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ORIGINAL RESEARCH

Assessing landscape-level effects of permanent grassland management and landscape configuration on open-land butterflies based on national monitoring data

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Abstract

Halting and reversing the ongoing insect decline requires in-depth knowledge on key drivers. Due to their sensitivity to habitat quality, butterflies are valuable indicators for grassland management intensity, including mowing. However, most studies examining mowing regime impacts on butterflies are limited to small spatial extents. Here, we tested the potential of citizen science butterfly monitoring data for assessing landscape-level effects of mowing regimes (number of mowing events and timing of the first event) and edge density (density of boundaries between different land-cover types) on butterfly richness, abundance, and community composition. We used generalised linear mixed-effects models to relate nationwide data from the German Butterfly Monitoring Scheme (DEBMS) to high-resolution satellite imagery on mowing events in permanent grasslands (grasslands excluded from crop rotation). As butterfly transects may not consistently be located within grasslands, we ran our models for different thresholds from 0 to 50%, representing increasing shares of the transect route situated within permanent grasslands (10% intervals). We did not find significant associations between mowing regimes and butterflies when focussing on species richness and abundance of all species inhabiting open land. However, we found strong positive associations of delayed mowing with the abundance of grassland specialists with increasing grassland shares per transect. Further, we found negative associations of delayed mowing with the annual number of generations and of more frequent mowing with the abundance of specialists, depending on the share of grassland per transect. Edge density had a positive association with species richness and abundance of species inhabiting open land, as well as abundance of grassland indicator species and grassland specialists in landscapes with a low grassland share per transect. Our findings underscore the importance of low-intensity managed permanent grasslands at the landscape scale for specialised butterflies. Additionally, we highlight the importance of a high density of boundaries for open-land and specialised butterflies, particularly in landscapes with highly fragmented permanent grasslands. To improve future analyses of

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grassland management impacts, we recommend expanding DEBMS monitoring sites to cover a larger grassland management intensity gradient and to place more transects within grasslands.

Keywords Conservation · Citizen science · Biodiversity · Landscape configuration · Mowing regimes · Satellite imagery

Introduction

In the face of the ongoing decline in invertebrate populations (Seibold et al. 2019; van Klink et al. 2022), mitigating the impacts of agricultural practices on pollinators has become of paramount importance (Kovács-Hostyánszki et al. 2017; Sutton et al. 2016). Over the past decades, intensive agricultural management has led to reduced habitat quality and landscape simplification, resulting in biotic homogenization (Gamez-Virues et al. 2015) and displacement of specialists by generalist species (Perović et al. 2015).

Low-intensity managed permanent grasslands are among the most biodiverse habitats in Europe and play a crucial role in supporting biodiversity and providing essential ecosystem services within agricultural landscapes (Bengtsson et al. 2019; Tamburini et al. 2022). However, these grasslands have faced substantial declines in extent and quality in recent decades, largely due to intensified management practices, land conversion, and abandonment (Estel et al. 2015; Schils et al. 2022). Among the various organisms dependent on low-intensity managed grasslands, particularly butterflies have undergone a sharp decline in species richness and abundance in Europe over recent decades (van Strien et al. 2019; van Swaay et al. 2020). To reverse the decline of butterflies by 2030, Member States of the European Union shall put in place restoration measures in agricultural ecosystems, such as reducing the intensity of permanent grassland management, as part of the EU Nature Restoration Law (European Commission 2022). Given their sensitivity to environmental changes, butterflies serve as valuable indicator organisms to evaluate the success of restoration measures (Settele et al. 2009). To date, more than 20 European countries have established citizen science Butterfly Monitoring Schemes, all adopting a uniform method facilitating data comparison and analysis across Europe (Van Swaay et al. 2020). An important outcome of these initiatives is the European Butterfly Indicator for Grassland species, providing insights into the status and trends of 17 widespread and specialist grassland butterflies (hereafter called “indicator species”) across Europe (Van Swaay et al. 2020). Recognized as a key EU biodiversity indicator, it has recently been included in the proposed EU Nature Restoration Law (European Commission 2022). Against this background, understanding the impact of grassland management intensity on butterflies becomes imperative for policy purposes, yet remains currently limited, particularly at national scales.

Within the three dimensions of grassland management intensity (fertilization, mowing, and grazing), mowing is one of the predominant management practices for European grasslands, playing a crucial role in shaping their ecological dynamics (van Klink et al. 2019). Mowing is frequently employed to maintain permanent grasslands, supported by the Common Agricultural Policy (CAP) of the EU (Bakker 2012; Settele et al. 2009). Less frequent mowing supports favourable microclimatic conditions for species adapted to warm and sunny grasslands by preserving high plant diversity and preventing shrub encroachment

(Bakker 2012). However, more intensive mowing regimes can also have adverse consequences (Schils et al. 2022). These include direct threats, such as increased mortality of grass-dwelling species due to cuts (Humbert et al. 2010; van de Poel and Zehm 2014), reduced availability of nectar and food plants due to changes in plant communities (WallisDeVries and Raemakers 2001), and increased predation risks (van Klink et al. 2015). Delayed first mowing events generally benefit butterflies by allowing them to complete their life cycles and reproduce before the cutting occurs, leading to higher survival rates (Settele et al. 2009; van de Poel and Zehm 2014; van Klink et al. 2019).

Previous work indicates that, in addition to permanent grassland management, the landscape context, particularly its configuration, also affects butterfly populations (Perović et al. 2015; Weibull et al. 2000). For instance, landscapes characterized by numerous edges may offer various green infrastructure elements like roadside ditches, field margins, or hedgerows. These elements can provide suitable breeding, foraging, and roosting conditions (Noordijk et al. 2009; Settele et al. 2009), and may serve as refuges for butterflies in landscapes with intensive grassland mowing regimes (Li et al. 2020). Moreover, such elements may act as corridors or stepping-stone habitats, facilitating butterfly movement across agricultural landscapes and supporting the survival of populations with limited dispersal abilities (Dover et al. 2000; Martin et al. 2019).

