

LETTER

Disentangling direct and indirect drivers of farmland biodiversity at landscape scale

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Abstract

To stop the ongoing decline of farmland biodiversity there are increasing claims for a paradigm shift in agriculture, namely from conserving and restoring farmland biodiversity at field scale (α -diversity) to doing it at landscape scale (γ -diversity). However, knowledge on factors driving farmland γ -diversity is currently limited. Here, we quantified farmland γ -diversity in 123 landscapes and analysed direct and indirect effects of abiotic and land-use factors shaping it using structural equation models. The direction and strength of effects of factors shaping γ -diversity were only partially consistent with what is known about factors shaping α -diversity, and indirect effects were often stronger than direct effects or even opposite. Thus, relationships between factors shaping α -diversity cannot simply be up-scaled to γ -diversity, and also indirect effects should no longer be neglected. Finally, we show that local mitigation measures benefit farmland γ -diversity at landscape scale and are therefore a useful tool for designing biodiversity-friendly landscapes.

KEYWORDSabiotic conditions, agricultural intensification, biodiversity, ecological focus area, farmland γ -diversity, landscape composition, landscape configuration, landscape design, multi-trophic species richness**INTRODUCTION**

Biodiversity is declining worldwide and intensified agricultural practices are considered to be one of the major drivers of this decline (IPBS, 2019). On the one hand, intensified management practices, such as increased fertiliser and pesticide inputs, have reduced biodiversity (Kleijn et al., 2009). On the other hand, to facilitate management, semi-natural landscape elements have been removed (Benton et al., 2003), which has simplified landscape complexity with negative consequences for biodiversity (Clough et al., 2014; Le Provost et al., 2021).

To counteract the negative effects of intensified agricultural practices on biodiversity, various conservation measures were implemented. However, despite

considerable efforts, we continue to lose farmland species (Díaz et al., 2019). As most previous efforts to conserve farmland biodiversity focused on biodiversity at local scale (i.e. biodiversity measured on a field patch), there is growing consensus that conservation efforts should additionally incorporate processes that affect farmland biodiversity at a larger scale (Ekroos et al., 2016). Accordingly, several recent studies called for conservation measures being designed from a landscape perspective (Landis, 2017; Tschardt et al., 2021). To meet these calls, knowledge on how intensified agricultural practices and other factors affect farmland biodiversity at the landscape scale are needed. Yet, studies on farmland biodiversity at the landscape scale are rare (but see Bennett et al., 2006; Billeter et al., 2007; Hendrickx

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et al., 2007; Dufлот et al., 2017; Zingg et al., 2019). Further, these studies, to the best of our knowledge, focus on the direct effects of drivers of farmland biodiversity only and neglect indirect effects.

Diversity at the landscape scale can be defined as γ -diversity (Lecoq et al., 2022), which is shaped by the local-scale biodiversity measured on a field patch (i.e. α -diversity), and the variation in species composition between different field patches (i.e. β -diversity). According to theory, α -diversity is largely determined by local abiotic conditions, land use and biotic interactions, as well as by landscape factors (e.g. Concepción et al., 2012). In contrast, β -diversity is largely determined by the diversity of resources and microclimates in a landscape (Mori et al., 2018). Accordingly, γ -diversity is most likely affected by all those factors, suggesting that the importance of factors known to affect farmland biodiversity varies between α - and γ -diversity. This idea is supported by for example Gossner et al. (2016), who found a moderate increase in land-use intensity to have a weak effect on α -diversity of belowground taxa, but to strongly reduce β -diversity.

As factors may affect α - and γ -diversity differently, local-scale management efforts to conserve and promote α -diversity might even have negative effects on γ -diversity. For example it is widely agreed that crop heterogeneity, which is increased either spatially (Alarcón-Segura et al., 2022; Sirami et al., 2019) or temporally (Marja et al., 2018), benefits biodiversity (Alignier et al., 2020; Tscharrntke et al., 2021). However, agri-environmental schemes that aim to promote farmland biodiversity currently largely ignore the benefits of increased heterogeneity, probably because they largely focus on α -diversity. Key elements of agri-environmental schemes are ecological focus areas (EFAs), i.e. patches on which low-intensity, biodiversity-friendly management is prescribed. Depending on the EFA type, they are non-productive set-aside sites or fields that provide less yield, but harbour generally more biodiversity compared to conventionally managed sites (Batáry et al., 2015; Boetzel et al., 2021; Kleijn et al., 2006; Knop et al., 2006). At landscape scale, however, the strict and uniform EFA management that is not designed from a landscape perspective, could lead to a decrease in the diversity of habitats in a landscape, resulting in fewer different niches available, which might have negative effects on farmland γ -diversity as it was suggested by Benton et al. (2003). To date, to our knowledge, we do not know whether this is indeed the case.

Here, we have examined the strength and direction of the direct and indirect effects of factors, which are known to affect the farmland α - and/or β -diversity, on farmland γ -diversity (Figure 1, see Supplementary 1 for detailed expectations). We focused on factors representing abiotic conditions, such as topography or climate, and on factors related to land use, such as land-use type, land-use intensity, conservation measures (i.e. EFAs)

and landscape heterogeneity (i.e. landscape composition and configuration). To disentangle the causal structure, we built structural equation models (SEM; Grace, 2006) based on a large dataset on plants, butterflies and birds collected in the farmland of 123 investigation squares of 1 km² each, evenly distributed over a large gradient of abiotic and land-use conditions in Switzerland. For quantifying farmland γ -diversity, we calculated an overall diversity measure, namely species richness per investigation square across different taxonomic groups (i.e. multitrophic species richness, MSR). We did so to assess the overall effect of factors on species diversity while being aware that the responses of individual taxa can differ (Allan et al., 2014). Additionally, to obtain a better mechanistic understanding of the underlying processes, as they are expected to respond distinctly to land-use factors (Gámez-Virués et al., 2015; Perović et al., 2015), we calculated a trait-specific farmland γ -diversity, that is the number of individuals per investigation square within specific trait groups. We classified plants regarding their dispersal ability, butterflies regarding their feeding specialisation, and birds regarding their migration behaviour. Species of a sessile taxa group like plants that are particularly limited in their dispersal ability may be especially sensitive to disturbances and the spatial arrangement of landscape features (e.g. Fahrig et al., 2011). More mobile species, however, may hardly shift to alternative habitats due to high feeding specialisation as in the case of certain butterflies, or migration-limited birds require a large number of different habitats within the landscape, especially during wintertime (Tscharrntke et al., 2012; Weibull et al., 2003). As we recorded the diversity of our organisms at the landscape scale, we analysed γ -diversity, compared the results to patterns of α - and β -diversity known from literature, and specifically asked the following questions (i) how do factors related to abiotic conditions and land use directly and indirectly affect landscape-scale MSR, and (ii) how do these relationships vary across specific trait groups with specific requirements, in particular requirements related to dispersal, food and overwintering?

METHODS

Study area

The study area was the Swiss farmland (45°81' N–47°81' N, 5°57' E–10°49' E; ~41.000 km²; Figure 2), which showed a strong species loss in the last decades (Bühler & Roth, 2011). Meadows and pastures (~58%) and arable land (~38%) accounted for the largest share of farmland, while orchards, vineyards and other uses accounted for only a small share (Bundesamt für Landwirtschaft BLW, 2021).

