

## Livestock density affects species richness and community composition of butterflies: A nationwide study

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### ARTICLE INFO

#### Keywords:

Conservation  
Farmland biodiversity  
Grazing  
Insect decline  
Livestock farming  
Management

### ABSTRACT

Extensively managed grasslands are globally recognized for their high biodiversity value. Over the past century, a continuous loss and degradation of grassland habitats has been observed across Europe that is mainly attributable to agricultural intensification and land abandonment. Particularly insects have suffered from the loss of grassland habitats due to land-use change and the decrease in habitat quality, either due to an increase in livestock density, higher mowing frequency, and an increase in nitrogen fertilization, or by abandonment. However, only a few studies have used nationwide datasets to analyse the effects of land cover and land-use intensity on insects. It further remains largely unexplored how these effects are modulated by species traits, i. e. habitat specialisation and mobility. Using nationwide butterfly data originating from the German Butterfly Monitoring Scheme, we investigated the effect of three indicators related to land cover and agricultural land-use intensity on species richness as well as trait composition of butterfly communities. Based on agricultural census data at the municipality scale, we calculated the share of permanent grasslands (measure of habitat availability), the total livestock density (proxy for organic fertilization) and the livestock density of domestic herbivores (proxy for management intensity in grasslands) within a 2 km buffer surrounding each butterfly transect. To analyse the relationships between butterflies and indicators of land cover and land-use intensity, we applied generalised linear mixed effect models. We found a negative relationship between butterfly species richness and the livestock density of domestic herbivores. Further, the ratio of butterfly generalist to specialist species shifted towards generalists and the size of butterflies increased with higher herbivore livestock density, indicating a shift in communities towards mobile habitat generalists. Our results are in accordance with previous studies carried out across smaller geographic extents, highlighting the importance of low herbivore livestock densities to halt the loss of pollinating insects and safeguard biodiversity and associated ecosystem services in agricultural landscapes. We here demonstrate that indicators based on livestock distribution data at the municipality scale can provide insights into processes and spatial diversity patterns of butterflies at the national level. Further, we highlight potentials and limitations of using agricultural census data to quantify and assess effects of land cover and land-use intensity on butterflies, and make recommendations for further research needs.

### 1. Introduction

Agricultural land makes up 39 percent of Europe's land cover (Eurostat, 2021) and thus has a major impact on many species, including rare and endangered ones, which are associated with farmland habitats

(Bengtsson et al., 2019; Loos et al., 2014). Over the past century European agricultural landscapes have changed considerably. Habitat loss and decline of habitat quality through agricultural intensification and abandonment of low-intensity farming have led to sharp declines in farmland biodiversity (Habel et al., 2019a; Warren et al., 2021).

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<https://doi.org/10.1016/j.ecolind.2023.109866>

Received 24 October 2022; Received in revised form 19 December 2022; Accepted 2 January 2023

Available online 5 January 2023

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Particularly insects have suffered from land-use intensification at local and landscape level, e.g. due to increased stocking density (van Klink et al., 2015), the use of pesticides (Brittain et al., 2010), higher fertilization intensity (Carvalho et al., 2019), and landscape simplification (Seibold et al., 2019). In addition, the abandonment of grassland management accompanied by woody plant encroachment is detrimental to species living in open habitats (Öckinger et al., 2006a; van Swaay et al., 2020). As a consequence of these processes, various studies have reported declines in insect abundance and biomass by several dozen percent in the past decades (Seibold et al., 2019; Warren et al., 2021). Insects play a vital role in the food chain and provide essential ecosystem services to agriculture such as pollination (Schowalter et al., 2018). To safeguard farmland biodiversity and associated ecosystem services, halting and reversing the loss of pollinating insects is one of the political headline targets of the EU biodiversity strategy for 2030 (European Commission, 2020). Therefore, profound knowledge on the impacts of land-use intensity at multiple spatial scales is pivotal to effectively conserve insects and to maintain the ecosystem services provided by them (Flohre et al., 2011).

Extensively managed grasslands are globally recognized for their high biodiversity value (Bengtsson et al., 2019). Numerous groups of insects depend on permanent grasslands (New, 2019; van Swaay et al., 2010) and therefore suffer from ongoing grassland conversion and the decrease in habitat quality in agricultural landscapes (Bengtsson et al., 2019; Schils et al., 2022; van Swaay et al., 2016; Warren et al., 2021). Accompanying the conversion of grasslands, land-use change often leads to increased fragmentation and reduced habitat connectivity, resulting in higher probabilities of species extinction and lower colonization rates (Hanski, 2011; Hanski, 2015). A loss in habitat quality is mainly attributed to either agricultural land abandonment or land-use intensification, i.e. an increase in the herbivore livestock density, in mowing events, and in nitrogen fertilization (Settele et al., 2009; van Swaay et al., 2020; Warren et al., 2021). Due to high nitrogen inputs and high stocking pressure, flowering plants are declining, vegetation structure becomes more homogenous, and microclimatic conditions on grasslands are changing. Insects are impacted not only by these indirect effects but also directly by increased mortality through grazing or mowing and reduced quality of food plants due to increased nitrogen inputs (Roth et al., 2021; Settele et al., 2009; van Klink et al., 2015).

