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RESEARCH ARTICLE

Biodiversity on old permanent versus restored grassland is driven by small-scale land-use intensity and habitat connectivity

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Central European grasslands with low land-use intensity potentially harbor high biodiversity, but have decreased in extent due to land-use intensification. We evaluated the success of a 30-year grassland restoration project on former arable fields in comparison to old permanent grassland in a floodplain in North Germany, taking into account the effects of land-use intensity and habitat connectivity. We analyzed restoration success by richness and abundance of target species groups of vascular plants and butterflies. Restoration was successful in establishing common plant species of agricultural grasslands. However, restoration failed to recover plant species of wet grasslands with respect to both richness and cover, which may be explained by the lack of wet site conditions on former arable fields. In general, higher land-use intensity reduced species richness and cover of mesotrophic and wet-grassland plants, while smaller distances to old permanent grassland increased richness of all but wet-grassland species. Butterfly species, including grassland specialists and red-list species, were favored by high cover of flowering forbs and, coherent to this, low land-use intensity. Surprisingly, higher cover of old permanent grassland in the surrounding landscape decreased species richness of butterflies, possibly due to a dilution effect. In conclusion, we recommend recreating wet microsites and introducing seeds of specialist and rare forbs for better restoration success, in addition to sowing of diverse seed mixtures. It is also important to keep land-use intensity low to allow for higher cover of host and nectar plants, which is vitally important for promoting butterflies, especially grassland specialists and red-list species.

Key words: agricultural grassland, floodplain, microsite, restoration, sowing, success, wet grassland, wetland

Implications for Practice

- Sowing low-diversity grass mixtures is ineffective for restoring target plant and butterfly communities, even after decades. However, achieving similar plant species richness to old grasslands is possible.
- Mowing twice a year is essential for developing flower-rich communities, which are crucial for butterfly restoration.
- Proximity to existing old grasslands can enhance the immigration of desired species over time. Effective recovery of wet-grassland species necessitates creating wet microsites and potentially introducing seeds.
- We recommend ongoing monitoring and adaptive management following restoration efforts, such as sowing high-diversity seed mixtures with regional genotypes and appropriate host plants, while also creating moist site conditions.

Introduction

Worldwide, land-use change by agricultural intensification, grassland fragmentation, and habitat loss are major threats to biodiversity (Sala et al. 2000; Fischer & Lindenmayer 2007; Díaz et al. 2018). Managed grasslands have the potential to be among the most species-rich habitats globally (Wilson et al. 2012). They deliver multiple, but underestimated, ecosystem services, such as fodder production, pollination, carbon storage, and biological control (Bengtsson et al. 2019). However, during the 20th century, Central European grassland ecosystems shifted from a preponderance of species-rich grasslands to more intensive land use, emphasizing highly productive grass species (Isselstein et al. 2005).

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Restoration of degraded grasslands addresses many current environmental problems simultaneously (Jochum et al. 2019; Schaub et al. 2020). Many factors, such as mowing frequency, nutrient availability, dispersal limitation of species due to grassland fragmentation, and former land use, have to be considered. Once grasslands have become species-poor, they generally have a low potential for naturally re-establishing locally extinct species (van Swaay et al. 2006; Oelmann et al. 2009). This might be especially relevant if grasslands were restored from arable land using low diversity, productivity-focused seed. Therefore, active introduction of plant species is increasingly implemented (Oelmann et al. 2009; Klaus et al. 2016; Temperton et al. 2019).

Traditionally, biodiverse and multifunctional grassland ecosystems in temperate Europe are maintained by low- to intermediate-intensity management and are a by-product of farming, originating from subsistence agricultural systems (Ellenberg & Leuschner 2010b). Typical traditional grasslands are mainly used as hay meadows, and more than 1,300 plant species are linked to those grassland communities in Europe (Dierschke & Briemle 2008; Kollmann et al. 2019). Agricultural grasslands with moderately productive to productive plant communities, traditionally generate species-rich to moderate species-rich meadows or pastures (Dierschke & Briemle 2008). These habitats are dependent on agricultural management and thus, land-use abandonment leads to succession and development of forest. Therefore, these habitats have experienced considerable degradation through either land-use intensification or land abandonment, as well as habitat loss and fragmentation due to land conversion (Stoate et al. 2009; Wesche et al. 2012; Kollmann et al. 2019).