Within the study area, we examined 123 investigation squares of each 1 km² (Figure 2). They were evenly

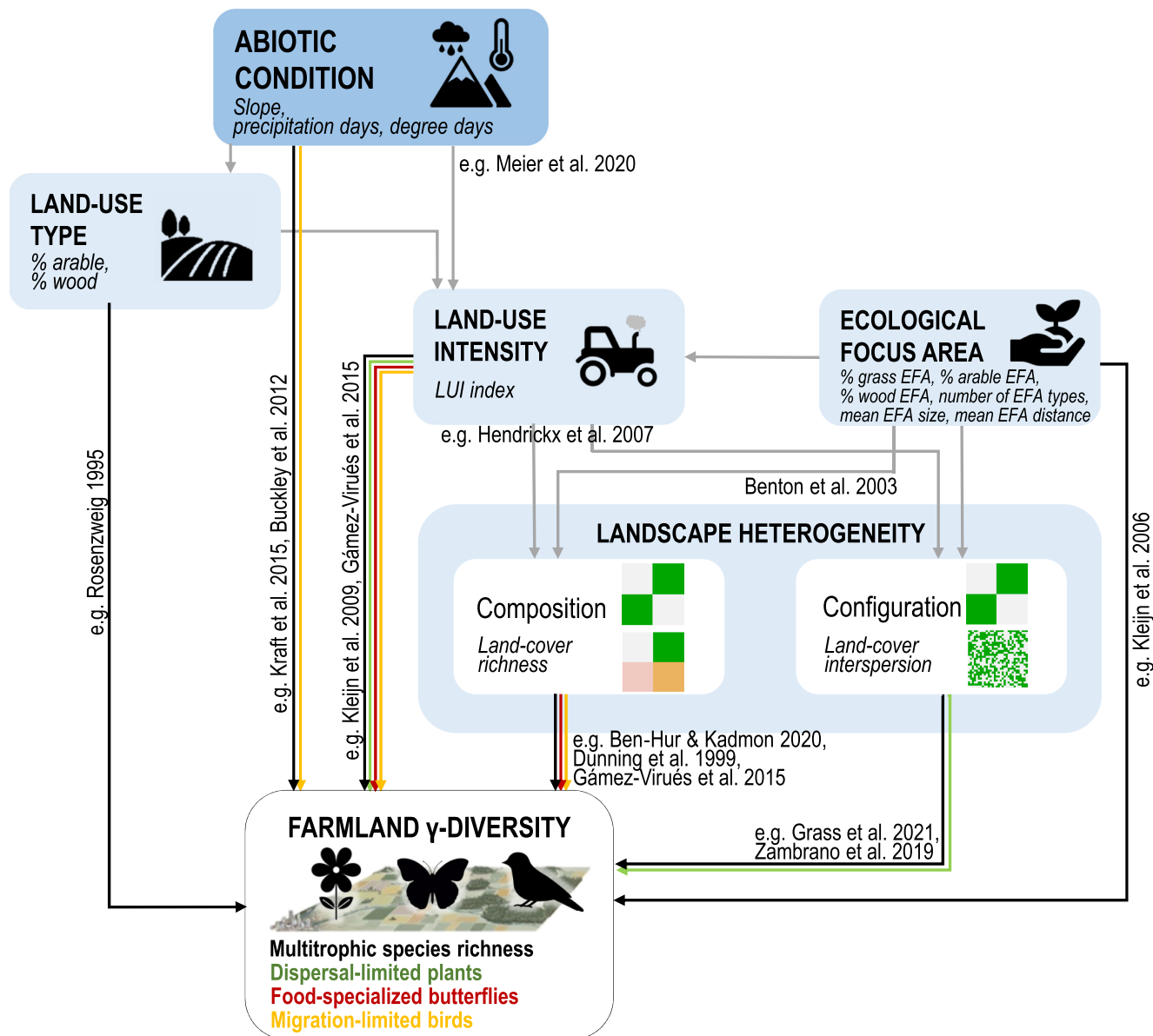


FIGURE 1 Hypothetical structural equation models (SEMs) representing hypothesised direct and indirect effects of abiotic conditions and land use (i.e. land-use type, land-use intensity, ecological focus areas (EFAs) and landscape heterogeneity) on farmland γ -diversity (i.e. multitrophic species richness (black), dispersal-limited plants (green), food-specialised butterflies (red) and migration-limited birds (yellow)). Grey arrows indicate indirect pathways which do not differ for the individual components of farmland γ -diversity. See supplementary 1 for the description of the individual expectations on direct and indirect relations.

distributed across a large gradient of abiotic conditions and land use. Within the investigation squares, we investigated exclusively the farmland by excluding buildings, settlement area, forest, water bodies, glaciers and rocks (Swisstopo, 2021).

Species data and metrics for farmland γ -diversity

Species surveys of vascular plants, butterflies, and birds were done in the same year and conducted between 2015

and 2019. During this 5-year period, each investigation square was visited once.

Data on vascular plant species were obtained from the ‘Swiss farmland biodiversity monitoring program’ (www.allema.ch). In each investigation square, first vegetation types were determined within 10 m² circular plots on a 50 × 50 m sampling grid (Figure 2), then on average 19 of these grid plots per investigation square were selected so that the frequency of their vegetation types was inversely proportional to the frequency of the vegetation types in the study area. On those plots (further referred to as vegetation plots), all vascular plant species and