Here, we use butterflies as model organisms to study the effect of land cover and land-use intensity. Butterflies vary in their mobility and are characterized by complex life histories, a rapid life cycle and a high sensitivity to habitat area and quality. Thus, butterflies are widely acknowledged as indicator organisms suitable to assess the effects of land cover and land-use intensity (Settele et al., 2009; van Swaay et al., 2020). Previous studies have demonstrated that agricultural landscapes with a high share of permanent grasslands promote a high taxonomic diversity of butterflies (Bergmann et al., 2018; Öckinger and Smith, 2006). However, high land-use intensity can outweigh the positive effects of a high share of grasslands (Zingg et al., 2018). Negative effects on butterfly diversity have been shown e.g. for high nitrogen inputs as well as high stocking pressure (Kruess and Tschardt, 2002; WallisDeVries and van Swaay, 2017). Furthermore, land cover and land-use intensity can be modulated by species traits in various ways (Lütolf et al., 2009; Perović et al., 2015; Warren et al., 2021). For instance, butterfly species with a wide use of different habitats (“habitat generalists”) are able to reproduce in other habitat types than grassland habitats (e.g. fallow land, shrubland and forests) and may therefore be less dependent on the presence of permanent grasslands (Ekroos et al., 2013; Öckinger and Smith, 2006). In contrast, grassland butterflies that depend on specific low-productive habitat types such as dry grasslands (“habitat specialists”) have been shown to respond more sensitively to permanent grassland availability and quality (Öckinger and Smith, 2006; Warren et al., 2021). However, grasslands that are mostly not fertilized and show low productivity have become scarce in present-day European agricultural landscapes (Peeters, 2009). Another main

ecological trait for species to deal with unsuitable conditions is their mobility (see e.g. Carvalho et al., 2019). Large butterflies are more mobile than smaller ones (Freire et al., 2021) and thus have the ability to make use of habitat patches dispersed over large distances. Compared to smaller species, they are less prone to extinction by isolation (Börschig et al., 2013; Luppi et al., 2018; Perović et al., 2015).

Large-scale studies covering a large variety of agricultural landscapes are of major importance when assessing the processes and drivers of biodiversity decline (Habel et al., 2019b). However, only a few studies have used nationwide datasets to analyse the effects of land cover and land-use intensity on insects (but see Bergmann et al., 2018; Lütolf et al., 2009; Roth et al., 2021; WallisDeVries and van Swaay, 2017). In the present study, we aimed to assess the effects of land cover and land-use intensity on butterflies across a large geographic extent covering Germany. We used agricultural census data at municipality scale to calculate three indicators. The first indicator (“Grassland Index”, GI) is related to land cover and quantifies the share of permanent grasslands, thus, provides a quantitative measurement of habitat availability. The second and third indicator are both related to land-use intensity and were calculated based on detailed information on the number of livestock units per unit of land area. While the second indicator (“Total Livestock Density Index”, TLDI) serves as a proxy for the amount of organic fertilizer input to agricultural land, the third indicator (“Herbivore Livestock Density Index”, HLDI) can be interpreted as an index of the demand for fodder and thus of grassland management intensity in terms of grazing or mowing. We then related these indicators to nationwide butterfly data originating from the German Butterfly Monitoring Scheme (Kühn et al., 2008).

We addressed the following hypotheses: (1) butterfly species richness is promoted by a high share of permanent grasslands, (2) high organic fertilizer input and high herbivore livestock density are associated with a low butterfly species richness, and (3) butterfly communities shift towards habitat generalists and mobile species if the share of permanent grasslands is low and land-use intensity is high. Furthermore, we highlight potentials and limitations of using agricultural census data to quantify and assess the effects of land cover and land-use intensity on butterflies.

## 2. Material and methods

### 2.1. Butterfly data

We used data on butterflies originating from the German Butterfly Monitoring Scheme (*Tagfalter-Monitoring Deutschland - TMD*, <https://www.ufz.de/tagfalter-monitoring>, hereafter called “DEBMS”) coordinated by the Helmholtz Centre for Environmental Research, UFZ. Data were collected by volunteers by within-year repeated transect walks between April and September since 2005. While the location and course of a transect was freely chosen by each volunteer, transect walks were done following standardized protocols (for details see Kühn et al., 2008). A transect consists of a variable number of sections, each 50 m in length. The total length of transects may thus vary. All counted butterfly individuals observed during the transect walk were reported at the species or species-complex level and revised by experts and the UFZ. Butterfly transects have been established in each federal state of Germany, spanning a total area of ca. 365,900 km<sup>2</sup>.

Prior to analysis, we filtered data on butterflies (Papilionoidea) according to various criteria: To ensure that determination skills of volunteers did not affect our results, we removed species that cannot be easily distinguished (i.e. *Melitaea aurelia/britomartis* and *Leptidea reali/sinapis*) as well as species groups, which were not determined to the species level. In the present study we focused on butterfly species that mainly breed in open land (“grassland species”). These were identified using habitat associations documented in Reinhardt et al. (2007) and Settele et al. (2015). In total 78 species were included in subsequent analyses (see Table A1).