Depending on their specific traits, butterflies respond differently to permanent grassland management (Perović et al. 2015; van Klink et al. 2019). While butterflies inhabiting open landscapes (i.e., butterfly species occurring outside of forests; hereafter called “open-land butterflies”) are generally adapted to permanent grasslands for breeding and foraging, grassland specialists with specific habitat requirements, such as the presence of particular food-plants, are expected to be particularly vulnerable to intensive mowing regimes, which can disturb their habitats and lead to the loss of food sources (Bruppacher et al. 2016). Similarly, species with a single generation per year may be more sensitive to mowing events due to increased mortality during their vulnerable life stages, whereas species with high reproductive capacity and shorter generation times can recover faster from intensive mowing regimes (Börschig et al. 2013; Szabó et al. 2022). Mobile species that are capable of long-distance movements may also be less affected by mowing intensity as they can effectively exploit resources at the landscape scale, potentially compensating for local disturbances (Börschig et al. 2013; Luppi et al. 2018).

Most studies assessing the impact of mowing regimes on butterflies have been restricted to small spatial extents (e.g. Bruppacher et al. 2016; Luppi et al. 2018; van Klink et al. 2019). In contrast, there has been limited exploration of large-scale butterfly monitoring data in relation to grassland management intensity (but see Kasiske et al. 2023; Meier et al. 2022). Further, recent studies on mowing regimes have yielded inconsistent findings, with some reporting positive, negative, or neutral effects, often attributed to significant confounding factors (Humbert et al. 2012; Tälle et al. 2018), such as landscape configuration (Perović et al. 2015; Weibull et al. 2000) and grassland productivity (Hautier et al. 2009). Given the continuous decline in butterflies across large spatial scales, as reported by the European Butterfly Indicator for Grassland species (van Swaay et al. 2020), there is an urgent need to inform policy regarding the potential drivers behind these negative trends so that effective counterstrategies can be developed.

Using the German Butterfly Monitoring Scheme as a case study, we aimed to assess the potential use of butterfly data collected through a nationwide citizen science monitoring scheme to get a better understanding of potential landscape-level determinants of butterfly diversity in open landscapes. Specifically, we investigated the impacts of grassland mowing regimes (number of mowing events and timing of the first mowing event), and edge density (density of boundaries between different land-cover types) on butterfly diversity across 286 landscapes (i.e., transect routes and their surroundings) in Germany between 2017 and 2021. We focused our analyses on the richness and abundance of open-land butterflies, along with the abundance of grassland indicator species and grassland specialists, to encompass different levels of habitat specialisations. Additionally, we explored whether specific traits within butterfly communities, such as mobility and voltinism, modulate the observed effects. Specifically, we asked the following questions:

1. How do grassland mowing regimes affect species richness and abundance of open-land butterflies at the landscape scale?
2. Does edge density affect open-land butterfly species richness and abundance and, if so, does this impact interact with the average number of mowing events?
3. Do the observed relationships differ among species with respect to habitat specialisation (i.e. abundance of grassland indicator species and grassland specialists) and to specific traits (mobility and voltinism)?

Materials and methods

Butterfly data

We obtained butterfly data 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, and the German Society for Butterfly Conservation - GfS. As the DEBMS is a component of the European Butterfly Monitoring Scheme (eBMS), its data contributes to the calculation of the European Butterfly Indicator for Grassland species (van Swaay et al. 2020). Surveys within the DEBMS have been conducted by volunteers through within-year repeated transect walks between April and September since 2005. Volunteers follow standardized protocols during the surveys (for details see Kühn et al. 2014), but are free to choose the length, location, and route of the transects. Different land-cover types are covered by this survey method (e.g. hedges, grasslands, arable land or forests) and the share of the transect route situated within permanent grasslands varies strongly (Fig. 1). All observed butterflies encountered during the transect walks are recorded and reported at the species or species-complex level. Butterfly transects have been established in each federal state of Germany, dispersed across an area of approximately 360,000 km² (Fig. 1).

Prior to the analysis, we excluded species complexes, which were not determined to the species level, and species that cannot be easily distinguished by volunteers (i.e. *Melitaea aurelia* / *britomartis* and *Leptidea juvernica* / *sinapis*). We did not anticipate effects of permanent grassland management on species primarily inhabiting forests and hence selected for butterflies that mainly reproduce in open land (i.e., species mainly occurring outside of forests), according to their habitat associations documented in Reinhardt et al. (2007), Rein-

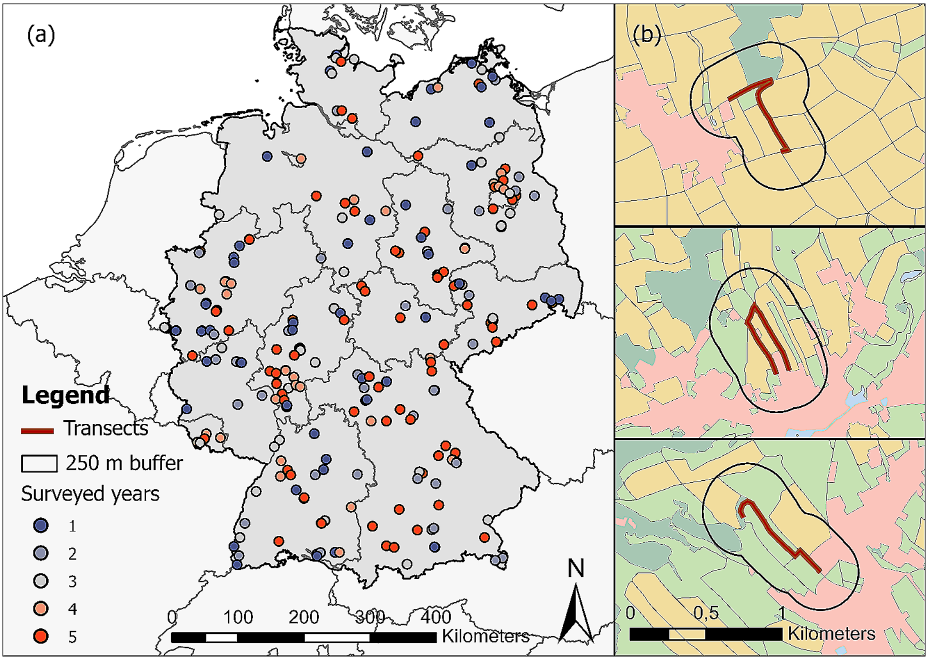

Fig. 1 (**a**) Centre points of the 286 butterfly transects across Germany used for the analyses. (**b**) Location of three example transects and their 250 m buffer. Background colours in (**b**) indicate different land-cover types based on the national Basic Digital Landscape Model (BDLM; Bundesamt für Kartographie und Geodäsie 2018). Yellow: arable land; light green: grasslands; dark green: forests; red: urban areas; blue: water bodies