Grassland loss and degradation reduce flower availability and reproduction sites for insects across landscapes (Tscharntke et al. 2005; Kleijn & van Langevelde 2006; Öckinger et al. 2012) and contribute to the current general insect decline. Both vascular plants and butterflies respond sensitively to changes in environmental conditions, for example, increased or reduced mowing frequency, fertilizer input, and shifts in soil moisture (van Swaay et al. 2006; Dierschke & Briemle 2008; Scherber et al. 2010). Therefore, they are considered to be useful indicator groups for assessing the ecological status of grassland ecosystems (Maccherini et al. 2009; Ellenberg & Leuschner 2010b).

Regarding butterfly species, habitat fragmentation and decreasing host plant availability are reported to be the most severe drivers of declines in diversity in Europe during the last decades, with a decrease of 19% in grassland butterfly species (van Swaay et al. 2006; Habel et al. 2013). Such trends are of great concern to nature conservation, because species diversity is shaped by the composition of the surrounding landscape and patch isolation and thus, habitat connectivity is shown to be an important factor for butterfly distribution (Öckinger et al. 2012; Damschen et al. 2019; Gallé et al. 2022). In general, colonization of habitats depends on the dispersal abilities of species and environmental requirements, as well as the quality of the surrounding landscape (Fahrig 2003; Löffler et al. 2020).

We compared (A) former arable, restored grassland to (B) old permanent grasslands (hereafter called old grasslands) in a flood plain, investigating the effects of land-use intensity and (1) distance to and (2) cover percentage of old grassland in the surrounding landscape (habitat connectivity metrics) on the diversity and community composition of butterflies and vascular plants. The aim was to find out if 30-year-old, species-poor sown grassland may be successfully re-colonized from the species pool of surrounding old grassland, including restoration target species. This seems especially important as species-poor sowing of grasslands is still common farming practice today (Spura 2002; Verband der Landwirtschaftskammern 2022). There is a summary of the overall framing and key outcomes of our study in Table 1.

We hypothesized that grassland restoration based on the sowing of species-poor, productivity-focused seed mixtures may not have led to the same species richness and community composition of plants and butterflies as in old grasslands even 30 years after the intervention. Further, we hypothesized that grassland restoration success in terms of species richness and abundance of plants and butterflies is positively affected by low land-use intensity and high habitat connectivity. These effects will differ between species groups. Furthermore, we hypothesize that the community composition of plants and butterflies is similarly determined by these factors. We used plant and butterfly species as indicator taxa to provide evidence of restoration success. Species were classified into groups according to their ecological characteristics, red-list status, and, in the case of plants, whether they were sown in the former restoration intervention or not.

Methods

Study Area

The study region was located in eastern Lower Saxony in northern Germany in the district of Gifhorn. The main land-use types are arable fields, coniferous and deciduous forests, intensively managed meadows and pastures, and small areas of heath and peatland. The study sites were distributed in and around the floodplain of river Ise (approx. 22.4 km^2 total area) and were managed by mowing for hay or silage production. In our study region, 300 ha of arable land was restored to grassland in 1991/1992 within a government-funded conservation project (Borggräfe et al. 2001) which caused a large increase in the area proportion of grasslands in contrast to many other regions in northern Germany. Farmers, at that time, were reluctant to sow the formerly productive arable land with an unproductive species-rich grassland seed mixture. Hence, a species-poor mixture containing six productive grass species and one legume species was used (*Festuca pratensis* [Meadow fescue], *Festuca rubra* [Red fescue], *Poa pratensis* [Smooth meadow-grass], *Agrostis gigantea* [Redtop], *Phleum pratense* [Timothy], *Lolium perenne* [Perennial ryegrass], and *Trifolium repens* [White clover]) (Borggräfe 1996). It was assumed that over time and under low to intermediate land use by different farmers, further plant species would immigrate from the surrounding remnants of old grassland into the former wet floodplain (Borggräfe et al. 2001). In our study, old grasslands have never been converted to arable land and have been managed since

Table 1. Overall framing and outcomes of the grassland restoration study.