To match the butterfly data with the indicators related to land cover and land-use intensity (see below), we included transect counts from the years 2007, 2010 and 2016 only. Because we focused on species living in open landscapes, only transects were kept, which had at least 10 % of open habitats (arable land, grassland, heathland, moors and bogs based on the Basic Digital Landscape Model, Bundesamt für Kartographie und Geodäsie (2018)) within a buffer of 2 km around their transect centre points. To skip very short as well as very long transects, we filtered for transects with a number of sections between 5 and 20. This criterion was shown to work well in previous studies using data from the DEBMS (Rada et al., 2019). Further, the number of repeated surveys per year differed between transects. Thus, we selected only transect-year combinations with a minimum of six surveys per year to allow on average for one survey per month within the season of six months. We did not consider single records of a species as established populations, and consequently, we excluded transect-species combinations where a species was reported only once. Additionally, transect-year combinations with less than two species per year were excluded. The selection process led to 388 transects and 704 transect-year combinations.

## 2.2. Species traits

First, we determined species-specific habitat breadth using published information on habitat associations of German butterflies (Reinhardt et al., 2020), supplemented and revised by expert knowledge. Habitat breadth was measured as the number of habitats used by a given species across Germany. Hence, the smaller the habitat breadth, the higher the degree of specialization. Mean habitat breadth of local butterfly communities was quantified by calculating the arithmetic mean of species-specific habitat breadth over all observed species on a given transect in a given year.

In addition, we quantified the size of a species based on the wing index given by Middleton-Welling et al. (2020). The index represents a robust measurement of overall size, independent from regional and inter-specific differences (Middleton-Welling et al., 2020). The mean wing index of butterfly communities was quantified by calculating the arithmetic mean of species-specific wing indices over all observed species on a given transect in a given year. Wing size has been shown to highly correlate with mobility, with larger species being more mobile than smaller ones (Freire et al., 2021). The final list of species and their characteristics are shown in Table A1.

## 2.3. Agricultural census data

To calculate indicators related to land cover and land-use intensity, we used agricultural census data at the municipality scale across Germany (mean size of a municipality is 38.5 km<sup>2</sup>). Agricultural census data are collected in predefined time intervals by regional statistical authorities at the level of individual farms and consist of 35 land-use and animal-stock categories. Here, we used the most recent census data covering the years 2007, 2010 and 2016. Due to data protection regulations in Germany, published data are aggregated at the county level and contain several gaps. To derive a complete data set at municipality resolution without violating data protection regulations, we made use of a Bayesian approach described by Gocht and Röder (2014). The approach estimates cropping hectares and livestock herd sizes by combining county-level data, distributional information of the micro-census as well as remote sensing land-use data. The resulting dataset is available for public uses as part of the Thünen Atlas (Gocht, 2021).

We derived area-weighted mean land-use data in a buffer radius of 2 km surrounding each butterfly transect centre point. Using this approach allows to mitigate possible uncertainties due to the spatial resolution of land-use data. The distance of 2 km corresponds to the landscape level and has been reported to correlate with the spatial dynamics of butterfly populations (Wilson and Roy, 2009). Overall, land-use data from 863 municipalities were used to derive area-weighted

mean indicator values.

## 2.4. Land cover and land-use intensity indicators

To analyse the effect of land cover and land-use intensity on butterflies we derived three different indicators: a “Grassland Index” (GI), a “Total Livestock Density Index” (TLDI) and a “Herbivore Livestock Density Index” (HLDI). The Grassland Index was quantified by calculating the share of permanent grasslands in the total utilized agricultural area (UAA). In the EU, permanent grassland is defined as land used to grow grasses or other herbaceous forage that has not been included in the crop rotation of the holding for a duration of at least five years (European Commission, 2004). The indicator ranged from 0 to 1 (mean =  $0.32 \pm 0.23$  standard deviation), where 1 means that all of the UAA within the buffer zone consists of permanent grasslands. The share of permanent grasslands was negatively correlated with the share of arable land ( $\tau = -0.79$ ,  $z = -31.31$ ,  $p < 0,001$ ) and can be interpreted as an indicator for the number of habitats suitable for colonisation by butterflies occurring in open habitats. The TLDI as well as the HLDI were both calculated based on the number of livestock units per ha reference area (LSU/ha) and thus indicate the pressure of livestock on the environment. The TLDI was calculated based on the number of livestock units of all domestic animals (cattle, pigs, poultry, sheep, goats, horses) per UAA (except sites without agricultural production, i.e. fallow land). Because all animals produce organic manure, which in most cases gets distributed within the utilized agricultural area, this indicator is suitable for indicating agricultural land-use intensity in terms of organic fertilizer input to agricultural land (Svanbäck et al., 2019). TLDI per transect ranged from 0.01 to 4.07 LSU/ha, with a mean of  $0.62 \pm 0.51$  LSU/ha. The HLDI was calculated using the number of domestic herbivore species (cattle, sheep, goats and horses) per area of permanent grasslands plus fodder crops on arable land (i.e. temporary grasslands). High herbivore livestock density can indicate high grazing pressure when animals are free-ranging on pastures. When they are kept in shelters and feedlots instead, a high herbivore density indicates a higher number of mowing events to meet the forage demand. Consequently, the HLDI can be interpreted as an index of the demand for fodder and thus of land-use intensity in grasslands. HLDI per transect ranged from 0.05 to 3.80 LSU/ha, with a mean of  $1.11 \pm 0.52$  LSU/ha. The spatial patterns of the three indicators across Germany are shown in Figure A.1.

We detected three transect-year combinations containing TLDI and HLDI values larger than 10 LSU/ha. Because these values were more than 10 times larger than the standard deviation of all the other transects-year combinations (Table A3), we expected them to be unreliable estimates and, consequently, excluded them from further analysis. This led to a final data set of 386 transects and 701 transect-year combinations for subsequent analysis (transect centre points are shown in Figure A.2).