hardt et al. (2020), and Settele et al. (2015). We excluded 27 forest-dwelling species during this process, resulting in a set of 48 open-land butterfly species used in our analyses (see Table S1). We matched butterfly data with data on grassland mowing regimes using transect counts between 2017 and 2021. We excluded transects shorter than 200 m and longer than 1000 m to minimize the impact of extreme values (mean transect length: *c*. 430 m, sd: *c*. 190 m). Further, we only selected transect-year combinations that had a minimum of six surveys per year and recorded a minimum of two butterfly species in a given year. Because we were mainly interested in revealing landscape-level impacts of grassland mowing regimes, we excluded transects that did not contain any permanent grasslands within a 250 m buffer (see Section. 2.3), for which we used remote sensing-based maps on mowing regimes across Germany (Schwieder et al. 2022; see Text S2). The selection of a 250 m buffer distance has previously been shown to account for the landscape context relevant for butterflies (Flick et al. 2012; Krauss et al. 2003; Perović et al. 2015). Our final data set encompassed approximately 416,000 individual butterflies observed on 286 transects (Fig. 1), covering 901 transect-year combinations.

We calculated species richness of open-land butterflies for each transect-year combination. To obtain a measure of abundance, we computed a Generalized Abundance Index (Dennis et al. 2016) (hereafter called “GAI”) for each butterfly species on a given transect in a given year, using the R package *rbms* version 1.1.3 (Schmucki et al. 2022) (for details see Text S1). By summing GAI values, we obtained the overall abundance of open-land butterflies for a given transect in a given year. In addition, we focused on habitat specialisation by calculating the abundance of grassland species included in the European Butterfly Indicator for Grassland species for each transect-year combination (van Swaay et al. 2016). This indicator encompasses seven widespread grassland species (*Ochlodes sylvanus*, *Anthocharis cardamines*, *Lycaena phlaeas*, *Polyommatus icarus*, *Lasiommata megera*, *Coenonympha pamphilus*, and *Maniola jurtina*) as well as ten specialised grassland species (*Cupido minimus*, *Cyaniris semiargus*, *Erynnis tages*, *Euphydryas aurinia*, *Phengaris arion*, *Phengaris nausithous*, *Lysandra bellargus*, *Lysandra coridon*, *Spialia sertorius*, and *Thymelicus acteon*). We expected this set of 17 indicator species to be generally more adapted to permanent grasslands than the entire set of 48 open-land species. Due to the rarity of three specialised species (*Euphydryas aurinia*, *Phengaris arion*, *Spialia sertorius*), we could not estimate GAI for them and excluded these species from our analysis (see Table S1). To assess whether the set of indicator species shows similar responses to grassland mowing regimes and landscape configuration as specialised grassland species, we also calculated abundance values for the subset of seven specialist species (see Table S1). This subset comprises species that predominantly reproduce in grassland habitats, possess highly-specific habitat requirements (such as specific food plants and the adaptation to specific microclimatic conditions), and are widely distributed across Europe (van Swaay et al. 2016). Due to their degree of habitat specialisation, we anticipated this set to display the highest sensitivity to grassland mowing regimes.

Species traits

To assess the landscape-level impacts of mowing regimes and landscape configuration on community composition, we calculated community-weighted mean (CWM) values for two species traits: mobility and voltinism. CWM values consider the relative abundance (using GAI values) of the species (limited to the 48 open-land butterflies) present on a transect in a specific year, indicating shifts in the average trait values in response to predictor variables. We derived the CWM wing index as an indicator for mobility (Freire et al. 2021; Kuussaari et al. 2014), representing a robust measure of overall wing size based on species-specific values from Middleton-Welling et al. (2020). Regarding voltinism, we calculated CWM values based on species-specific values for the maximum number of generations per year, provided by Middleton-Welling et al. (2020), which we supplemented with German observations from the DEBMS. The final list of species and their traits are shown in Table S1.

Mowing regimes

We assessed the influence of grassland mowing regimes using high-resolution (10 m x 10 m) data on mowing regimes across Germany, derived from Sentinel-2 and Landsat 8 satellite imaginary for the years 2017 to 2021 (Schwieder et al. 2022). These maps provide information on the number of mowing events (further called “mowing frequency”) and the day of the first mowing event (further called “timing of mowing”) per year, covering all permanent grasslands (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) in Germany. We excluded temporary grasslands from our study as they are part of the crop rotation on arable land, regularly sown and ploughed (Schils et al. 2022), and therefore do not provide suitable breeding habitats for butterflies. Permanent grasslands can be managed through mowing, grazing, or a combination of both. It is important to note that the algorithm used does not allow for the direct differentiation between meadows and pastures (Schwieder et al. 2022). Grazing schemes with high stocking density can lead to comparable changes in the spectral signal, similar to biomass removal by mowing, potentially causing the algorithm to detect these grazing events as mowing. However, the algorithm may fail to detect grazing with lower stocking density, where minimal biomass removal occurs (Schwieder et al. 2022). To account for the landscape context and to mitigate uncertainties due to potential misclassification, we calculated a grassland area-weighted mean for mowing frequency and timing of mowing within a 250 m buffer surrounding each butterfly transect (see Text S2 for further details).

Edge density

To assess landscape configuration, we calculated the edge density (in km/ha) within 250 m buffers as the density of boundaries between land-cover types based on the national Basic Digital Landscape Model (BDLM; Bundesamt für Kartographie und Geodäsie 2018). We classified eight land-cover types, including permanent grasslands, arable land, urban areas, traffic infrastructure, forests, small woody features, semi-natural land, and water bodies (Table S2). Streets, railroads, and streams, which were defined as line features in the BDLM, were buffered with a radius of two meters to represent realistic areas. We excluded boundaries within forests and urban areas (e.g., streets within cities) from the analysis, as our focus was on species inhabiting open landscapes. The calculated edge density is expected to capture various vegetation structures at the boundaries that may benefit butterflies. For instance, a low intensity managed strip of grassy and herbaceous vegetation may exist between a grassland and a forest, where different management practices converge. Given the infrequent updates of the BDLM and minimal expected changes in edges between land-cover types over five years, we used the edge density of the year 2018 for the entire analysis.

