and grain, may result in a greater variety of environmental conditions and different land-use intensities, ultimately increasing the hypervolume of the trait space due to the variety of niches supplied (Blonder, 2018). Our findings align with a positive functional richness-area relationship reported by Karadimou et al. (2016) and with a positive association between functional richness and species richness, observed by Pakeman (2011). The positive relationship between taxonomic diversity and spatial scale, described by the species-area relationship (MacArthur and Wilson, 1967; Palmer and White, 1994), was therefore proven to also apply to functional richness in our study, similar to what Suárez-Castro et al. (2022) had expected for the relationship between functional richness and species richness.

Our results showed a hump-shaped trend of functional evenness across spatial scales. We found a slight increase of evenness from the plot to farm scale and a non-significant trend of slightly decreasing evenness from the farm to regional scale, which partly aligns with the results by Karadimou et al. (2016), who reported a negative functional evenness-area relationship. Our findings also fit to the theory by Hillebrand et al. (2008) that regional species evenness is lower in anthropogenically shaped habitats due to reduced heterogeneity and dominant species. The detected hump-shaped trend in our study can be attributed to ecological assembly processes, for which environmental variation and dominance effects play a role (Hillebrand et al., 2008; Weiher et al., 2011). At the plot scale, priority effects as part of assembly processes, where the order and timing of species arrivals shape the local dominance, can lead to divergent plant communities even under similar abiotic conditions (Chase, 2003; Fukami, 2015; Stroud et al., 2024). We conclude that the inclusion of multiple species and thereby a decreased

dominance can lead to a more even filling of the trait space at the intermediate large farm scale. However, at the regional scale, certain environmental conditions and land-use practices might dominate and select specific traits, leading to high densities in one part of the trait space.

We found that functional divergence decreased by 5% from the plot to the farm scale. This fits to the conclusion by de Bello et al. (2013c) that divergence, quantified as functional dissimilarity of co-occurring species, is mainly driven by competition at smaller spatial scales, while environmental filtering acts at larger spatial scales. Karadimou et al. (2016) reported a case-specific functional divergence-area relationship. A decrease of functional divergence at the larger farm scale could also be a result of an underlying sampling effect, whereby larger areas have a greater probability of including species with similar, centrally clustered traits. This is similar to what is theorised by Suárez-Castro et al. (2022) for the relationship of functional divergence and species richness. However, sampling intensity, which also increases with spatial scale, was reported to be less influential for functional divergence and dispersion compared to evenness and richness (van der Plas et al., 2017).

4.2. Land-use intensity effects on functional diversity from plots to farms

Our findings suggest that the influence of land-use intensity on functional diversity was rather weak at both the plot and farm scale and not consistent across regions. Accordingly, we could not clearly confirm or reject our second hypothesis that (i) functional diversity is highest in extensively managed grasslands at the plot and farm scale and (ii) that functional diversity increases with greater spatial variation of land-use intensity within farms. Nevertheless, some region-specific results of land-use intensity effects on functional richness are consistent with our hypothesis. In the Schwäbische Alb region, functional richness was highest under extensive grazing intensity, as demonstrated at both the plot and farm scale. However, this pattern was not detectable in the other two regions nor with regard to mowing and fertilisation. Moreover, we found that a higher spatial variation of the fertilisation intensity within farms was associated with greater functional richness in the Hainich-Dün and the Schwäbische Alb regions, but not in the Schorfheide-Chorin region, which had a quite homogeneous fertilisation regime. The variation of mowing and grazing intensity within farms had no effect on functional richness in any of the three regions. The other indices functional evenness and functional divergence showed no effects in response to land-use intensity and their spatial variation at the farm scale. This aligns with the study of Rosa et al. (2025), who demonstrated that land use had a stronger impact on functional richness than on functional evenness and divergence in northern bioregions.

Our results provide support for the intermediate disturbance hypothesis (Connell, 1978) in one of the three regions. In the Schwäbische Alb region, functional richness was highest at intermediate grazing intensity at both the plot and farm scale (Fig. 3). Similarly, the standard deviation of specific leaf area and leaf dry matter content showed a hump-shaped response to farm-level grazing intensity across all regions (Fig. 4). This region-specific finding implies that farms with very intensive grazing are homogenising plant communities by selecting few disturbance-tolerant species with similar traits (Buzhdygan et al., 2020; Grime, 1973; Laliberté et al., 2013). Similarly, Laliberté et al. (2013) reported that the trait space was almost filled at low productivity, while an increased productivity decreased functional variation at the metacommunity scale.

At the farm scale and across regions, leaf trait shifts were predominantly detected at the lower end of the land-use intensity gradient, as has been shown for shifts in community structure at distinct intensity thresholds (Le Bagousse-Pinguet et al., 2025). This shift was particularly clear in the trait space regression at the farm scale for leaf dry matter content (Fig. 4 and Fig. S5), which decreased with mowing intensity. This is in line with the findings of Busch et al. (2018), who reported a decrease of the functional diversity index Rao's Q of the leaf dry matter content in response to the mowing intensity at the plot scale.