We checked for pairwise correlations between the indicators related to land cover and land-use intensity (Kendall’s correlation coefficient), but found no problematic collinearity ( $\tau > 0.5$ , Dormann et al. (2013)). There was a weak positive correlation ( $\tau = 0.396$ ,  $z = 15.688$ ,  $p < 0.001$ ) between GI and HLDI, indicating a tendency towards an increasing number of herbivore livestock units with an increasing share of grasslands per utilized agricultural area. Another positive correlation between TLDI and HLDI ( $\tau = 0.432$ ,  $z = 17.091$ ,  $p < 0.001$ ) indicated a tendency of an increasing total livestock density with an increasing herbivore livestock density. Because the given collinearity ( $\tau < 0.5$ ) was not expected to severely distort model estimation (Dormann et al., 2013), we decided to use both indicators in subsequent analyses.

A comparison of indicator values in municipalities surrounding butterfly transects against values across all municipalities in Germany indicated that the transects displayed a fairly representative cross-selection of agricultural landscapes (Figure A.3). However, on average, transects were located in landscapes with a slightly smaller share of permanent grasslands and lower TLDI and HLDI values,

indicating that land use in the surroundings of the transects was slightly less intense than on average throughout Germany. Still, roughly 80 % of all municipalities in Germany (with at least 10 % UAA) were characterized by mean land-use indicator values which were within the 95 % range of the values of landscapes around transects. Those municipalities that were not well-represented by the transects occurred mainly in the north-western parts of Germany, as well as in the southern parts, near the Alps (Figure A.3).

Prior to analysis we checked for the annual rate of change of land cover and land-use intensity indicator values of transects. Between 2007 and 2016 there was an annual reduction of GI, TLDI and HLDI values by ca. 0.5 %, 0.3 % and 1.2 % respectively. Because we assume the annual rate of change on transects to be too small to reveal effects on species richness and ecological traits of butterflies, we decided to use a space-for-time substitution approach, that is a commonly used study design allowing for broad-scale hypothesis testing (Davison et al., 2021).

## 2.5. Statistical analyses

To analyse the relationships between the response variables (species richness, habitat breadth and wing index) and predictor variables (GI, TLDI and HLDI), we applied generalised linear mixed effect models (GLMM). While the focus of our analyses was on the effect of the indicators related to land cover and land-use intensity, we also controlled for possible confounding effects of the sampling design (e.g. number of transect sections) and the location of transects (e.g. latitudes and longitudes). The model structure was as follows:

$$y \sim GI + TLDI + HLDI + n\ surveys + n\ sections + year + Natura2000 + lat + long + (1 | transect\ ID) + mat(position + 0 | group)$$

where “n surveys” was the number of surveys within the year of interest (log-transformed), “n sections” indicated the number of sections of a transect, “year” (2007, 2010, 2016) was a factor variable, and “Natura2000” was a binary variable indicating whether the transect centre point was situated within or outside of an area protected by the Natura2000 network. We used the binary “Natura2000” variable, because of the known effects of Natura2000 sites on species richness in DEBMS transects (Rada et al., 2019). The variable was used as a static parameter, because the data set is not updated annually (Bundesamt für Naturschutz, 2017). Because transects were not distributed within a systematic sampling grid, latitudes (“lat”) and longitudes (“long”) of the transect centre points were introduced in the analysis as explanatory variables to account for potential trends in factors related to geography (see e.g. Gutiérrez, 2009). The “transect ID” was added as a random effect with a random intercept to account for possible transect-specific effects. If necessary, the Matérn correlation function term “mat(position + 0 | group)” was included to correct for spatial autocorrelation in residuals (see paragraph below), where “position” is a factor containing the coordinates as numeric interpretable levels and “group” is a dummy grouping variable.

Prior to analysis we centred all continuous variables on their respective means. To get positive values for the wing index (which otherwise can be negative in some cases), the minimum value was added to all values. For species richness and habitat breadth we fitted generalised linear mixed effect models (GLMMs) with a gaussian error distribution. For the wing index we fitted GLMMs with a gamma error distribution and a logarithmic link function. Models for each response variable were fitted with restricted maximum likelihood (REML) to evaluate parameter estimates. Significant residual spatial autocorrelation was detected for species richness and wing index using the package

*DHARMA* (Hartig, 2022) (observed Moran’s I ( $\pm$ SD) is 0.076 ( $\pm$ 0.017;  $p < 0.001$ ) and 0.050 ( $\pm$ 0.017;  $p = 0.002$ ), respectively (Figure A.4). Thus, a Matérn correlation function term was implemented into the models for both response variables (Rasmussen and Williams, 2006). To test whether the effect of land cover and land-use intensity indicators was constant throughout years, we included an interaction term between the indicators and year. Since this approach performed worse (higher AIC scores) and did not reveal any significant ( $p < 0.05$ ) interactions (results are not shown here), we removed the term from our models. To test for a unimodal relationship of species richness in response to HLDI, we further included a quadratic term of HLDI. However, the squared term was non-significant and thus was removed from the model. To avoid overfitting, we then selected the most parsimonious model for each response based on the lowest AIC by backwards selecting of the indicators related to land cover and land-use intensity when  $\Delta$ AIC  $\geq 3$  (Burnham and Anderson, 2002). Final models were checked for normality of residuals and homogeneity of variance using the R package *DHARMA* version 0.4.5 (Hartig, 2022). No problematic collinearity (variance inflation factor  $< 2$ ; Zuur et al. (2010)) of predictors were found in the final models according to the R *performance* package version 0.8.0 (Lüdecke et al., 2021). To quantify the percentage of variability in the response explained by the predictors, we calculated pseudo- $R^2$  for final models as squared correlation between the response variable and the predicted values. To further examine the robustness of our final models, we used a validation set approach by randomly dividing the data set into a training set (70 % of all transects) and a validation set (remaining 30 % of transects) (James et al., 2021). For each set we predicted new response values and calculated the root-mean-square