Representativeness of butterfly transects

Since the selection of butterfly transect locations was based on volunteer decisions, there is a possibility of non-random dispersion of transects across different landscapes, potentially leading to biases such as a preference of volunteers to place transects near human populated areas (Kühn et al. 2008). Therefore, we evaluated the representativeness of the transects for each predictor variable by randomly sampling 10,000 different landscapes (250 m buffer surrounding randomly selected points) across Germany for the year 2020 and compared the mean values of mowing frequency, timing of mowing, edge density, and landscape-level grassland proportions between random samples and our transects. Furthermore, we computed the mean distance from transects to the nearest edge to assess whether transects predominantly align with edges or are situated within open land, such as grasslands (further details given in Text S3).

Statistical analyses

To analyse the relationships between our response variables (species richness, abundance of open-land butterflies, abundance of indicator species and grassland specialists, wing index, and voltinism) and predictor variables, we applied generalised linear mixed-effects models (GLMM). While the focus of our analyses was on grassland mowing regimes and edge density, we also controlled for possible confounding effects of the sampling design and the location of transects. Key components of the sampling design included the annual survey count, transect length, and the specific year of survey (Table 1). The geographical location of the transects was delineated by their coordinates (Table 1). To account for differences in habitat availability, we further included the proportion of permanent grasslands within the 250 m buffer surrounding each transect. Moreover, we considered whether the transect fell within an area protected by the Natura2000 network (see Table 1 for a detailed description). The model structure utilized in our analysis was as follows:

Table 1 Predictor variables used for model building

Predictor	Description
Edge density	Edge density in km/ha within the 250 m buffer, measured as the density of boundaries between different land-cover types
Mowing frequency	Mean number of mowing events within the 250 m buffer
Timing of mowing	Mean day of the first mowing event within the 250 m buffer
Grasslands	Proportion of permanent grasslands within the 250 m buffer, derived from Blickensdörfer et al. (2022).
log(Surveys)	Number of surveys conducted within the year of interest (log-transformed). Because the number of surveys was used to calculate the abundance, already, this variable was used for the species richness models only.
log(Length)	Length of each transect in meter (log-transformed)
Year	Year as factor variable encompassing the years 2017 to 2021
Natura2000	Binary indication whether the transect centre point was located within or outside of an area protected by the Natura2000 network. As Natura2000 areas often cover landscapes with a high biodiversity value (such as calcareous grasslands), they are expected to impact butterflies, independent of the grassland management. Their positive impact on butterflies in DEBMS transects has previously been shown by Rada et al. (2019). The variable was used as a static parameter due to the lack of annual updates in the dataset (Bundesamt für Naturschutz 2017).
Latitude	y-Coordinates of the transect centre points to account for potential geographic trends (Gutiérrez 2009)
Longitude	x-Coordinates of the transect centre points to account for potential geographic trends (Gutiérrez 2009)
Random effect	Transect ID as random intercept

$$y \sim \text{Edge density} * \text{Mowing frequency} + \text{Timing of mowing} \\ + Grasslands + \log(Surveys) + \log(Length) + Year \\ + Natura2000 + Latitude + Longitude + \text{Random effect}$$

To assess whether the density of edges in the surrounding landscapes modulates the effects of mowing frequency on butterflies, we incorporated the interaction between edge density and mowing frequency in all models. Given the known large inter-annual variability in butterfly populations (Kühn et al. 2022), we employed pooled models encompassing all five consecutive years. To investigate whether the effects of mowing regimes become more pronounced when transect routes are increasingly situated within permanent grasslands compared to those covering other land-cover types, we established several models using different transect subsets based on the share of each transect route situated within grasslands, ranging from 0 to 50% (10% intervals). Out of the full set of 286 transects, the sample size decreased to 55 transects for a threshold of 50% ($n_{\geq 0\%} = 286$, $n_{>10\%} = 146$, $n_{>20\%} = 116$, $n_{>30\%} = 88$, $n_{>40\%} = 65$, $n_{>50\%} = 55$). Prior to analyses, we standardized all continuous variables by centring them on their respective means. We then examined pairwise correlations using Kendall`s correlation coefficient among response variables, but found no problematic collinearity with all $\tau < 0.7$ (Dormann et al. 2013; for details see Text S 4). To ensure positive values for the wing index, we added the minimum value to the standardized values. Abundance index values were rounded to integers to represent counts. We fitted GLMMs using the *glmmTMB* package version 1.1.5 (Magnusson et al. 2021). To analyse species richness and the abundance of open-land butterflies, as well as the abundance of indicator species and grassland specialists, we used either a Poisson error distribution with a logarithmic link function or a negative binomial distribution with linear parameterization (“nbinom1”). We selected the appropriate distribution based on visual inspection of model performance plots concerning normality of residuals and homogeneity of variance, using the *DHARMa* package version 0.4.6 (Hartig 2022). For wing index and voltinism, we fitted GLMMs either with a Gaussian error distribution or a gamma distribution with a logarithmic link function. We evaluated parameter estimates using restricted maximum likelihood (REML) estimation. We checked for significant ($p < 0.05$) residual spatial autocorrelation based on the global model covering all transects, by calculating the Moran’s I coefficient using the *DHARMa* package version 0.4.6 (Hartig 2022). We detected no significant residual spatial autocorrelation. Building upon the full model, we set up 11 individual models for each response and each transect subset. This involved exploring all possible combinations of timing and frequency of mowing, edge density, and the interaction between mowing frequency and edge density. Additionally, we included one model without any of these three variables as a baseline model. All other variables were held constant in each model. Subsequently, we identified a top model set for each response variable consisting of models with a difference in Akaike Information Criterion (ΔAIC) less than 6 (Harrison et al. 2018; Richards 2008) in comparison to the model with lowest AIC values. We averaged across this model set to obtain average coefficient estimates. We used the “*dredge*” and “*model.avg*” functions from the *MuMIn* package version 1.47.1 (Bartoń 2022) for model selection and averaging, respectively. We calculated pseudo-R^2 values to assess the goodness-of-fit of our averaged models by squaring the correlation between the response variable and the predicted values. To examine the robustness of final models, we compared the root-mean-square error (RMSE) of a training set and a validation set using repeated cross-validation (Guisan and

Zimmermann 2000; James et al. 2021). Deviations between the RMSE estimates of the training and validation set indicate potential problems with model fit and lower robustness (for further information see Text S5).

All calculations were performed using R Statistics, Version 4.2.1 (R Core Team 2022). The R packages *ggeffects* version 1.1.4 (Lüdecke 2018) in combination with *ggplot2* version 3.4.1 (Wickham 2016) were used to visualize the results.