Overall Framing	*Expectations*	*Key Outcomes*	*Suggested Restoration Measures*
Restoration intervention 30 years ago from arable land with low-diversity seed mixture typically used in agriculture to sow productive agricultural grassland. Old permanent grassland embedded into an agricultural landscape was used to compare restoration success. Old grassland plant communities are partly degraded regarding their ecological potential.	Grassland restoration based on sowing of species-poor, productivity-focused seed mixtures may not lead to the same species richness and community composition of plants and butterflies as in old grasslands even 30 years after the intervention. Not enough source plant communities to re-colonize the restored grassland with target restoration plant communities.	Grassland restoration by sowing low-diversity grass mixtures is not a successful method to restore target restoration plant and butterfly communities, even after decades. Nevertheless, total plant species richness increases to the same level as old grassland and does not differ anymore.	Adjusted restoration after subsequent monitoring, such as sowing of high diversity seed mixtures with regional genotypes including appropriate butterfly host plants and creating moist site conditions with wet grassland communities.
Land-use intensity of the study sites ranged between 0.6 and 4.2 (wide gradient from low to intermediate high land-use intensity).	Grassland restoration success in terms of species richness and abundance of plants and butterflies is positively affected by low land-use intensity and high habitat connectivity.	Low land-use intensity is a prerequisite for flower and species-rich plant communities which are vitally important for restoring butterfly communities.	Implementation of low land-use intensity as a prerequisite for flower and species-rich plant communities, which are vitally important for restoring butterfly communities.
Within a 500 m buffer around the study sites, we detected the cover of old permanent grassland and calculated nearest neighbor distance and composition as landscape connectivity metrics.		Immigration of target restoration plant species can be improved over longer time by initial small distances to old grassland.	Monitoring, conservation and hay transfer of old grassland communities with target restoration plant communities including host plants.

they became grassland by human land use of the floodplain. Therefore, the old grassland habitats are characterized by wet ground depressions resulting in natural microsites. The general age of the grassland is not known, and land-use intensity before the 1990s can be assumed to have been low.

Study Sites

We surveyed vascular plant and butterfly species on 28 grassland study sites to test the effects of former restoration interventions (restored vs. old grassland), land-use intensity, and grassland connectivity on species richness, abundance, and community composition of plants and butterflies. We selected 14 grassland sites out of 66 (300 ha) that had been restored 30 years ago on ex-arable land and 14 sites that have continuously been managed as old permanent grassland (Fig. 1). For both grassland types, we selected the same compositional gradient of plant-available soil moisture and soil types (Table S1). The area of the selected grassland study sites was 4.1 ± 0.45 ha (mean ± SE) for restored grassland (ranging from 1.7 to 7.2 ha) and 3.8 ± 0.54 ha (mean ± SE) for old grassland (ranging from 1.1 to 6.5 ha). The selection of sites further considered comparable gradients of land-use intensity and compositional gradients of old grassland cover in the vicinity for both grassland types. The dispersion of sites scattered through the landscape will be explained in the landscape analysis section.

We assessed land-use intensity using a specific land-use intensity index for meadows (LUI_m) calculated based on Blüthgen et al. (2012) that integrates nitrogen input and mowing. For this purpose, we collected land-use information in structured interviews of the managing farmers asking for total nitrogen input per year and mowing frequency. The respective study sites ranged between 0 and 150 $kg\ N\ ha^{-1}\ yr^{-1}$ and 1.5 and 3.5 cuts yr^{-1} across our study sites. The values of LUI_m ranged between 0.6 and 4.2, which represents a wide gradient from low to intermediate high intensity of agricultural grassland meadows (*Molinio-Arrhenatheretea* R. Tx. 1937, Dierschke 1997, 2004; Blüthgen et al. 2012).

Sampling Methods

Vascular plants were recorded between the middle of May and the end of June in both 2020 and 2021 at all sites, using the same plots in both years. Species names followed the nomenclature of Rothmaler (2017). We conducted the surveys on a total of 25 m^2 (Dierschke 1994) divided into five 1-m^2 plots and one 20-m^2 plot per site. The plots were evenly spread over the site in areas that represented different vegetation structures and moisture levels and were randomly selected by throwing a frame in each area of the study site. Cover percentages of species were assessed visually in each plot.