error (RMSE). We run this process over 100 iterations, and afterwards, compared the mean RMSE over all iterations between both data sets. If the resulting RMSE estimates of training and validation set are very different from each other, this indicates potential problems with the model fit and thus a low robustness (for further information see Text A.1).

All calculations were performed with R Statistics, Version 4.2.1 (R Core Team, 2022) using the R package *glmmTMB* version 1.1.2.9 (Magnusson et al., 2021). We used the R packages *ggeffects* version 1.1.1 (Lüdecke, 2018) in combination with *ggplot2* version 3.3.5 (Wickham, 2016) to visualize the results.

## 3. Results

Per transect-year-combination, on average 14.7 ( $\pm$ 6.4 SD) grassland butterfly species were observed. Most common species were *Aglais io*, *Maniola jurtina* and *Pieris rapae*, that were recorded at least once in more than 90 % of all transects (Table A1). Mean habitat breadth and wing index was 6.8 ( $\pm$ 0.6 SD) and 0.029 ( $\pm$ 0.011 SD), respectively.

From the set of three indicators for land cover and land-use intensity only the Herbivore Livestock Density Index (HLDI) showed significant relationships with butterfly community metrics (Table 1). There was a weak negative association between HLDI and species richness, although this effect was not statistically significant ( $p = 0.06$ , Table 1, Fig. 1). Further, habitat breadth as well as wing index increased with increasing HLDI values per landscape (see Table 1, Fig. 1), indicating a shift in communities towards larger habitat generalist species with increasing herbivore stocking rate.

While there was an inconsistent effect of the factor year, the location of a transect affected all community metrics under study. Species

**Table 1**

Results of the GLMMs for butterfly species richness, habitat breadth and wing index. Shown are parameter estimates, standard error, z-value and significance. Values are given only for covariables remaining in the variable set after backwards selection. For each model pseudo-R<sup>2</sup> was calculated as squared correlation between the response variable and the predicted values. RMSE is given for a validation and test dataset based on cross-validation. Significant ( $p < 0.05$ ) estimates are in bold characters.

	Species richness				Habitat breadth				Wing index			
	Estimate	±SE	z value	p value	Estimate	±SE	z value	p value	Estimate	±SE	z value	p value
Intercept	<b>14.42</b>	<b>0.39</b>	<b>36.93</b>	<b>&lt;0.001</b>	<b>6.82</b>	<b>0.04</b>	<b>164.25</b>	<b>&lt;0.001</b>	<b>-3.51</b>	<b>0.03</b>	<b>-117.47</b>	<b>&lt;0.001</b>
GI	0.27	0.31	0.87	0.385	–	–	–	–	–	–	–	–
TLDI	-0.45	0.42	-1.06	0.288	–	–	–	–	–	–	–	–
HLDI	-0.78	0.42	-1.85	0.064	<b>0.16</b>	<b>0.05</b>	<b>3.12</b>	<b>0.002</b>	<b>0.09</b>	<b>0.03</b>	<b>2.65</b>	<b>0.008</b>
2010	-0.03	0.24	-0.14	0.890	0.04	0.05	0.91	0.361	-0.04	0.02	-1.70	0.885
2016	<b>-0.74</b>	<b>0.28</b>	<b>-2.69</b>	<b>0.007</b>	0.08	0.05	1.74	0.081	-0.01	0.03	-0.40	0.693
Natura2000	<b>3.09</b>	<b>0.62</b>	<b>4.99</b>	<b>&lt;0.001</b>	-0.08	0.07	-1.24	0.213	<b>-0.19</b>	<b>0.05</b>	<b>-4.25</b>	<b>&lt;0.001</b>
n sections	<b>1.45</b>	<b>0.28</b>	<b>5.10</b>	<b>&lt;0.001</b>	0.00	0.03	-0.02	0.980	<b>-0.04</b>	<b>0.02</b>	<b>-1.96</b>	<b>0.050</b>
n surveys	<b>2.18</b>	<b>0.18</b>	<b>11.85</b>	<b>&lt;0.001</b>	0.02	0.02	0.73	0.464	-0.01	0.02	-0.39	0.699
longitude	<b>1.08</b>	<b>0.35</b>	<b>3.08</b>	<b>0.002</b>	<b>-0.07</b>	<b>0.03</b>	<b>-2.41</b>	<b>0.016</b>	-0.02	0.02	-0.71	0.475
latitude	<b>-0.97</b>	<b>0.34</b>	<b>-2.88</b>	<b>0.004</b>	<b>0.16</b>	<b>0.03</b>	<b>5.62</b>	<b>&lt;0.001</b>	<b>0.05</b>	<b>0.02</b>	<b>2.06</b>	<b>0.039</b>
pseudo-R <sup>2</sup>	0.31				0.08				0.09			
RMSE training	0.35				0.08				0.35			
RMSE validation	0.37				0.09				0.37			

richness was significantly higher inside Natura2000 sites than outside, which is in line with the results of Rada et al. (2019). Moreover, butterfly communities had a smaller wing index inside Natura2000 sites than outside. The effect of the Natura2000 sites for species richness and wing index was consistently higher than the effect of indicators related to land cover and land-use intensity.