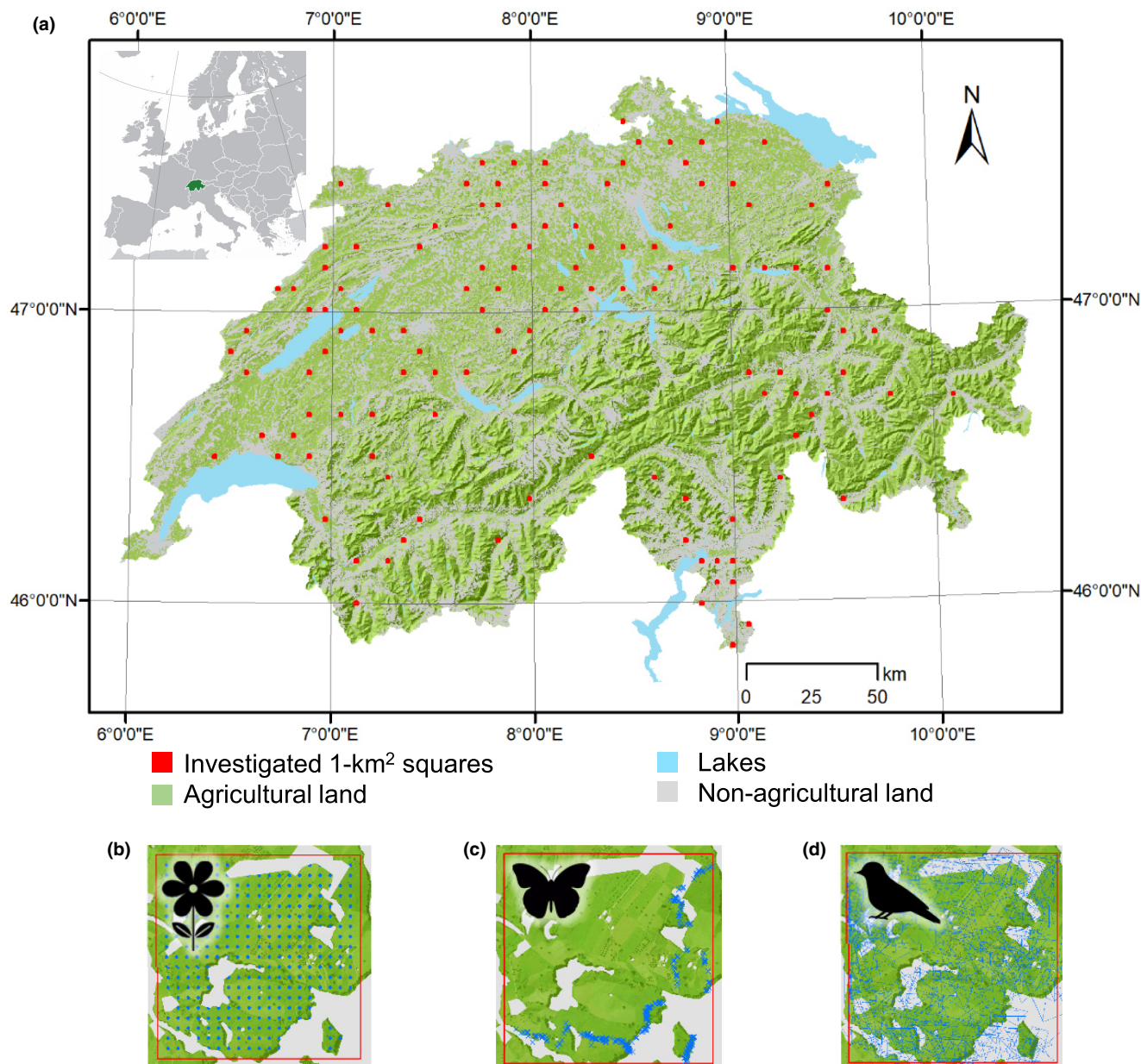


FIGURE 2 The location of the study area in Europe and the 123 1-km² investigation squares within the study area (a). Sampling of farmland within an exemplary investigation square in terms of (b) vegetation types and plant species on a sampling grid, (c) butterfly occurrences along transects and (d) bird territories across the entire area.

their percentage cover were determined once at the peak of flowering in the year of survey. Invasive plant species were also recorded, but these were only found on 2% of the vegetation plots and therefore not specially treated in the analyses.

Data on butterfly species (i.e. *Hesperiidae*, *Lycaenidae*, *Nymphalidae*, *Papilionidae* and *Pieridae*) were obtained from the ‘Swiss Biodiversity Monitoring’ (www.biodiversitymonitoring.ch). Each investigation square was surveyed along a 2.5 km transect (width 10 m) at seven time points during the year of survey. During the survey, the identity of all observed butterfly species and the coordinates of their position were recorded. For our

analyses, we included all observations within the farmland (Figure 2).

Bird data originated from the common breeding bird survey of the Swiss Ornithological Institute (www.vogelwarte.ch). Each investigation square was surveyed at three time points in the year of recording. Based on the individual observations of the birds, ornithologists delineated the breeding bird territories and indicated the number of individuals per territory. For our analyses, all territories were included which had their centroid within the farmland (Figure 2).

As a metric for overall farmland γ -diversity, we estimated the number of plant, butterfly and bird species

in the farmland of each investigation square, and then calculated the multitrophic species richness (MSR) across all taxonomic groups (Allan et al., 2014). For this purpose, the species richness values of each taxonomic group were first z-standardised (i.e. by subtracting the mean and dividing by the standard deviation), and then the mean of these standardised values was calculated.

The abundances of species with specific traits related to dispersal, food and overwintering were analysed to gain a better mechanistic understanding of the factors driving farmland γ -diversity, as they are expected to respond differently to abiotic conditions and land use. We used plants to investigate effects from dispersal limitation. Non-dispersal-limited plants were defined as species that disperse primarily by long-distance dispersal through anthropochory, dyszoochory, endozoochory, epizoochory, trichometeorochory and cystometeorochory (Landolt et al., 2010; Vittoz & Engler, 2007), while dispersal-limited plants were defined as plant species that exhibit other dispersal modes (see Table S0). Based on this classification, we calculated the percentage cover of (non-)dispersal-limited plants by summing the percentage cover of (non-)dispersal-limited plants per vegetation plot, and then calculating the mean of the vegetation plot values per investigation square. We used butterflies to investigate effects from food specialisation. Food-specialised butterfly species were defined as species that feed as caterpillars on one single plant species, several plant species of one genus or several plant species of one family (i.e. monophagous to oligophagous; Fauna Indicativa, <http://www.cscf.ch/cscf/de/home/projekte/fauna-indicativa.html>). The remaining species were defined as food-non-specialised butterflies (see Table S0). Based on these traits, we calculated the abundance of food-(non-)specialised butterflies by summing the number of individuals from food-(non-)specialised species per investigation square. We used birds to investigate effects from wintering requirements. Migration-limited bird species were defined as species that are resident (Storchová & Hořák, 2018), all others were defined as migratory (see Table S0). Based on this classification, we calculated the abundance of migration-limited (or migratory) birds by summing the number of individuals from migration-limited (or migratory) species per investigation square.

The species richness values of the individual components of MSR were each strongly correlated (>0.6), whereas the abundances of individuals with specific traits were only weakly correlated with each other and with MSR (<0.6) (Table S1). All metrics were generated using R version 4.1.2 (R Core Team, 2021).

Data on abiotic condition and land use

As drivers of farmland γ -diversity, we tested abiotic and land-use variables that have been shown to

explain spatial patterns of α - and/or β -diversity, and thus possibly explain farmland γ -diversity (Table S3). Only variables with a Pearson correlation of $|r_p| < 0.6$ and a Variance Inflation Factor < 5 in relation to the farmland γ -diversity metrics were selected to reduce multicollinearity (Table 1, Table S2). An exception was made for slope and LUI index, which were correlated with $r_p = -0.8$ (Table S2), therefore slope was only used as an explanatory variable of the LUI index, but was omitted in the other paths. Abiotic conditions were described with a 25 m grid resolution by slope ($^{\circ}$) (Swisstopo, 2005), yearly precipitation days (d) and annual degree-days using a 0°C threshold ($^{\circ}\text{C}\cdot\text{d}$) (Hijmans et al., 2005; Zimmermann & Kienast, 1999). To characterise land use, shares of land-use types (i.e. % arable and % wood) were derived by classifying the vegetation types assessed on the grid plots (see above) (Figure 2) into grass, arable and wood (for classification see Table S4). Further, land-use intensity (i.e. LUI index) was derived by classifying the vegetation types into a land-use intensity index (for details see Meier et al., 2020). Two measures of landscape heterogeneity were analysed: First, landscape composition, which was defined as land-cover richness based on the number of different vegetation types grouped into 14 classes. Second, landscape configuration, which was defined as land-cover interspersion based on the interspersion-index of 14 classes of vegetation types (R-library 'landscapemetrics', function 'lsm_l_iji'; Hesselbarth et al., 2019). Furthermore, several characteristics of ecological focus areas (EFAs) were derived from polygon data of the authorities, in particular the share of grass EFAs, the share of arable EFAs, the share of wood EFAs, the number of different EFA types, the mean EFA patch size and the mean nearest distance between EFA patches. To account for the area effect in farmland γ -diversity, we added the share of farmland in the 1 km^2 investigation squares as a co-variable. A detailed description of the explanatory variables can be found in Supplementary 2. All explanatory variables were generated with R version 4.1.2 (R Core Team, 2021).