Scaling up from plots to farms, while accounting for the spatial heterogeneity in land use and abiotic factors, still revealed land-use intensity effects on functional richness in some regions, but effects were rather weak and comparable between the plot and farm scale. Although there is evidence that environmental filtering effects on the diversity of plant functional traits are scale-dependent (Biswas et al., 2024; de Bello et al., 2013b, 2013c; Carmona et al., 2020; Laliberté et al., 2013), our results did not allow us to conclude such scale dependence for land-use intensity effects. Hence, our study cannot validate the theoretical presumption of land use effects being more pronounced at increasing spatial scales because environmental heterogeneity effects become less influential at larger spatial scales (Wiens, 1989) through the statistical averaging effect (Doak et al., 1998). Correlation analyses and models that additionally included within-farm abiotic variation showed no significant effects on the functional diversity indices, although it was assumed that the spatial heterogeneity at the farm scale influences the availability of different niches (Blonder, 2018) and thus also the variety of functional strategies (Biswas et al., 2024).

We suspect that aggregating plots with a homogeneous management regime reveals stronger patterns at the farm scale, whereas aggregating heterogeneously managed plots might obscure site-specific effects and thus may show weaker patterns. Disentangling the interactive effects of land-use intensity variation and abiotic variation requires further investigation to understand underlying effects of farm-level land-use intensity on plant functional diversity when aggregating plot-level data.

4.3. Land-use intensity effects on farm-to-regional functional dissimilarity

Our cross-scale analysis, which compared trait spaces between the farm and regional scale, revealed a trend of higher farm-to-regional functional dissimilarity for farms with a grazing intensity below the regional average (i.e. farms with no or very little grazing). This is consistent with our third hypothesis that farms with a lower land-use intensity than the regional average exhibit higher farm-to-regional functional dissimilarity. However, no clear patterns were found regarding mowing and fertilisation intensity due to the rather weak and inconsistent responses of functional dissimilarity across regions. Region-specific responses to extensification were also found by Schreiner et al. (2026), who analysed trait distribution moments in an extensification experiment in the same grassland fields as in our study. For instance, nutrient availability is especially high in the Schorfheide-Chorin region due to historically drained peatland (Blüthgen et al., 2012; Klaus et al., 2011) and thus eliminates the demand for a high fertilisation intensity. Such regional specificity could explain why we were unable to detect consistent effects related to fertilisation intensity on the functional dissimilarity in our study.

We demonstrated that narrower farm-level trait probability density distributions, which manifest themselves in lower farm-level functional richness, have a higher farm-to-regional functional dissimilarity. This is in accordance with remarks by Blonder (2016) and Carmona et al. (2019) that if one distribution is much narrower than the other, the dissimilarity between these two will be high. Similarly, according to Chase (2003), the dissimilarity between a local unit (here, the farm trait space considered as alpha diversity) and the region (here, the regional trait space considered as gamma diversity) is strongly influenced by how large the regional species pool is. The patterns of land-use intensity effects on farm-level functional richness were consequently also reflected in our analysis of the farm-to-regional functional dissimilarity. For instance, farm-level functional richness increased from no grazing to extensive grazing in the region Schwäbische Alb, while the farm-to-regional dissimilarity decreased sharply from no to the regional average grazing intensity. Nevertheless, it should be noted that even if there is a strong correlation between farm-level functional richness and

farm-to-regional functional dissimilarity, the latter also encompasses information on shifts in the trait space at the farm scale in relation to the regional trait space and thereby includes regional context dependency. Hence, we believe that the farm-to-regional functional dissimilarity, combined with farm-level functional richness, can help prioritise management interventions by identifying farms that constitute conservation potential for maintaining high regional functional diversity.

4.4. Limitations and outlook

In this study, we address the spatial mismatch between the farm scale (where farmers plan management interventions) and the plot scale (where vegetation surveys are conducted) by explicitly investigating plant functional diversity at the farm scale. However, it must be stressed that this scale can conflict with the scale of ecological organisation, since organisms do not follow arbitrarily defined spatial boundaries (Chave, 2013; Levin, 1992).

Our analysis was limited to three leaf traits. Thus, it should be emphasised that the choice of traits could influence functional diversity and its ecological implications differently (Zhu et al., 2017). In addition, semi-natural grasslands in the Biodiversity Exploratories study regions are generally more extensively managed than the average land-use intensity of other federal states in Germany (Reinermann et al., 2023), resulting in an uneven distribution along the land-use intensity gradient. A steeper gradient and a larger sample of grassland farms would likely reveal stronger and more significant effects on farm-level plant functional diversity and farm-to-regional functional dissimilarity. Moreover, the actual association of plots to a respective farm might be incomplete, as some farms can include additional fields not covered by permanently installed research plots and vegetation surveys.

We recommend that future studies should investigate plant functional diversity at the farm scale using designs that encompass a larger sample of farms with their entire field composition, include field data from several (bio)regions with various management regimes and incorporate additional plant traits to capture manifold functional strategies within the trait space. Furthermore, it would be interesting to compare effects of abiotic variation and land use on the functional dissimilarity among plots within farms and among farms to complement our study's findings on facets of alpha diversity and cross-scale beta diversity at the management- and socioeconomic-relevant farm scale.