The pseudo-R<sup>2</sup> of final models ranged between 0.31 for species richness and 0.08 for habitat breadth. Root-mean-squared error for the validation set ranged between 0.35 for species richness and wing index and 0.08 for habitat breadth. There were only minor differences between the RMSE of the validation and training datasets, thus, indicating robust models.

#### 4. Discussion

##### 4.1. High herbivore livestock density is negatively associated with butterfly species richness

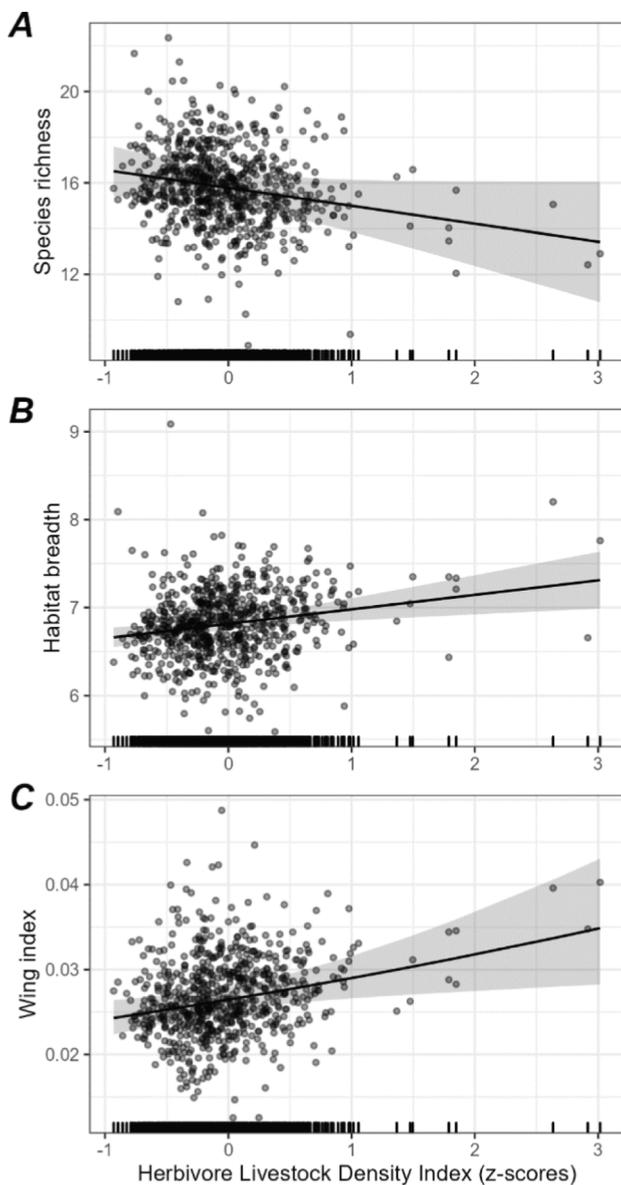
Grazing by domestic herbivores has historically dominated and shaped most of the central European landscapes over centuries (Kapfer, 2019). Along with agricultural intensification in the middle of the 20th century, landscapes with highly productive grasslands experienced an accumulation of livestock (Peeters, 2009). In contrast, landscapes with less productive grasslands experienced a decline in the number of small farms leading to habitat loss caused by the abandonment of grazing and mowing (Peeters, 2009; Schils et al., 2022). Both processes are known as major threats to species living in open land, e.g. for grassland butterflies (Warren et al., 2021). To stop and reverse abandonment, grazing is often seen as an essential tool for nature conservation purposes (Kapfer, 2019; Stewart and Pullin, 2008). However, whereas intensifying land use of a nearly abandoned pasture might result in positive effects, intensification of an extensively managed pasture might cause declines (Rakosy et al., 2022). Thus, understanding the consequences of different livestock densities is of major importance (Batáry et al., 2010). In accordance with our second hypothesis, the taxonomic diversity of grassland butterflies was negatively related to the Herbivore Livestock Density Index (HLDI). This result corroborates the review of van Klink et al. (2015) which has demonstrated a negative effect of high grazing intensity at arthropod diversity, mainly at local scales. Van Klink et al. (2015) have underlined that high management intensity can directly affect arthropod diversity due to increased mortality rates by grazing and trampling or mowing, especially in less mobile species and less mobile stages, i.e. in immature stages. Moreover, high management intensity has been shown to cause negative indirect effects as well, such as a homogenisation of plant communities and a dominance of grasses, resulting in a loss of food