Structural equation models

We used structural equation models (SEMs) to separate direct and indirect effects of abiotic conditions and land use on farmland γ -diversity (Grace, 2006). Therefore, we first built a priori theoretical SEMs reflecting hypothesised relationships among all variables (Figure 1 and Supplementary 1). To test if patterns were due to traits, we also calculated SEMs for inverse trait groups (e.g. migration limited and migratory birds). Based on the theoretical SEMs, we calculated empirical SEMs to investigate whether important paths between variables were missing or variables could be omitted, to evaluate how strongly and

TABLE 1 Variables used as dependent variables (i.e. farmland γ -diversity) and as explanatory variables (i.e. share of farmland, abiotic condition and land use). The values always refer only to the farmland within the 1 km² investigation squares (i.e. means and standard deviations over all 123 investigation squares)

Category	Variable	Description	Unit	Mean \pm SD
Farmland γ -diversity	MSR	Multitrophic species richness (averaged standardised species richness of plants, butterflies and birds)	—	0.00 \pm 0.77
	Dispersal-limited plants	Percentage cover of plants with low dispersal ability	%	2.91 \pm 3.12
	Food-specialised butterflies	Abundance of food-specialised butterflies	—	51.62 \pm 75.78
	Migration-limited birds	Abundance of migration-limited birds	—	86.07 \pm 41.74
Share of farmland	% agriculture	Share of farmland	%	67.71 \pm 20.85
Abiotic condition	Slope	Mean slope	°	11.86 \pm 7.03
	Precipitation days	Mean yearly precipitation days	d	36.18 \pm 4.14
	Degree days	Mean annual degree-days (0°C threshold)	°C d	2778.74 \pm 567.86
Land use				
Land-use type	% arable	Share of land-use “arable”	%	6.27 \pm 11.20
	% wood	Share of land-use class “wood”	%	2.84 \pm 8.29
Land-use intensity	LUI index	Mean land-use intensity index derived from habitat types	—	0.59 \pm 0.22
Landscape heterogeneity				
Composition	Land-cover richness	Number of detailed land-cover types	—	7.45 \pm 1.72
Configuration	Land-cover interspersation	Interspersation (spatial intermixing) of the detailed land cover types	%	54.12 \pm 14.43
Ecological focus area	% grass EFA	Share of grass EFAs	%	12.43 \pm 11.79
	% arable EFA	Share of arable EFAs	%	0.13 \pm 0.48
	% wood EFA	Share of wood EFAs	%	0.74 \pm 0.96
	Number of EFA types	Number of different EFA types	—	4.29 \pm 1.75
	Mean EFA size	Mean EFA patch size	m ²	3074.75 \pm 12226.38
	Mean EFA distance	Mean nearest distance between EFA patches	m	352.62 \pm 130.99

in which direction which paths explained the patterns. Missing paths were identified by high modification indices and large residual correlations between pairs of variables and were subsequently incorporated in the model. Variables that did not explain patterns were identified by omitting them from the model and checking if there was no difference in model fit compared to the model with the variable included. As measures of model fit, we used model Chi-squared (good fit indicated by $\text{Chisq } p\text{-value} > 0.05$), Comparative Fit Index (good fit indicated by $\text{CFI} > 0.90$) and Root Mean Square Error of Approximation (good fit indicated by $\text{RMSEA} < 0.08$, and its lower 90% confidence interval, RMSEA_{90} , close to 0). For these calculations, all variables were z-standardised to obtain standardised coefficients. SEMs were constructed using the ‘piecewiseSEM’ package version 2.1.2 in R (Lefcheck, 2016). Indirect effects and total effects of variables were calculated by multiplying the standardised coefficients of the involved paths and summing all resulting products using the ‘semEff’ package version 0.6.0 in R (Lefcheck, 2016). All data analysis was done with R version 4.1.2 (R Core Team, 2021).

RESULTS

Relationships among explanatory variables and overall effect on γ -diversity

Across all analysed farmland γ -diversity metrics, that is MSR and the abundance of trait groups with specific requirements for dispersal, food and overwintering (Figure 3, Table 2 and Table S5), we found that abiotic conditions were directly related to farmland γ -diversity, though the direction of the effect varied among the farmland γ -diversity metrics. However, shallow slopes, moist and warm climates were all indirectly, strongly negatively related to farmland γ -diversity, because these conditions were associated with increased land-use intensity. Increased land-use intensity was furthermore positively related to increasing shares of arable land and decreasing shares of woody habitats and grass EFAs. Increasing land-use intensity was directly strongly negatively related to farmland γ -diversity, and was indirectly negatively related to it over landscape heterogeneity. Contrarily, landscape heterogeneity was positively associated with a high number of EFA types