Results

On average, 13.7 (sd=6.2) open-land butterfly species were observed per transect-year-combination. The most frequently encountered species were *Maniola jurtina*, *Aglais io*, *Pieris rapae*, and *Pieris brassicae*, which were recorded in over 85% of all transects (see Table S1). The estimated mean abundance for open-land species was 149.2 (sd=95.7), while for the subset of 14 indicator species it was 63.5 (sd=46.9). When considering the subset of seven grassland specialists, the estimated mean abundance was 4.5 (sd=12.0). Open-land butterflies in transect communities, on average, exhibited a mean wing index of 0.057 (sd=0.014) and 2.0 (sd=0.4) generations annually.

Landscape characteristics

While, on average, the landscapes within the 250 m buffers around the transects comprised about 13% (sd=16%) permanent grasslands, approximately 19% (sd: 26%) of each transect route was directly situated within permanent grasslands. Landscape-level mowing frequency varied from 0 to 5 times per year, with an average of 1.5 (sd=0.7). The timing of mowing ranged between day 94 (beginning of April) and day 281 (beginning of October), averaging day 177 (end of June; sd=27 days). Edge density at the landscape scale ranged from 0.00 to 1.23 km/ha, with a mean of 0.20 km/ha (sd=0.15 km/ha).

Effects on butterflies

The fixed effects of the averaged models explained between 16% (abundance of open-land butterflies) and 71% (species richness of open-land butterflies) of the variation in the respective target variable (Table 10). Minimum values for the standardized root-mean-squared error (RMSE) for the validation set ranged between 0.13 for voltinism and 2.31 for grassland specialists. There were only minor differences between the RMSE of the validation and training set, thus, indicating robust models (Table S10).

Effects of grassland mowing regimes

Throughout the five-year study period, we observed no significant associations between mowing regimes and open-land butterflies at the landscape scale. A higher share of transect routes situated within grasslands did not influence the impact of mowing regimes (Fig. 2, Table S 4 – Table S9).

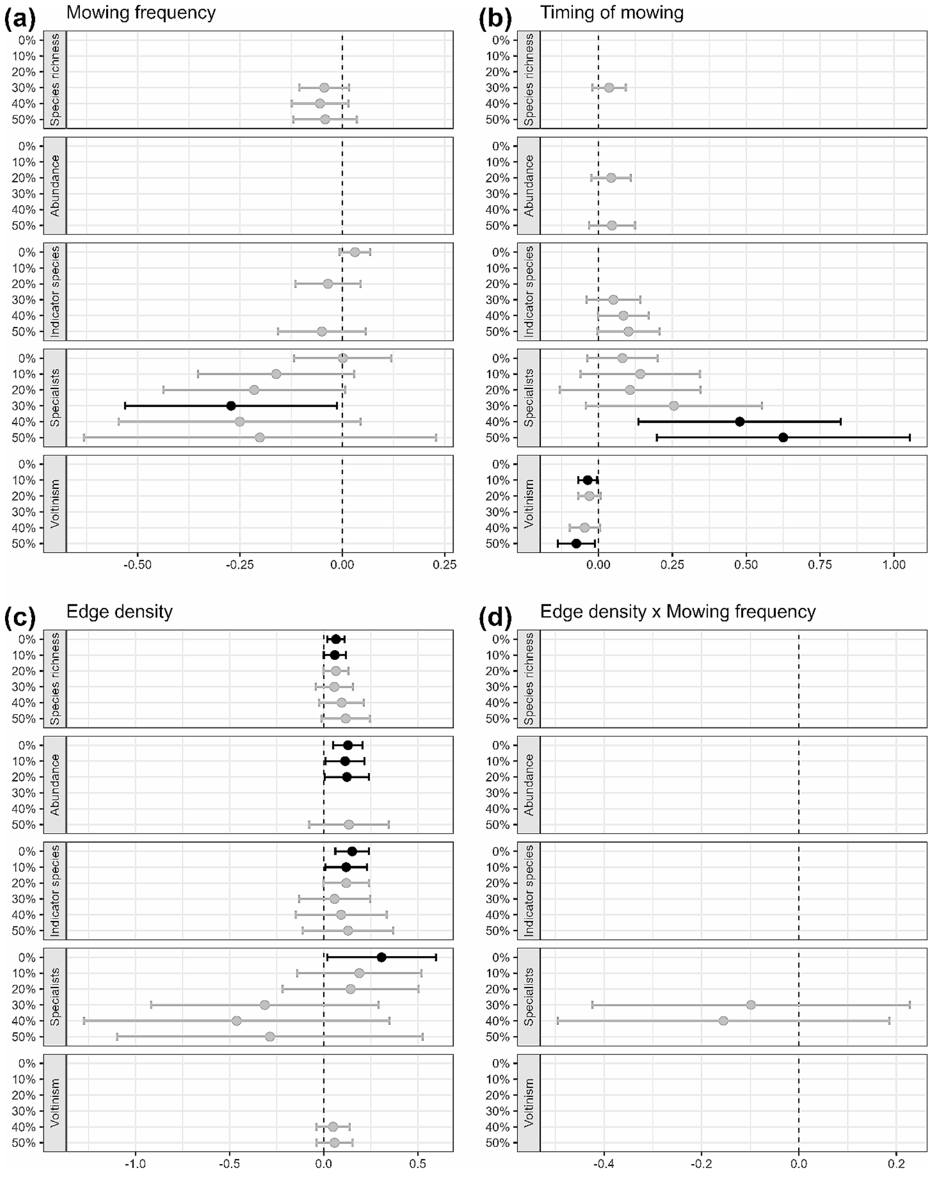

Fig. 2 Scaled parameter estimates (as points) and their respective 95% confidence intervals (as horizontal lines) for (**a**) mowing frequency, (**b**) timing of mowing, (**c**) edge density, and (**d**) the interaction between mowing frequency and edge density for different thresholds (0 – 50%) regarding the share of transect routes situated within grasslands ($n_{\geq 0\%} = 286$, $n_{>10\%} = 146$, $n_{>20\%} = 116$, $n_{>30\%} = 88$, $n_{>40\%} = 65$, $n_{>50\%} = 55$) using conditional model average-coefficients (see Table 1 for further details on predictor variables). Results are shown for species richness ("Species richness") and abundance ("Abundance") of open-land butterflies, abundance of indicator species ("Indicator species") and grassland specialists ("Specialists"), as well as voltinism ("Voltinism"). Results for wing index are not shown, as none of the predictors were included in the best model sets. Non-significant results, where confidence intervals include zero, are displayed in grey, while significant estimates are shown in black. Missing points / confidence intervals indicate variables not present in the best model set. Note the different x-axis scale in the four panels

Effects of edge density

We observed significant positive effects of edge density at the landscape scale on species richness and abundance of open-land butterflies for transect subsets with the lowest grassland share, ranging from 0 to 10% and 0–20%, respectively (Fig. 2). However, for transects with higher grassland shares, the effects became non-significant, despite a slight increase in effect sizes on species richness. Notably, the interaction between edge density and mowing frequency was not included in the top model sets for any response variable (Fig. 2, Table S4 – Table S9).