Based on literature, all recorded vascular plant species were assigned to the following groups to derive restoration success: The majority of all species recorded were typical of the phytosociological class *Molinio-Arrhenatheretea*, which comprises historically species-rich agricultural grasslands, including plant

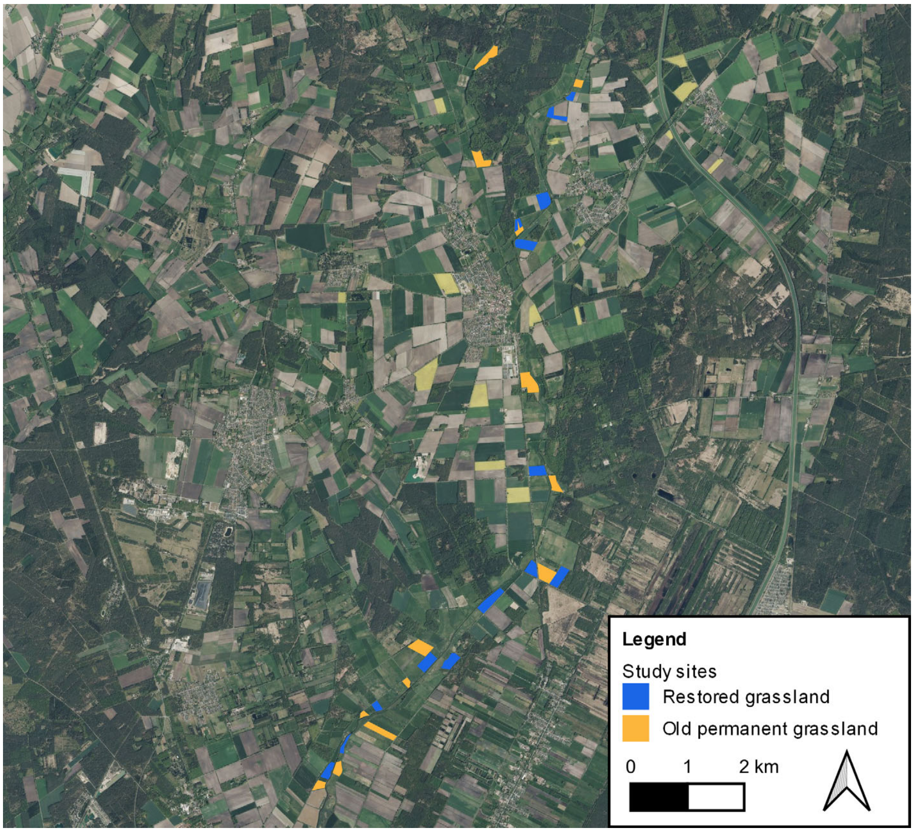


Figure 1. Map of the study sites of restored grassland (blue) and old permanent grassland (yellow) in the study region.

communities of grasslands with low and intermediate intensity, but also highly cultivated grassland with high yield. This group is called "agricultural grassland species" in the following and represents a higher-order group including many species of the other following groups. The group "non-sown grassland species" were those which were not sown in the restoration process when arable land was converted to grassland. Further, we used Ellenberg indicator values to define groups by the species' habitat requirements. Ellenberg indicator values range from one to nine on an ordinal scale and characterize the plant species' niche optima with respect to for example nutrient supply (Ellenberg N) and soil moisture (Ellenberg F; Dierschke & Briemle 2008; Klaus et al. 2012; Kleinebecker et al. 2018). Here, we classified species with low Ellenberg values for nutrient supply (Ellenberg *N* value 0–6) as mesotrophic grassland species and high Ellenberg moisture values (Ellenberg *F* value 7–10) as wet grassland species. We used these two indicator values, because typical wet and low nutrient indicating grassland species generally became rare in floodplain grassland habitats (Oelmann et al. 2009; Wesche et al. 2012). These historically characteristic agriculturally used plant groups are restoration target species groups and their presence can be expected for successful grassland restoration. Regarding nature conservation quality, we classified two further restoration target species groups, namely flowering forbs and red-list plants (Klotz et al. 2002; Garve 2004; Ellenberg & Leuschner 2010a). Using these classifications, species might belong to multiple groups and may be assigned to both mesotrophic and wet grassland species or even multiple groups. We cumulated species richness for all species groups over the six plots per study site and over both years. Cover percentages were calculated as weighted means over all plots and the two surveys per study site, using plot sizes as weights.