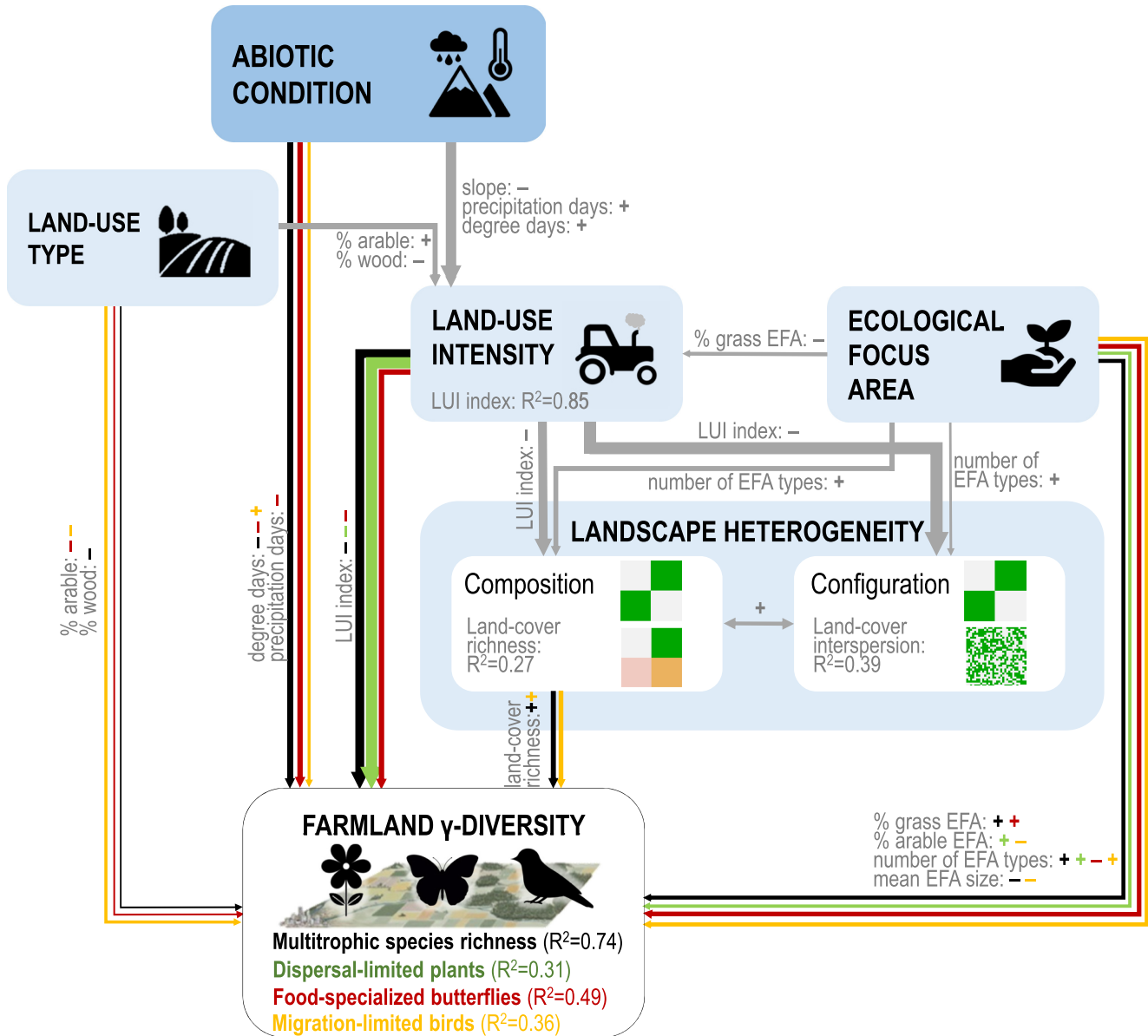


FIGURE 3 Structural equation models (SEMs) representing direct and indirect effects of abiotic conditions and land use (i.e. land-use type, land-use intensity, ecological focus areas (EFAs) and landscape heterogeneity), on farmland γ -diversity (i.e. multitrophic species richness (black), dispersal-limited plants (green), food-specialised butterflies (red) and migration-limited birds (yellow)). Shown are the final SEMs, and only variables that were retained in the final SEMs. Line thickness of paths is proportional to the values of the standardised coefficients (if variables are presented as groups, the largest standardised coefficient is used). The direction of the standardised coefficients is indicated with a '+' or '-' behind the explanatory variable. The amount of explained variance is indicated by ' R^2 '. The exact values of standardised coefficients, standardised errors and significance values are given in Table S5.

in the landscape: they introduced land-cover types (i.e. changing landscape composition), and interspersed the management units of the agricultural landscape (i.e. changing landscape configuration). High land-cover richness was directly strongly positively related to farmland γ -diversity, while land-cover interspersions was not related to farmland γ -diversity. In addition to the positive indirect relationship of EFAs with farmland γ -diversity through their overall negative association with land-use intensity and positive association with landscape heterogeneity, EFAs also were mostly directly positively related to farmland γ -diversity.

Direct and indirect effects on multitrophic species richness

Multitrophic species richness (MSR; model fit: Chisq p -value = 0.11, CFI = 0.98, RMSEA = 0.06 and RMSE_90 = 0.00; Figure 3 and Table 2) was indirectly more strongly related to abiotic conditions (via land-use intensity and landscape composition) than directly. A higher wood share was directly related to a lower MSR, but indirectly to a higher MSR. Land-use intensity was directly and indirectly strongly related to MSR (via landscape composition). Share of

TABLE 2 Standardised direct, indirect and total effects of all explanatory variables on all endogenous explanatory variables, that is land-use intensity (LUI index), landscape composition (land-cover richness), landscape configuration (land-cover interspersions), and on farmland γ -diversity, that is multitrophic species richness (MSR), the abundance of dispersal-limited plants, food-specialised butterflies and migration-limited birds

	LUI index			Land-cover richness			Land-cover interspersions		
	Direct	Indirect	Total	Direct	Indirect	Total	Direct	Indirect	Total
Share of farmland	0.084		0.084	0.157	-0.038	0.120		-0.052	-0.052
Abiotic condition	-0.392		-0.392	0.175	0.175	0.175		0.243	0.243
Precipitation days	0.141		0.141	-0.063	-0.063	-0.063		-0.087	-0.087
Degree days	0.114		0.114	-0.051	-0.051	-0.051		-0.071	-0.071
Land-use type	0.129		0.129	-0.058	-0.058	-0.058		-0.080	-0.080
% wood	-0.133		-0.133	0.059	0.059	0.059		0.082	0.082
LUI index				-0.447		-0.447		-0.619	-0.619
Landscape composition									
Landscape configuration									
Ecological focus area	-0.151		-0.151	0.067	0.067	0.067		0.093	0.093
% grass EFA									
% arable EFA									
% wood EFA									
Number of EFA types				0.217		0.217		0.128	0.128
Mean EFA size									
Mean EFA distance									
MSR									
	Dispersal-limited plants			Food-specialised butterflies			Migration-limited birds		
	Direct	Indirect	Total	Direct	Indirect	Total	Direct	Indirect	Total
Share of farmland	0.004		0.004	-0.046	-0.046	-0.046	0.171	0.266	0.266
Abiotic condition	0.160		0.160	0.215	0.215	0.215	0.077	0.040	0.040
Precipitation days	-0.058		-0.058	-0.077	-0.077	-0.077	-0.130	-0.014	-0.014
Degree days	-0.179		-0.179	-0.062	-0.062	-0.062	-0.160	-0.012	-0.012
Land-use type	-0.110		-0.110	-0.071	-0.071	-0.071	-0.025	-0.013	-0.013
% wood	0.054		0.054	0.073	0.073	0.073	0.026	0.013	0.013
LUI index	-0.300		-0.300	-0.547	-0.547	-0.547	-0.195	-0.101	-0.101
Landscape composition	0.244		0.244				0.226		0.226
Landscape configuration									
Ecological focus area	0.100	0.062	0.161	0.083	0.083	0.083	0.183	0.015	0.015
% grass EFA									
% arable EFA				0.162	0.162	0.162	-0.108	-0.108	-0.108
% wood EFA									
Number of EFA types	0.172	0.053	0.225	0.123	0.123	0.123	-0.125	0.049	0.222
Mean EFA size	-0.103		-0.103						
Mean EFA distance							-0.114	-0.114	-0.114

grass EFAs, the number of EFA types and smaller-sized EFA patches were directly and indirectly (via land-use intensity and landscape composition) positively related to MSR.

Direct and indirect effects on dispersal-limited plants, food-specialised butterflies and migration-limited birds

The abundance of dispersal-limited plants (model fit: $\text{Chisq } p\text{-value} = 0.05$, $\text{CFI} = 0.97$, $\text{RMSEA} = 0.07$ and $\text{RMSE}_{90} = 0.00$; [Figure 3](#) and [Table 2](#)) was only indirectly related to abiotic conditions and land-use shares (via land-use intensity), while it was directly negatively related to high land-use intensity. Landscape heterogeneity was not related to the abundance of dispersal-limited plants. Increasing shares of arable EFAs and number of EFA types were directly positively related to the abundance of dispersal-limited plants, while increasing shares of grass EFAs were indirectly positively related, negatively to the abundance of dispersal-unlimited plants ([Table S5](#) and [S6](#)), respectively.

The abundance of food-specialised butterflies (model fit: $\text{Chisq } p\text{-value} = 0.7$, $\text{CFI} = 0.98$, $\text{RMSEA} = 0.07$ and $\text{RMSE}_{90} = 0.00$; [Figure 3](#) and [Table 2](#)) was directly more strongly related to abiotic conditions than indirectly through land-use intensity. Land-use shares were only indirectly related to the abundance of food-specialised butterflies through land-use intensity, while a high land-use intensity was directly negatively related to it. Landscape heterogeneity was not related to it. Increasing shares of grass EFAs and decreasing number of EFA types were directly positively related to the abundance of food-specialised butterflies (but not to food non-specialised butterflies, [Table S5](#) and [S6](#)), and also indirectly via land-use intensity.