Effects on community composition

When analysing all transects, landscapes with higher edge density showed a significantly higher abundance of indicator species and grassland specialist species. Voltinism and wing index, however, were not significantly affected by either mowing regimes or edge density (Fig. 2). With an increasing grassland share per transect, the positive effect of edge density on indicator species and grassland specialists became non-significant. Effect sizes for mowing regimes on grassland specialists increased with higher shares of transect routes situated within grasslands. In turn, higher mowing frequencies had a statistically significant negative impact on specialists for transects with more than 30% grassland share. Additionally, delayed mowing had a significantly positive association with specialists on transects with at least 40% and 50% grassland share. A significantly lower number of generations per year was associated with delayed mowing in transects with at least 10% and 50% grassland share. Effects on indicator species were similar to those on all open-land butterflies (Fig. 2, Table S4–Table S9).

Confounding factors

The remaining covariates, namely Natura2000 areas, coordinates, the number of surveys, and transect length, often showed similar or larger effect sizes in comparison to landscape-level mowing regimes and edge density (see Table S4- TableS9). Specifically, Natura2000 areas displayed statistically significant positive relationships with species richness, abundance of indicator species, as well as the abundance of specialists, and a significant negative relationship with wing index, when all transects got used (Table S4). These findings correspond with the conclusions drawn by Rada et al. (2019), demonstrating a positive impact of Natura2000 areas on butterflies using data from the DEBMS. Additionally, our observations aligned with geographical patterns showing positive north-south and west-east gradients. For instance, the eastern regions of Germany showed a higher species richness and greater open-land butterfly abundance compared to the western parts. Conversely, the northern areas of Germany displayed fewer species of open-land butterflies and a diminished specialist abundance compared to the southern regions. A comprehensive listing of model outputs, encompassing coefficients for all covariates, is provided in Table S4- Table S9.

Representativeness of transects

For approximately 66% of all randomly sampled landscapes across Germany, values for mowing frequency, timing of mowing, and edge density collectively fell between the 2.5% and 97.5% percentiles of the respective transect values (Table S3). This illustrates that DEBMS transects effectively sample a majority of the gradient of permanent grassland management intensity and edge density conditions of landscapes in Germany (Figure S1). When considering each landscape characteristic individually, values for approximately 75–95% of randomly sampled landscapes were between the 2.5% and 97.5% percentiles of the respective transect values (Table S3). Nevertheless, transects, on average, were located in landscapes exhibiting lower frequencies of mowing events and a delayed timing of the initial mowing event, compared to the random sample (Figure S1). The least degree of representativeness was observed for edge density, with *c*. 20% of randomly sampled landscapes characterized by lower configurational complexity compared to transects (Figure S1, Table S3). The average distance of randomly sampled points from the nearest edge was 42 m (sd = 66 m). In contrast, the average distance of transects from the nearest edge was about 13 m (sd = 34 m) (Figure S2), suggesting that transects are frequently located in close proximity to edges. Regions in Germany that were less represented by the transects, characterized by high grassland management intensity but low edge density, are distributed across whole Germany, but particularly prevalent in north-eastern and southern Germany (Figure S3, Figure S4).

Discussion

Permanent and low-intensity managed grasslands have declined in quality and extent in recent decades across Europe (Estel et al. 2015; Schils et al. 2022). While understanding the impact of permanent grassland management on pollinators is vital for policy to develop restoration measures counteracting biodiversity loss, research across large spatial scales is lacking. By focussing on the German Butterfly Monitoring Scheme as a case study, we aimed to explore the feasibility of using nationwide citizen science butterfly data in combination with high-resolution satellite imagery to assess the landscape-level effects of grassland mowing regimes and landscape configuration on butterflies in open landscapes.

Effects of grassland mowing regimes

In our first research question, we aimed to investigate the influence of grassland mowing regimes on open-land butterflies at the landscape scale. Contrary to our assumption, we did not find a significant negative relationship between mowing regime intensity (i.e. a high frequency of mowing events and an early initial cut) and the richness and abundance of open-land butterflies. We consider several potential explanations for this finding. Firstly, despite their similarity to randomly sampled landscapes across Germany, the landscapes surrounding our transects generally had a low proportion of permanent grasslands (approximately 13% on average; Figure S1), potentially posing challenges when exploring research questions related to grassland management at a landscape scale. However, we expect landscape-level effects of grassland management to become detectable (i.e. via larger and significant effect sizes) with increasing shares of transect routes situated within permanent grasslands. However, as the results for open-land butterflies remain stable along the gradient of grassland shares, the availability of grassland habitat in the near surrounding of a transect may not be crucial for this species set in general. Further, our calculation of mowing regime indicators as averages across transect buffers might mask the effects of landscapes characterized by polarized management practices, i.e. low- and high-intensity grassland management within the same landscape. Average indicator values might indicate intermediate, and thus suitable conditions for butterflies (Dumont et al. 2009; Jerrentrup et al. 2014), yet the reality at plot scale could render these conditions unsuitable. This challenge may impact the interpretation of mowing effects and merits consideration in future studies analysing management impacts at the landscape scale. It is further noteworthy that the literature on mowing regime effects on butterflies reports complex and varying relationships (Humbert et al. 2012; Tälle et al. 2018). Confounding factors such as mowing techniques (Humbert et al. 2010; Steidle et al. 2022) and biomass productivity (Tälle et al. 2018; van de Poel and Zehm 2014) might also explain the weak effects of our mowing regime indicators on richness and abundance of open-land butterflies. Specifically, butterflies that prefer sparser and warmer habitats may benefit from more frequent mowing in productive grasslands with fertile soil as it prevents the development of dense vegetation and cooler microclimates (Roth et al. 2021; WallisDeVries and van Swaay 2006). These complex interactions can mask direct mowing effects, leading to fluctuations across diverse regions (Tälle et al. 2018). Furthermore, the years 2018, 2019, and 2020 experienced significant heatwaves and drought in various regions of Germany (Deutscher Wetter Dienst 2018, 2019, 2020). Although these drought conditions were correlated with reduced mowing frequency, especially in 2018 (Schwieder et al. 2022), butterflies adapted to open landscapes may have suffered from a lack of food and nectar plants during this period (Kühn et al. 2019), potentially masking any positive effects of low grassland management intensity.