Diurnal butterflies (Lepidoptera: Hesperidae and Papilionidea) and burnet moths (Lepidoptera: Zygaenidae, hereafter also called butterflies) were sampled from 17 May 2020 until 7 September 2020 with four survey rounds in five 80-m transects placed through the 1-m^2 vegetation plots on each study site. The survey followed the standard protocol by Pollard 1977 and butterflies were released immediately after identification (following Krauss et al. 2003). Identification and nomenclature followed Settele et al. (2015) for butterflies and Plattner et al. (2010) for burnet moths. We classified butterfly species as grassland specialists if they were associated with open grassland habitats and their larval host plants depended on low to intermediate-intensity grasslands (Settele et al. 2015). Further, we classified red-list butterfly species based on literature (van Swaay et al. 2006; Theunert 2008; Plattner et al. 2010; Bellmann & Ulrich 2016; Ulrich 2018). For all butterfly groups, butterfly species richness was cumulated over the five transects per study site and survey round. Abundance was calculated as the cumulated counts of individuals per species over the five transects per study site and survey round. Furthermore, cover percentage of flowering forbs and number of flowering forb species were recorded on each transect to characterize the availability of nectar resources.

Landscape Analysis

To calculate landscape metrics, we created a landcover map in QGIS (QGIS Development Team 2020) with arable land, old and restored grassland, forested land, water, woody structures, and semi-natural land, such as heath and field margins, as land-cover categories based on geodata from the German Basic Digital Landscape Model (BKG 2018), Copernicus Grassland High Resolution Landcover Maps (CLMS 2018), Copernicus Small Woody Features High Resolution Landcover Maps (CLMS 2015), and old on-site mappings of land-cover types and restoration sites by former project managers (Aktion Fischotterschutz 1990). In order to assess habitat connectivity, we calculated (i) distance to the nearest neighboring old grassland and (ii) cover of old grassland in a 500 m buffer around each of the grassland sites, excluding the area of the respective study sites in R (R Core Team 2022). The spatial cover of old grassland ranged from 2.5 to 61 ha within a 500 m buffer around both types of grassland study sites. For statistical analyses, we used (1) distance to the nearest neighboring old grassland as a measure of isolation (lower isolation means higher connectivity) and (2) cover of old grassland in a 500 m buffer in order to assess effects of habitat amount at the landscape level on colonization and, thus, restoration success (higher habitat amounts means higher connectivity).

Statistical Analysis

Cover sums of plants, abundance of butterflies, and species richness of both were cumulated over plots or transects per site and sampling occasions per year and calculated for both all species and the above-mentioned species groups. Restored versus old grassland, cover percentage of flowering forbs (in case of butterflies), land-use intensity (LUI_{m}), habitat connectivity (distance to the nearest neighboring old grassland and cover of old grassland in a 500 m buffer) and the interactions of any two of these were used as explanatory variables (Table 2). For both taxa, we applied generalized linear models (GLM) to detect effects on species richness and abundance of species groups. Models of species richness and abundance (butterflies) were fitted with Poisson distribution and, in case of overdispersion, with negative binomial distribution using log link. Models of cover sums of plants were fitted with binomial or quasibinomial distribution and logit link, respectively. For all models, we used the MASS package (Venables & Ripley 2002) of R software (R Core Team 2022). We performed a mix of hypothesis-based and forward selection modeling to test for significant effects because the sample size did not allow testing all predictors and interactions in one model. First, we built local-factor models with restoration versus old grassland type and LUI_m as predictors. In the case of butterflies, we also included percent flowering plants in the local-factor model. Subsequently, we added one of the landscape factors, distance to old grassland or cover of old grassland, to the predictors in separate models. Likewise, we performed forward selection modeling to test for interactions.

Further, we applied constrained correspondence analysis (CCA) to analyze the variability in community composition of plants and butterflies, focusing on the target restoration species groups, wet and mesotrophic grassland plant species. According to our hypotheses, we used the same explanatory variables for vascular plants and butterflies, namely restoration versus old grassland type, LUI_{m}, distance to old grassland, and cover of old grassland. To visualize the variability in community composition, the results were displayed in ordination biplots. Prior to the CCA, community data were Wisconsin-transformed using the package vegan of R software (Oksanen et al. 2020). We then performed a permutation test with 9,999 permutations to assess statistical significance. For the plotting of the figures, we used the package ggplot2 in R (Wickham 2016).

Results

On the 28 grassland study sites, we recorded a total of 106 vascular plant species, of which 99 were not sown on the sites. Regarding the phytosociological classification, 69% of plant species (73) were typical agricultural grassland species. With respect to site conditions, 65 plant species were mesotrophic, and 26 were wet grassland plant species. Further, there were eight red-list plant species (Table S2). The vegetation plots had a mean species richness of 13.3 species/m^2, ranging from 6.8 species/m^2 up to 23.1 species/m^2. The highest cover percentages were found for *Holcus lanatus* (Velvet grass), *Poa pratensis*, and *Alopecurus pratensis* (Meadow foxtail) (Table S4).