The abundance of migration-limited birds (model fit: $\text{Chisq } p\text{-value} = 0.10$, $\text{CFI} = 0.98$, $\text{RMSEA} = 0.06$ and $\text{RMSE}_{90} = 0.00$; [Figure 3](#) and [Table 2](#)) was directly and indirectly related to abiotic conditions in opposite directions (via land-use intensity and landscape composition). Increasing arable shares were directly negatively related to the abundance of migration-limited birds, increasing wood shares to the abundance of migratory birds ([Table S5](#) and [S6](#)), respectively. Land-use intensity was only indirectly negatively related to the abundance of migration-limited birds via landscape composition, but it was directly positively related to the abundance of migratory birds. Besides the positive indirect relationships between EFAs and the abundance of migration-limited birds, an increasing number of EFA types, smaller-sized EFAs and decreasing shares of arable EFAs were directly positively related to it.

DISCUSSION

Strong negative direct and indirect relationships of land-use intensity and γ -diversity

High land-use intensity was positively related to shallow slopes, moist and warm climates, large arable shares, and negatively related to high shares of woody elements a EFAs in the landscape. For its part, it had a strong direct negative relationship with farmland γ -diversity (MSR, dispersal-limited plants and food-specialised butterflies), which is in line with previous studies that focused on farmland α -diversity (e.g. Allan et al., 2015; Hendrickx et al., 2007; Kleijn et al., 2009), β -diversity (e.g. Gossner et al., 2016; Karp et al., 2012), γ -diversity (e.g. Billeter et al., 2007; Hendrickx et al., 2007) or species with low dispersal and high feeding specialisation (e.g. Gámez-Virués et al., 2015; Mangels et al., 2017). Interestingly, in contrast to migratory birds, non-migratory birds were not directly related to land-use intensity. One reason might be that non-migratory farmland birds breed less often on the ground than migratory farmland birds (Storchová & Hořák, 2018) and hence are less affected by an intense management. Further, in order to survive the winter, they are often less specialised on insects (Storchová & Hořák, 2018), which might make them less susceptible to low abundances of insects in intensively managed farmland.

Because of the negative relationship between land-use intensity and landscape heterogeneity (Bergholz et al., 2022; Liu et al., 2018) and between landscape heterogeneity and farmland γ -diversity (Lecoq et al., 2022), several studies suggested that land-use intensity affects farmland γ -diversity not only directly but also indirectly through a change in landscape heterogeneity (e.g. Benton et al., 2003; Gossner et al., 2016; Hendrickx et al., 2007; Landis, 2017). Indeed, here we show that part of the negative relationship between land-use intensity and farmland γ -diversity (MSR as well as migration-limited birds) was explained by the negative relationship of land-use intensity with both components of landscape heterogeneity. Landscape composition was most likely negatively affected through the elimination of small, semi-natural areas in intensively used farmland, landscape configuration through merging smaller management units into larger units, respectively. However, the negative relationship may also have resulted from a homogenisation of the landscape leading to an increase in land-use intensity. Nevertheless, specific measures to promote landscape heterogeneity in areas with high land-use intensity could mitigate the negative effects of land-use intensity on farmland biodiversity (Perović et al., 2015). In sum, our results suggest that land-use intensity is directly and indirectly a key driver for the ongoing decline of farmland biodiversity.

Positive direct and indirect relationships of EFAs and γ -diversity

Similar to their well-known, largely positive effects of EFAs on α -diversity (e.g. Batáry et al., 2015; Boetzl et al., 2021; Kleijn et al., 2006; Knop et al., 2006) and the rare existing studies on their effect on γ -diversity (Zingg et al., 2019), our results showed that EFAs were generally positively related to farmland γ -diversity, both through a direct positive relationship with it, and through modifying factors that were in turn related to farmland γ -diversity, such as land-use intensity. The importance of the different EFA types or characteristics of EFAs, however, varied between trait groups.

For example we found a direct positive relationship between the share of grass EFAs and MSR, food-specialised butterflies, respectively, but not for the other trait groups. We assume that this resulted from the biodiversity-friendly local management of grass EFAs, such as delayed mowing, which facilitates reproduction of plants and insects. Arable EFAs directly benefitted mainly dispersal-limited plants, probably because they were sown in the arable EFAs and thus dispersal limitation in these areas was not limiting. Interestingly, increased mean size of EFAs had a negative effect on MSR and migration-limited birds, which is in contrast to findings on the effects of patch sizes due to fragmentation on γ -diversity in general (Chetcuti et al., 2020; Fahrig, 2017), but consistent with the negative trend of EFA size on butterfly richness in the study of Zingg et al. (2019). A reason for these contrasting findings might be that in fragmentation studies the focal habitat usually harbours a specialised community of rare and specialised species. Fragmentation increases the edge length, thereby adding more generalist species, but reducing the number of specialists in the focal habitat by decreasing habitat size. As EFAs are known to fail to promote rare and specialised species (e.g. Kleijn et al., 2015), the positive effect of fragmentation on habitat generalists due to increased edge length might drive our results.

In addition to their direct positive relationship with farmland γ -diversity, EFAs also had an indirect relationship with it by modifying other drivers of farmland γ -diversity, such as land-use intensity or landscape heterogeneity. In particular, a large share of EFAs was related to a lower land-use intensity, a high number of different EFA types related to a higher landscape heterogeneity, respectively. The finding of an indirect, positive relationship of EFAs farmland γ -diversity by reducing land-use intensity in a landscape was expected, although to our knowledge this has hardly been quantified so far. On the other hand, the indirect, positive relationship with farmland γ -diversity by increasing landscape heterogeneity was unexpected, because previous studies proposed that due to their strict

management practices EFAs would not promote landscape heterogeneity (Benton et al., 2003).

Overall, our results suggest that EFAs have on top of their direct positive effect also a positive indirect effect on farmland γ -diversity by modifying the landscape. They are thus an important conservation tool to halt the ongoing loss of farmland biodiversity. In particular, the indirect positive effect on farmland biodiversity through a reduction in land-use intensity seems to be valuable. Our results also indicate that their effectiveness could further be improved by establishing many different EFA types to increase land-cover richness. For example new EFA types could be included, which are specifically designed for rare and specialised species or for providing more food and shelter resources for resident species in winter. In that way, EFAs would more strongly promote farmland γ -diversity and contribute to biodiversity-friendly landscapes (Grass et al., 2021; Landis, 2017; Tschardt et al., 2021).

Mixed relationships of landscape heterogeneity and land-cover types with γ -diversity

Other than expected from studies focusing on α -diversity, landscape heterogeneity showed mixed relationships with farmland γ -diversity. Increasing land-cover richness (i.e. landscape composition) was positively related to MSR and the abundance of migration-limited birds, which is in line with previous studies (Ben-Hur & Kadmon, 2020; Billeter et al., 2007; Gámez-Virués et al., 2015; Hendrickx et al., 2007; Tschardt et al., 2012). However, in contrast to the landscape-moderated insurance hypothesis (Tschardt et al., 2012), we found no such positive relationships with food-specialised butterflies. Interestingly, we found a negative relationship with land-use intensity and a positive relationship with grassland EFAs with them. It seems that they were more dependent on low land-use intensity (e.g. late mowing) than on high land-cover richness, which might be related to the availability of host plants for reproduction.