Effects of edge density

Our second research question focused on the effects of edge density as a proxy of landscape configuration. Consistent with previous studies indicating positive effects of structural heterogeneity on butterfly populations (see e.g. Börschig et al. 2013; Martin et al. 2019; Perović et al. 2015), we observed positive effects of edge density on species richness and abundance of open-land butterflies, especially in landscapes with low shares of transect routes situated within permanent grasslands. Edges, such as roadside ditches or field margins, play a crucial role in supplying butterfly habitats within agricultural landscapes, typically exhibiting characteristics beneficial to butterflies, including herbaceous vegetation hosting food plants and nectar sources (Lebeau et al. 2016). These linear elements may provide suitable habitats in intensively cultivated landscapes, thereby serving as refuge for pollinators countering the pressures of intensive farming (Li et al. 2020; Settele et al. 2009). Further, edges may generally experience lower disturbance levels compared to adjacent managed habitats (Smart et al. 2002) and can provide protection from predation, drought, and wind, particularly when they are managed less intensively (Dover et al. 1997; Weibull et al. 2000). However, the positive effects associated with edges might decline if management intensifies. For example, frequent mowing of edges like field boundaries can increase butterfly mortality within these areas (Steidle et al. 2022). Additionally, agricultural practices such as fertilization and pesticide usage can impact insects in edges bordering agricultural fields and thereby threaten butterfly communities (Braak et al. 2018).

Even though we expected edge density to mediate the effect of the mowing frequency (Perović et al. 2015), we found no statistically significant interaction between them. This may be attributed to the relatively modest effect size associated with mowing frequency, making it challenging to detect interactions. Nevertheless, our results indicate context-dependent effects of edges. In some situations, edges may not only serve as refuges from unsuitable permanent grassland management but also act as independent habitats, irrespective of the agricultural practices in the surrounding areas. Particularly in open landscapes with highly fragmented permanent grasslands, edges can offer sufficient habitat quality, acting as island-like habitats for open-land butterflies (Dover and Sparks 2000). This is confirmed by the significant positive edge effect in our models when only a small share of the transect route is situated within permanent grasslands. It is important to note that the landscape variable “edge density” in our study encompassed various boundaries connecting different land-cover types. Hence, edges may be characterized by linear elements such as roadside ditches, hedgerows, or strips of herbaceous vegetation at a boundary e.g. between arable land and grassland. However, our study lacks information on the vegetation structure and quality of boundaries, which would be beneficial for further interpretation of our findings (Ries and Sisk 2008). Further, we did not anticipate edges between patches of the same land-cover type, potentially leading to an underestimation of the true edge density in our landscapes. Despite these limitations, our results support the assumption that boundaries between land-cover types may provide suitable habitat conditions for butterflies (Li et al. 2020). Our results further underscore the significance of heterogenous landscapes characterized by features like small agricultural fields and bordering structures, such as field margins, as well as low-intensity management practices for promoting biodiversity and safeguarding butterfly populations at the landscape level (Li et al. 2020; Luppi et al. 2018; Perović et al. 2015).

Community composition

In our third research question, we aimed at investigating the potential effects of mowing regimes and edge density on habitat specialisation and specific traits. Although we did not find significant effects related to wing index, we did observe variations in community composition, particularly regarding habitat specialisation and voltinism. Transects situated in landscapes with higher edge density tended to harbour greater abundance of indicator species (i.e. species included in the European Butterfly Indicator for Grassland species) and grassland specialists in landscapes with low shares of transect routes situated within grasslands. The significant positive effect suggests that even though edges might not act as suitable habitats for grassland specialists on their own, they may serve as dispersal corridors, facilitating butterfly movement between grasslands, especially in landscapes characterized by strong fragmentation and reduced habitat quality (Wilson and Roy 2009). For transects with high grassland shares, delayed and, to some extent, reduced mowing events positively influenced specialists’ abundance. Delayed mowing was also associated with more species having fewer generations when a significant share of the transect was situated within grasslands. These results align with prior research emphasizing the importance of species traits and habitat specialisation in determining susceptibility to (high) management intensity (e.g. Bruppacher et al. 2016; Perović et al. 2015). However, there is evidence that responses to land use can also vary significantly among species (Scherer and Fartmann 2023; van de Poel and Zehm 2014). For example, species like *Phengaris nausithous* benefit from early mowing before June (Reinhardt et al. 2007), while others like *Phengaris alcon* require late cuts, preferably no earlier than September (Bayrische Akademie für Naturschutz und Landschaftspflege 2007). These species-specific variations likely introduce additional uncertainties, that may lead to wider confidence intervals in model outcomes, especially when the number of species is small. Nevertheless, the significant effects of mowing regimes on grassland specialists and voltinism highlight the importance of incorporating habitat specialisation and specific traits in the design of grassland management strategies for the conservation of diverse butterfly populations (Tälle et al. 2018).

Given Article 9 of the proposed Nature Restoration Law (European Commission 2022) suggesting the evaluation of the entire set of 17 indicator species typical of European grasslands (van Swaay et al. 2020; van Swaay and Warren 2012), we extended our analysis to examine the sensitivity of this species set to mowing regimes and edge density. In contrast to grassland specialists, the set of indicator species showed weaker and non-significant effects of mowing regimes. While the set of indicator species includes both grassland specialists and widespread grassland species, our results suggest that rather than analysing both groups together, distinguishing between both groups may be more effective, when assessing the effects of permanent grassland management on butterfly diversity. Specifically, our results highlight that specialists demonstrate higher sensitivity to mowing regimes compared to the set of indicator species of the European Butterfly Indicator for Grassland species.