plants and nectar sources for insects (Rakosy et al., 2022; WallisDeVries et al., 2016; WallisDeVries and Raemakers, 2001). Although we found a linear negative relationship between species richness and herbivore stocking density, negative effects can be expected on the opposite extreme of the gradient as well, i.e. without any active management (Settele et al., 2009; van Swaay et al., 2020). In the long term, succession due to extremely low management intensity or the abandonment of grassland management leads to woody plant encroachment into grasslands accompanied by unfavourable microclimatic conditions and, consequently, the disappearance of grassland butterflies (Öckinger et al., 2006a; van Swaay et al., 2020). Following the intermediate disturbance hypothesis (Connell, 1978), the highest diversity can be assumed at intermediate frequencies of disturbance, which is in line with a few studies that found unimodal relationships with the most positive effects at low to intermediate stocking densities (Dumont et al., 2009; Jerrentrup et al., 2014; Pöyry et al., 2006). However, agricultural census data do not contain information on abandoned grasslands because farmers need to manage permanent grasslands regularly to comply with the CAP's "minimum maintenance" requirement in order to receive payments. As a consequence, the linear relationship seen in our results could possibly be explained by the land-use intensity gradient which is covered only partly by agricultural census data, especially in terms of abandonment.

##### 4.2. Butterfly communities shift towards habitat generalists and mobile species with increasing herbivore livestock density

In line with our third hypothesis, butterfly communities shifted towards habitat generalists and large, mobile species with increasing livestock density of domestic herbivores. Hence, our results support the findings of several studies carried out across smaller spatial extents, that have demonstrated a higher number of mobile butterflies with higher land-use intensity (e.g. Börschig et al., 2013; Luppi et al., 2018; Perović et al., 2015).

Although we focused on grassland species, the ones with broader habitat ranges might also occur in other habitats, e.g. in open forests or alongside hedgerows. Consequently, such species might be able to avoid unsuitable conditions (i.e. highly managed grasslands), by making use of the surrounding habitat patches. In contrast to habitat specialists, they might still be found on transects at low-quality sites because of immigration from neighbouring high-quality habitats. Accordingly, a decrease in grassland quality can be assumed to particularly affect habitat specialists that have already experienced much more pronounced declines in the past decades than generalists (Eskildsen et al., 2015; Habel et al., 2019b; Laussmann et al., 2021).



**Fig. 1.** Relation of butterfly species richness (A), habitat breadth (B) and wing index (C) to Herbivore Livestock Density Index (HLDI). Shown are partial residuals (effect of the HLDI when all other predictors are held fixed at their means) of the observations (black dots) and the regression line (black line) with 95 % confidence intervals (shaded area around the fit) based on the final model.

#### 4.3. No association of butterflies with the grassland index (GI) and the total livestock density index (TLDI)

Contrary to our hypotheses, species richness and ecological traits of butterflies were neither significantly related to the Grassland Index (GI) nor to the Total Livestock Density Index (TLDI). Since landscapes with a high share of permanent grasslands are likely to contain a large variety of micro-habitats for butterflies, they are also likely to promote species richness (Bergmann et al., 2018; Öckinger and Smith, 2006). In contrast to our first hypothesis, our results were in line with studies that did not find an effect of the amount of grasslands in the surrounding landscapes on local butterfly communities (e.g. Carrié et al., 2018; Loos et al., 2014). The absence of a significant effect may be linked to other factors not covered by our model and interacting with the share of grasslands, such as landscape composition and configuration (Carrié et al., 2018). In support of this, Ekroos et al. (2013) reported decreasing species richness of butterflies with increasing distance to semi-natural grasslands.

Additionally, the result might indicate the importance of habitat quality which potentially negotiates the effect of habitat quantity (Zingg et al., 2018). Studies reporting positive effects of habitat quantity mainly focused on grasslands of high habitat quality, i.e. semi-natural and calcareous grasslands (e.g. Ekroos et al., 2013; Öckinger and Smith, 2006). Besides the differentiation between temporary and permanent grasslands, agricultural census data do not offer further information about the quality of grasslands. According to our results, this differentiation seems not to be sufficient to efficiently assess the effect of the share of grasslands on butterflies across large geographic extents. Hence, our result indicates that additional data on landscape configuration and the quality of permanent grasslands is needed to better understand their effects on butterflies.

One of the parameters determining grassland quality is the total amount of nitrogen fertilizers applied. Accordingly, it is considered as one of the key factors affecting the status and trend of butterflies (Roth et al., 2021; WallisDeVries and van Swaay, 2017). Several studies have shown a negative effect of high nitrogen inputs on butterflies due to a homogenization of vegetation, the dominance of grasses and, consequently, a change in microclimatic conditions (Carvalho et al., 2019; Roth et al., 2021). Although the here presented results support our second and third hypothesis in terms of herbivore livestock density, we could not detect a significant effect of organic fertilizer input on both, butterfly species richness and community composition. An underlying assumption in our study is that the Total Livestock Density Index (TLDI) is representative for the total organic nitrogen input in agricultural land. However, besides manure from local livestock rearing, additional sources of nitrogen might contribute to nitrogen input, such as the import by manure transportation (McMillan, 2018). Manure transportation, however, is prominent especially in landscapes with the highest manure production rates in Germany (McMillan, 2018), and thus can be assumed to be relevant only for a few spatially restricted regions containing a minority of butterfly transects, especially in municipalities not represented by the DEBMS (see Figure A.3). The application of synthetic nitrogen fertilizers as an additional source of nitrogen in grasslands is considered to be less relevant in comparison to organic fertilizers (Flisch et al., 2009). Besides direct nitrogen input, atmospheric deposition is known to have a large impact as well (Nijssen et al., 2017) and, consequently, might act as another source of uncertainty to our data. Several studies have demonstrated that the effect of nitrogen input may depend on species characteristics, such as host plant association (see e.g. Carvalho et al., 2019; Öckinger et al., 2006b). For example, nettles usually prefer nitrogen-rich sites (Reif et al., 1985) and, consequently, we expect nettle-feeders to be less sensitive against high nitrogen input. In line with this expectation, nettle-feeding butterfly species (e.g. *A. io*, *A. urticae*, *V. atalanta*) can be found in a majority of agricultural landscapes and belong to the most common ones in our dataset (Table A1). Another explanation for missing effects might be that land-use intensity often varies between years (Allan et al., 2014) and insects eventually lag behind and rather react to long-term effects of eutrophication (Carvalho et al., 2019).