In contrast to the positive effects of higher configurational heterogeneity in the surroundings of a patch on α -diversity through increasing cross-habitat spill-over (Fahrig et al., 2011; Grass et al., 2021; Zambrano et al., 2019), increasing landscape configuration was not related to farmland γ -diversity. One explanation for this unexpected result could be that spill-over effects at field scale were often observed in sessile or barely mobile organism groups. This idea is supported by the positive relationship of landscape configuration with plant species diversity that we have found (Table S5). Spill-over effects at field scale might be less important for mobile organism groups such as butterflies and birds (Perović et al., 2015). For those organism groups, spill-over effects

probably take place on a larger spatial scale, for example from non-farmland to farmland.

Interestingly, the share of arable land was not only indirectly negatively related with farmland γ -diversity by increasing land-use intensity and reducing landscape heterogeneity, but also directly with the abundance of overwintering birds. This suggests that arable land provides poor habitats for overwintering organisms (Redhead et al., 2018). It also seems that the small share of arable EFAs cannot compensate the lack of suitable winter habitats in landscapes that are dominated by arable land, so EFA shares should be increased there.

Strong indirect relationships of abiotic conditions and γ -diversity

Except for the abundance of migration-limited birds, harsher abiotic conditions were not generally negatively related to farmland γ -diversity. This is in contrast to what is widely known for local communities regarding environmental filtering (Kraft et al., 2015), but see Buckley et al. (2012) for similar findings on birds. Our findings might be explained by the fact that farmland γ -diversity is assembled by various communities that all require slightly different abiotic factors (Udy et al., 2021). Therefore, the effects are only evident in communities that are clearly dependent on favourable conditions, such as, for example migration-limited birds, which have to maintain their metabolism even under temporarily very harsh conditions.

Indirectly, however, more favourable abiotic conditions were clearly negatively related with farmland γ -diversity by favouring intensive land-use. In particular, the absence of steep slopes (i.e. enabling the use of heavy machines), high precipitation (i.e. no water limitation) and high temperatures was directly positively related with land-use intensity (Meier et al., 2020), indirectly negatively with farmland γ -diversity, respectively. To our knowledge, we were able to show such indirect relationships empirically for the first time. They turned out to be rather strong and should therefore be taken into account when designing biodiversity-friendly landscapes.

Recommendations for improving conservation measures

Our results show that a paradigm shift in the design of biodiversity conservation in agriculture would be important—away from optimising local management to promote local biodiversity, towards redesigning agricultural landscapes to promote biodiversity-friendly landscapes. Specifically, our results suggest that key for halting the ongoing decline of farmland biodiversity is a reduction of land-use intensity at the landscape scale, particularly in areas with favourable abiotic conditions

(i.e. shallow slopes, humid and warm climate). This could be achieved on the one hand by a particularly high share of EFAs in those landscapes, and on the other hand by reducing the intensity on conventionally managed fields (Alarcón-Segura et al., 2022; Alignier et al., 2020; Marja et al., 2018; Sirami et al., 2019). In addition, the EFA landscape design could be improved by specifically aiming at increasing landscape heterogeneity through adding many EFAs (also small ones) and EFAs that are suitable habitats throughout the year.

CONCLUSIONS

By revealing the causal structure of factors that were directly and indirectly related to farmland γ -diversity, our results provide one of the rare pieces of evidence on the drivers of the large-scale declines in farmland biodiversity. We found that when focusing on farmland γ -diversity, the direction and strength of the effects of factors might deviate from what is known from α - or β -diversity. Therefore, knowledge on farmland α - or β -diversity cannot simply be up-scaled to γ -diversity. Moreover, the direction and strength of factors related to farmland γ -diversity depended on whether their direct and indirect relationship was considered. We thus conclude that it is important to consider both, the direct and indirect pathways, which is currently rarely done. Finally, we show, how management, for example overall land-use intensity or specific management actions designed for promoting biodiversity at the local scale (i.e. EFAs), are related to farmland γ -diversity at the landscape scale. Thus, reducing land-use intensity in an area combined with a high share of EFAs would benefit farmland γ -diversity. Further studies examining the effects of management on farmland γ -diversity are needed, however, to improve our knowledge on designing biodiversity-friendly landscapes aimed at halting the on-going loss of farmland γ -diversity.

AUTHOR CONTRIBUTIONS

ESM, EK and GL designed the study. ESM and GL prepared the data. ESM performed the analyses. ESM and EK wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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DATA AVAILABILITY STATEMENT

The data supporting the results and R code used to check for multicollinearity and to generate the SEMs are archived on DRYAD (DOI: <https://doi.org/10.5061/dryad.r7sqv9sg3>).

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REFERENCES

- Alarcón-Segura, V., Grass, I., Breustedt, G., Rohlf, M. & Tschardt, T. (2022) Strip intercropping of wheat and oilseed rape enhances biodiversity and biological pest control in a conventionally managed farm scenario. *Journal of Applied Ecology*, 6, 1513–1523.
- Alignier, A., Solé-Senan, X.O., Robleño, I., Baraibar, B., Fahrig, L., Giralt, D. et al. (2020) Configurational crop heterogeneity increases within-field plant diversity. *Journal of Applied Ecology*, 57, 654–663.
- Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tschardt, T. et al. (2014) Interannual variation in land-use intensity enhances grassland multidiversity. *Proceedings of the National Academy of Sciences*, 111, 308–313.
- Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., Blüthgen, N. et al. (2015) Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition. *Ecology Letters*, 18, 834–843.
- Batáry, P., Dicks, L.V., Kleijn, D. & Sutherland, W.J. (2015) The role of Agri-environment schemes in conservation and environmental management. *Conservation Biology*, 29, 1006–1016.
- Ben-Hur, E. & Kadmon, R. (2020) Heterogeneity–diversity relationships in sessile organisms: a unified framework. *Ecology Letters*, 23, 193–207.
- Bennett, A.F., Radford, J.Q. & Haslem, A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation*, 133, 250–264.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecology and Evolution*, 18, 182–188.
- Bergholz, K., Sittel, L., Ristow, M., Jeltsch, F. & Weiss, L. (2022) Pollinator guilds respond contrastingly at different scales to landscape parameters of land-use intensity. *Ecology and Evolution*, 12, 1–11.
- Billetter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I. et al. (2007) Indicators for biodiversity in agricultural landscapes: a pan-European study. *Journal of Applied Ecology*, 45, 141–150.
- Boetzel, F.A., Krauss, J., Heinze, J., Hoffmann, H., Juffa, J., König, S. et al. (2021) A multitaxa assessment of the effectiveness of Agri-environmental schemes for biodiversity management. *Proceedings of the National Academy of Sciences of the United States of America*, 10, 118.
- Buckley, L.B., Hurlbert, A.H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, 21(9), 873–885.
- Bühler, C. & Roth, T. (2011) Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. *Diversity and Distributions*, 17, 1089–1098.
- Bundesamt für Landwirtschaft BLW. (2021). Agrarbericht. www.agrarbericht.ch. Available at: https://www.agrarbericht.ch/download/documents/b2/0t71qpkqyscuou5vbtv8x3ellxjrhb/ab2l_l_landwirtschaftliche_nutzflaeche_nach_nutzungsarten_datenreihe_d.xlsx. Last accessed 16 May 2022.
- Chetcuti, J., Kunin, W.E. & Bullock, J.M. (2020) Habitat fragmentation increases overall richness, but not of habitat-dependent species. *Frontiers in Ecology and Evolution*, 8, 1–12.
- Clough, Y., Ekroos, J., Báldi, A., Batáry, P., Bommarco, R., Gross, N. et al. (2014) Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology Letters*, 17, 1168–1177.
- Concepción, E.D., Diaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y. et al. (2012) Interactive effects of landscape context constrain the effectiveness of local Agri-environmental management. *Journal of Applied Ecology*, 49, 695–705.
- Diaz, S., Settele, J., Brondizio, E.S., Ngo, H.T., Agard, J., Arneeth, A. et al. (2019) Pervasive human-driven decline of life on earth points to the need for transformative change. *Science*, 80, 366.
- Duflot, R., Ernout, A., Aviron, S., Fahrig, L. & Burel, F. (2017) Relative effects of landscape composition and configuration on multi-habitat gamma diversity in agricultural landscapes. *Agriculture, Ecosystems and Environment*, 241, 62–69.
- Ekroos, J., Ödman, A.M., Andersson, G.K.S., Birkhofer, K., Herbertsson, L., Klatt, B.K. et al. (2016) Sparing land for biodiversity at multiple spatial scales. *Frontiers in Ecology and Evolution*, 3, 1–11.
- Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, 48, 1–23.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J. et al. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, 14, 101–112.
- Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H. et al. (2015) Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, 6, 8568.
- Gossner, M.M., Lewinsohn, T.M., Kahl, T., Grassein, F., Boch, S., Prati, D. et al. (2016) Land-use intensification causes multi-trophic homogenization of grassland communities. *Nature*, 540, 266–269.
- Grace, J.B. (2006) *Structural equation modeling and natural systems*. Cambridge: Cambridge University Press.
- Grass, I., Batáry, P. & Tschardt, T. (2021) *Combining land-sparing and land-sharing in European landscapes*. In: *Advances in Ecological Research*, pp. 251–303.
- Hendrickx, F., Maelfait, J.-P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S. et al. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, 44, 340–351.
- Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K. & Nowosad, J. (2019) Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography (Cop.)*, 42, 1648–1657.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.
- IPBS. (2019) *Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services*. Bonn.
- Karp, D.S., Rominger, A.J., Zook, J., Ranganathan, J., Ehrlich, P.R. & Daily, G.C. (2012) Intensive agriculture erodes β -diversity at large scales. *Ecology Letters*, 15, 963–970.

- Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., Esteban, J., Fernández, F. et al. (2006) Mixed biodiversity benefits of Agri-environment schemes in five European countries. *Ecology Letters*, 9, 243–254.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E., Clough, Y. et al. (2009) On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society B: Biological Sciences*, 276, 903–909.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R. et al. (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, 6, 7414.
- Knop, E., Kleijn, D., Herzog, F. & Schmid, B. (2006) Effectiveness of the swiss Agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology*, 43, 120–127.
- Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. & Levine, J.M. (2015) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29, 592–599.
- Landis, D.A. (2017) Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, 18, 1–12.
- Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W. et al. (2010) Flora indicativa - Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. *Haupt, Bern*, 7, 378.
- Le Provost, G., Thiele, J., Westphal, C., Penone, C., Allan, E., Neyret, M. et al. (2021) Contrasting responses of above- and below-ground diversity to multiple components of land-use intensity. *Nature Communications*, 12, 3918.
- Lecoq, L., Mony, C., Saiz, H., Marsot, M. & Ernout, A. (2022) Investigating the effect of habitat amount and landscape heterogeneity on the gamma functional diversity of grassland and hedgerow plants. *Journal of Ecology*, 110, 1871–1882.
- Lefcheck, J.S. (2016) piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7, 573–579.
- Liu, Q., Buyantuev, A., Wu, J., Niu, J., Yu, D. & Zhang, Q. (2018) Intensive land-use drives regional-scale homogenization of plant communities. *Science of the Total Environment*, 644, 806–814.
- Mangels, J., Fiedler, K., Schneider, F.D. & Blüthgen, N. (2017) Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. *Biodiversity and Conservation*, 26, 3385–3405.
- Marja, R., Viik, E., Mänd, M., Phillips, J., Klein, A.-M. & Batáry, P. (2018) Crop rotation and Agri-environment schemes determine bumblebee communities via flower resources. *Journal of Applied Ecology*, 55, 1714–1724.
- Meier, E.S., Indermaur, A., Ginzler, C. & Psomas, A. (2020) An effective way to map land-use intensity with a high spatial resolution based on habitat type and environmental data. *Remote Sensing*, 12, 1–22.
- Mori, A.S., Isbell, F. & Seidl, R. (2018) β -Diversity, community assembly, and ecosystem functioning. *Trends in Ecology & Evolution*, 33, 549–564.
- Perović, D., Gámez-Virués, S., Börschig, C., Klein, A.M., Krauss, J., Steckel, J. et al. (2015) Configurational landscape heterogeneity shapes functional community composition of grassland butterflies. *Journal of Applied Ecology*, 52, 505–513.
- R Core Team. (2021). R: a language and environment for statistical computing.
- Redhead, J.W., Hinsley, S.A., Beckmann, B.C., Broughton, R.K. & Pywell, R.F. (2018) Effects of Agri-environmental habitat provision on winter and breeding season abundance of farmland birds. *Agriculture, Ecosystems & Environment*, 251, 114–123.
- Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A. et al. (2019) Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences*, 116, 16442–16447.
- Storchová, L. & Hořák, D. (2018) Life-history characteristics of European birds. *Global Ecology and Biogeography*, 27, 400–406.
- Swisstopo. (2005). DHM25 - Das digitale Höhenmodell der Schweiz [DHM25—Digital terrain model of Switzerland]. <http://www.swisstopo.admin.ch/internet/swisstopo/d>.
- Swisstopo. (2021). swissTLM3D - Topografische Landschaftsmodell der Schweiz [swissTLM3D - Topographic landscape model of Switzerland].
- Tscharntke, T., Grass, I., Wanger, T.C., Westphal, C. & Batáry, P. (2021) Beyond organic farming—harnessing biodiversity-friendly landscapes. *Trends in Ecology & Evolution*, 36, 919–930.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P. et al. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87, 661–685.
- Udy, K., Fritsch, M., Meyer, K.M., Grass, I., Hanß, S., Hartig, F. et al. (2021) Environmental heterogeneity predicts global species richness patterns better than area. *Global Ecology and Biogeography*, 30, 842–851.
- Vittoz, P. & Engler, R. (2007) Seed dispersal distances: a typology based on dispersal modes and plant traits. *Botanica Helvetica*, 117, 109–124.
- Weibull, A., Östman, Ö. & Granqvist, Å. (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation*, 12, 1335–1355.
- Zambrano, J., Garzon-Lopez, C.X., Yeager, L., Fortunel, C., Cordeiro, N.J. & Beckman, N.G. (2019) The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? *Oecologia*, 191, 505–518.
- Zimmermann, N.E. & Kienast, F. (1999) Predictive mapping of alpine grasslands in Switzerland: species versus community approach. *Journal of Vegetation Science*, 10, 469–482.
- Zingg, S., Ritschard, E., Arlettaz, R. & Humbert, J.Y. (2019) Increasing the proportion and quality of land under Agri-environment schemes promotes birds and butterflies at the landscape scale. *Biological Conservation*, 231, 39–48.

SUPPORTING INFORMATION

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

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