Limitations and implications

For approximately 70% of randomly selected landscapes across Germany, values for mowing frequency, timing of mowing, and edge density were between the 2.5% and 97.5% percentiles of the respective transect values. This suggests that our results are broadly representative of a majority of German landscapes with permanent grasslands in their surroundings. However, there are limitations when generalizing our conclusions to broader contexts and applying our findings to landscapes with low edge density and high-intensive mowing regimes (Figure S3, Figure S4), as these landscapes are not well represented in our data.

The remote sensing products utilized in our analyses allow an assessment of management intensity on permanent grasslands, although they might be influenced by external factors such as differences in cloud cover and cannot distinguish between meadows and pastures (Schwieder et al. 2022). Still, the observed mowing regime patterns in Germany are supported by other studies (Reinermann et al. 2023). Additionally, Weber et al. (2023) applied the approach to estimate grassland use intensity in Switzerland. Through independent validation, they demonstrated that the algorithm may detect grazing events but with a substantially higher omission rate compared to mowing events. As grazing with low stocking pressure generally has a minor influence on the vegetation index (Weber et al. 2023), we anticipate that mainly intensive grazing, characterized by high biomass removal within short timeframes, may be identified as mowing events by the algorithm. This can lead to comparable detrimental effects on butterflies as observed in mowing events (Rakosy et al. 2022; van Klink et al. 2015). Future studies should prioritize refining the differentiation between grazing and mowing events, considering that grazing is anticipated to yield distinct effects on biodiversity compared to mowing (Bussan 2022). For instance, grazing with low stocking pressure might enhance structural heterogeneity in grasslands compared to mowing, leading to positive effects on biodiversity (van Klink et al. 2015).

Regarding the observed modest effects of mowing regimes on butterfly populations at the landscape scale, we assume that they may partly be due to a dilution effect (Didham et al. 2020). In unmown grasslands, where resources like nectar are evenly distributed, butterflies tend to exhibit a more even distribution, leading to fewer butterflies along edges. Conversely, mown grasslands can concentrate butterflies along unmown edges, resulting in increased abundances along these edges (van Klink et al. 2019). Given that our transects were frequently located in landscapes with notably high edge densities and in close proximity to edges (Figure S1, Figure S2), some may follow paths or tracks where a higher butterfly abundance could be observed when management intensity in neighbouring grasslands is high (Li et al. 2020). Consequently, the placement of transects may introduce a potential source of uncertainty into the analysis, impacting the precision of estimates for mowing regimes and leading to enlarged confidence intervals. In line with that, our results highlight variations in effects based on subsets of transects with different shares of transect routes situated within grasslands. This underscores the importance of careful planning when establishing transect routes for monitoring schemes, especially in alignment with specific research questions. Unfortunately, in our study, increasing thresholds considerably reduced the sample size, resulting in wider confidence intervals and decreased statistical power to detect effects. To enhance the sensitivity of models in future studies examining the impacts of grassland management intensity, we recommend incorporating a larger sample of transects with routes situated within permanent grasslands, where these effects are more likely to manifest. Although similar RMSE values for both training and validation data highlighted the robustness of our results (Table S10), disproportionally large RMSE values for specialists and low R^2 values for wing index and voltinism indicate that a substantial amount of variation remained unexplained by the fixed effects employed in our study. Similarly, as underscored by relatively large coefficients like the location within Natura2000 areas (Table S4), our results highlight the influence of several confounding factors beyond mowing regimes, such as climate (McDermott Long et al. 2017), mowing techniques (Humbert et al. 2010; Steidle et al. 2022), or biomass productivity (Tälle et al. 2018; van de Poel and Zehm 2014).

Conclusions

Despite certain limitations, the combination of citizen science data and high-resolution satellite imagery generally provides a valuable approach for investigating key determinants of insect decline at large spatial scales. We observed that DEBMS transects are broadly representative of a large portion of Germany's landscapes in terms of mowing regimes and edge density. While specific aspects, such as the correlation between mowing regimes and butterfly diversity, may require further investigation using larger subsets of transects situated within permanent grasslands, our study generally highlights the suitability of the DEBMS for assessing the impacts of management intensity on permanent grasslands and landscape configuration, particularly when focusing on grassland specialists.

We here demonstrate that certain butterfly species can benefit from low mowing frequencies and delayed mowing at the landscape scale, depending upon their habitat specialisation and specific traits. Additionally, our results highlight the ecological importance of edges as valuable habitats for insects in open landscapes. On the one hand, edges can serve as suitable habitats for grassland species, and on the other hand, they may play a crucial role as dispersal corridors and can provide additional resources for specialists in landscapes with fragmented grasslands. Consequently, our findings underscore the importance of heterogeneous landscapes and implementing low-intensity management practices in permanent grasslands and adjacent habitats.

To improve future, large-scale analyses and the suitability of the DEBMS for assessments of permanent grassland management, in line with suggestions outlined in the proposed EU Nature Restoration Law (European Commission 2022), we recommend adjustments and augmentations to the DEBMS to yield more robust outcomes concerning grassland-related research questions. This could include adding transects located specifically within landscapes characterized by intensive mowing regimes and low edge density (Figure S 4), and transects containing a substantial share of permanent grasslands in their immediate surroundings.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10531-024-02861-6.

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Author contributions T.K., J.D., A.H., S.K., E.K., J.S. and M.M. conceptualized the idea; T.K., S.K. and M.M. defined the questions and methodological approach; J.S., E.K., M.M. and A.H. led the curation of biodiversity data as part of the DEBMS; M.S. led the curation of land-use data; T.K. carried out the analyses and led the writing as well as visualization; S.K., C.L., J.D., M.M., M.S., P.D., and E.K. contributed to the writing. All authors participated in the discussion and agreed on the final version of the manuscript.

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Data availability Data on mowing regimes can be accessed from the Thünen Atlas (https://atlas.thuenen.de/search/?title__icontains=Grassland%20mowing%20detection&abstract__icontains=Grassland%20mowing%20detection&purpose__icontains=Grassland%20mowing%20detection&f_method=or&limit=20&offset=0&type__in=raster). Butterfly data are stored at the Helmholtz-Centre for Environmental Research - UFZ and can be made available for scientific research upon request (www.tagfalter-monitoring.de).

Declarations

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Competing interests J.D. is a member of the editorial board of the journal Biodiversity and Conservation. The authors declare that they have no additional known financial or non-financial competing interests or personal relationships that could have appeared to influence the work reported in this paper.

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