#### 4.4. Data limitations

With regard to land use in agricultural landscapes in Germany, one of the most consistent data set openly available is the agricultural census data. They comprise some of the most relevant factors for farmland biodiversity. We here show that a majority of agricultural landscapes in Germany is covered by butterfly transects of the DEBMS, especially at intermediate land-use intensities (Table A3). Thus, our results demonstrate that data originating from the DEBMS in combination with agricultural census data are generally well suited for analysing patterns of butterfly diversity across most German agricultural landscapes. However, data at municipality scale often show large uncertainties due to coarse spatial and thematic resolution of census data. Even though we found a significant relationship between herbivore livestock density and

butterflies, we do not know whether livestock is free-ranging on pastures or kept in shelters and feed-lots. Further, there is no information on the duration of grazing and the grazing system. A high livestock density in a municipality, thus, does not necessarily indicate high grazing pressure in grasslands. Hence, agricultural census data alone do not allow to draw conclusions concerning the differentiation between effects of grazing and mowing, which has been shown to affect species differently (Korrmann et al., 2019; WallisDeVries and Raemakers, 2001).

Whereas the RMSE for each model was nearly similar for the training and the validation data set, indicating robust model estimates, the fixed variables in the final models explained only 8 % and 9 % of the total variation in habitat breadth and wing index, respectively (Table 1). This indicates that a large amount of variation could not be attributed to the indicators and covariates used in the final models. Thus, additional parameters not considered in this study may have an effect on community composition in terms of habitat specialization and wing index. This is supported by studies showing that landscape configuration can affect species differently, depending on their degree of specialization (Ekroos et al., 2013; Krauss et al., 2003; Perović et al., 2015). Although the implementation of e.g. the edge density as a proxy for connectivity and refuge habitats might potentially increase the total variance explained by the model, there is no such information available in the agricultural census data. Accordingly, our study highlights the need for more precise data on land cover and land-use intensity at the national level, particularly for drivers that are likely to affect species living in open land, such as landscape configuration, as well as spatial patterns and intensity of mowing and livestock grazing.

## 5. Future prospects

Our study demonstrates that indicators related to grassland management intensity based on livestock distribution data can provide insight into processes and spatial diversity patterns of butterflies at the national level. The results add to the growing evidence that high management intensity in grasslands has detrimental effects on butterflies (e.g. Kruss and Tschamtkke, 2002; Öckinger et al., 2006b; Zingg et al., 2018). Nevertheless, our study illustrates that the explanatory power of agricultural census data to detect effects of land cover and land-use intensity on butterflies across large geographic extents is limited. Thus, we emphasize the need for additional information and better spatial resolution of data describing the distribution of livestock, mowing frequency and mineral fertilizer inputs. Future analysis should therefore incorporate other data sources, such as the Integrated Administration and Control System (IACS), that could help to partly address these limitations by providing more detailed information on livestock at the farm scale (Lomba et al., 2017). Unfortunately, such data often underlie strict data protection regulations, which prove an obstacle to its use in scientific analyses. During the past years, the availability of high-resolution, multi-spectral and multi-temporal satellite data has increased tremendously (Schwieder et al., 2022), enabling for example the mapping of mowing events for permanent grasslands in Germany (Schwieder et al., 2022). Accordingly, a natural follow-up of this study is the use of such high-resolution data to enhance our understanding of the effects of grassland management intensity on butterfly diversity at the national level.

## CRedit authorship contribution statement

**Toni Kasiske:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Jens Dauber:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing. **Alexander Harpke:** Conceptualization, Data curation. **Sebastian Klimek:** Conceptualization, Funding acquisition, Data curation, Methodology, Writing – review & editing. **Elisabeth Kühn:** Conceptualization, Data curation, Writing – review & editing. **Josef Settele:** Conceptualization, Supervision, Data curation. **Martin**

**Musche:** Conceptualization, Data curation, Methodology, Writing – review & editing

## 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.

## Data availability

The authors do not have permission to share data.

## Acknowledgements

We express our sincere gratitude to all volunteers taking part in the German Butterfly Monitoring Scheme and collecting data in the field. We thank Sebastian Neuenfeldt and Norbert Röder for providing the agricultural census data. Funding was provided by the German Federal Ministry of Food and Agriculture as part of the joint project “Monitoring der biologischen Vielfalt in Agrarlandschaften” (MonViA, Monitoring of biodiversity in agricultural landscapes). M.M. was supported by the projects eLTER PLUS (grant number 871128) and EUROPABON (grant number 101003553) funded under the EU’s research and innovation funding programme HORIZON 2020. Finally, we would like to thank two anonymous reviewers for their very constructive comments on an earlier version of that manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2023.109866>.

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