5. Conclusion

Our study contributes to filling the gaps in understanding land-use intensity effects on plant functional diversity by explicitly considering intraspecific trait variation and comparing diversity across spatial scales through the implementation of the trait probability density framework (Carmona et al., 2016) in combination with a bootstrapping approach (Maitner et al., 2023).

We provide evidence that functional richness and evenness increased, while functional divergence decreased from the plot to farm scale in managed semi-natural grasslands. However, we did not find evidence for scale-dependent effects of land-use intensity on plant functional diversity at the plot and farm scale, as effects were weak and inconsistent across regions. Using a cross-scale approach that explicitly compares farm-level and regional-level trait spaces, which has not yet been investigated to our knowledge, we identified more consistent patterns of farm-to-regional functional dissimilarity in response to farm-level grazing intensity across regions. This shows that our cross-scale approach between the farm and regional scale revealed clearer and stronger patterns of land-use intensity effects in contrast to our multi-scale approach at the plot and farm scale. Moreover, we detected that farm-to-regional functional dissimilarity was highly negatively associated with farm-level functional richness. Findings of our study underscore the necessity to investigate land-use intensity effects on plant functional diversity at multiple as well as across spatial scales, rather than limiting analyses to the plot scale.

Further investigation of the farm scale as focal scale of analysis in social-ecological systems like semi-natural grasslands offers a pathway towards farm-targeted assessments and scale-aware policy design for optimising land-use practices that promote plant functional diversity within a regional context. Maximising both farm-level functional richness and farm-to-regional functional dissimilarity along the trade-off between these two diversity facets, in addition to a qualitative assessment of the species composition, could help identify farms with a high diversity of complementary plant strategies. This information could further be used to harmonise the planning of management practices and conservation measures across individual farms. Furthermore, this combined approach provides potential for assessing the success of eco-schemes implemented through the Common Agricultural Policy, such as by quantifying a farm's contribution to the regional trait space after farm-level livestock density has been reduced.

CRediT authorship contribution statement

Sophia N. Meyer and **Felix Nößler** contributed equally to the work and share first authorship. **Sophia N. Meyer:** Writing – original draft, Writing – review & editing, Conceptualization, Investigation, Data curation, Methodology, Formal analysis, Software, Validation, Visualization, Project administration. **Felix Nößler:** Writing – original draft, Writing – review & editing, Conceptualization, Investigation, Data curation, Methodology, Formal analysis, Software, Validation, Visualization. **Oksana Buzhdygan:** Writing – review & editing, Conceptualization, Supervision. **Felix May:** Writing – review & editing, Conceptualization, Supervision. **Lisa-Maricia Schwarz:** Writing – review & editing, Investigation, Data curation. **Judith C. Niedersen:** Writing – review & editing, Investigation, Data curation. **Javier Muro:** Writing – review & editing, Investigation. **Olena Dubovyk:** Writing – review & editing, Project administration, Funding acquisition. **Britta Tietjen:** Writing – review & editing, Supervision, Conceptualization. **Anja Linstädter:** Writing – review & editing, Conceptualization, Supervision, Investigation, Project administration, Funding acquisition.

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Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Writefull in order to improve the language of the text. After using this service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110475.

Data availability

This work is based on data elaborated by the project Sensing Biodiversity Across Scales (SeBAS) and the Botany core project of the Biodiversity Exploratories program (DFG Priority Program 1374). Raw and processed data and all scripts to reproduce the results can be found on Zenodo with the doi: 10.5281/zenodo.17062118 (Meyer & Nößler, 2026). The raw data files can be also found in the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q) with the dataset IDs 31893 version 3 (Vegetation records for grassland EPs, 2008 - 2024), ID 24807 version 2 (Leaf traits of most abundant plant species from all EPs, 2017/2018), ID 31971 version 1 (Plant trait measurements from grassland experimental plots (2020–2023)), ID 31501 version 6 (Topographical parameters (slope, aspect, elevation) for all forest and grassland experimental plots (EP)) and ID 31655 version 5 (Soil carbon, nitrogen and sulfur concentrations - soil sampling campaign 2021, all experimental plots (EPs), 0-10 cm). The mowing, grazing and fertilisation intensities are based on information from the landowners (Vogt et al., 2019) and were downloaded with the land-use intensity (LUI) calculation tool (Ostrowski et al., 2020) from the Biodiversity Exploratories Information System. Due to privacy concerns, we cannot publish the dataset with ID 10462 (EP-polygon) and ID 31767 (Land use in grasslands: raw data from annual landowner interviews - revised in 05/2024). We additionally anonymised the assignment of plots to farms, originating from the dataset ID 31767. Polygon data on borders of Germany were used for the illustration of the study sites in Germany for Figure 1a: © EuroGeographics for the administrative boundaries. The icons used for Figure 1b originate from Phylopic (https://www.phylopic.org/) and all have the CC0 1.0 Universal Public Domain Dedication license.

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