As for butterflies, 25 species, one of them a burnet moth, were identified among 349 recorded individuals. We classified 12 butterfly species as grassland specialists and 8 as red-list species (Table S3). Summed over the transects, we found a mean number of 6 species per study site, ranging from 3 to 12 species per study site. The most abundant species of butterflies were *Coenonympha pamphilus* (Small Heath), *Maniola jurtina* (Meadow brown) and *Pieris napi* (Green-veined white) (Table S5).

Vascular Plants

Total species richness did not differ between old and restored grassland habitats, whereas total plant cover sums were significantly but only slightly lower (approximately −3%) on restored grassland sites (Table S6; Fig. S1). Agricultural grassland species richness was significantly higher on restored compared to old grassland (17.3 vs. 14.2 species), but did not show effects for cover sums. In contrast, wet grassland species richness (6.6 vs. 10.4 species) and cover sums (16% vs. 35%) were significantly lower on restored grassland (Table S6; Fig. 2). Mesotrophic, red-list, non-sown, and flowering plant species did not differ between restored and old grassland.

We found the LUI_m to be an important factor determining plant species richness and cover sums of different plant groups. While total and agricultural grassland species plant cover sum was significantly, but only scantily higher when LUI_m was high (+1.3% at maximum LUI_m), species richness of these groups was not affected (Table S6). Contrastingly, species richness and cover sums of mesotrophic, wet, and red-list grassland plants were significantly lower under higher LUI_m. From min. to max. LUI_m, species richness of the mentioned groups declined by 31, 67, and 100%, respectively. Regarding

Table 2. Concept of causal linkages for the hypothesized connections between landscape or field factors (explanatory variables) and response variables with expected effects (left column) and effects from tested models (right column).

		Landscape scale				*Field scale*					
Factors from hypotheses		Habitat connectivity				Restoration status		Land-use intensity		Flower availability (for butterflies)	
Explanatory variables		distance to the nearest neighbouring old grassland		cover of old grassland in a 500 m buffer		restored grassland		LUI_m		cover of flowering forbs	
Response groups plants	**Response variables**	**Expected effects** (left column) | **Effects from tested models** (right column)									
Species including intensified grassland species	Total species richness	–	–	+	ns	+	ns	–	ns	NA	NA
	Total cover sum	no	ns	no	ns	–	–	+	+	NA	NA
	Agricultural grassland species richness	–	ns	+	ns	+	+	–	ns	NA	NA
	Agricultural grassland species cover sum	no	ns	no	ns	–	ns	+	+	NA	NA
Restoration target species	Mesotrophic grassland species richness	–	–	+	ns	–	ns	–	–	NA	NA
	Mesotrophic grassland species cover sum	–	ns	+	ns	–	ns	–	–	NA	NA
	Wet grassland species richness	–	ns	+	ns	–	–	–	–	NA	NA
	Wet grassland species cover sum	–	ns	+	ns	–	–	–	–	NA	NA
Nature conservation target species	Red-list species richness	–	ns	+	ns	–	ns	–	–	NA	NA
	Red-list species cover sum	no	ns	no	ns	–	ns	–	–	NA	NA
	Flowering forb species richness	–	ns	+	ns	–	ns	–	ns	NA	NA
	Flowering forb cover sum	no	ns	no	ns	–	ns	–	–	NA	NA
Immigration indicator species	Non-sown plant species richness	–	–	+	ns	–	ns	–	ns	NA	NA
	Non-sown plant species cover sum	–	ns	+	ns	–	–	–	ns	NA	NA
Response groups butterflies	**Response variables**	**Expected effects** (left column) | **Effects from tested models** (right column)									
Species including intensified grassland species	Total species richness	–	ns	+	ns	–	ns	–	–	+	+
	Total species abundance	–	ns	+	–	–	ns	–	–	+	+
Restoration target species	Grassland species richness	–	ns	+	–	–	ns	–	–	+	+
	Grassland species abundance	–	ns	+	–	–	ns	–	–	+	+
Nature conservation target species	Grassland species richness	–	ns	+	–	–	ns	–	–	+	+
	Red-list species abundance	–	ns	+	–	–	ns	–	–	+	ns

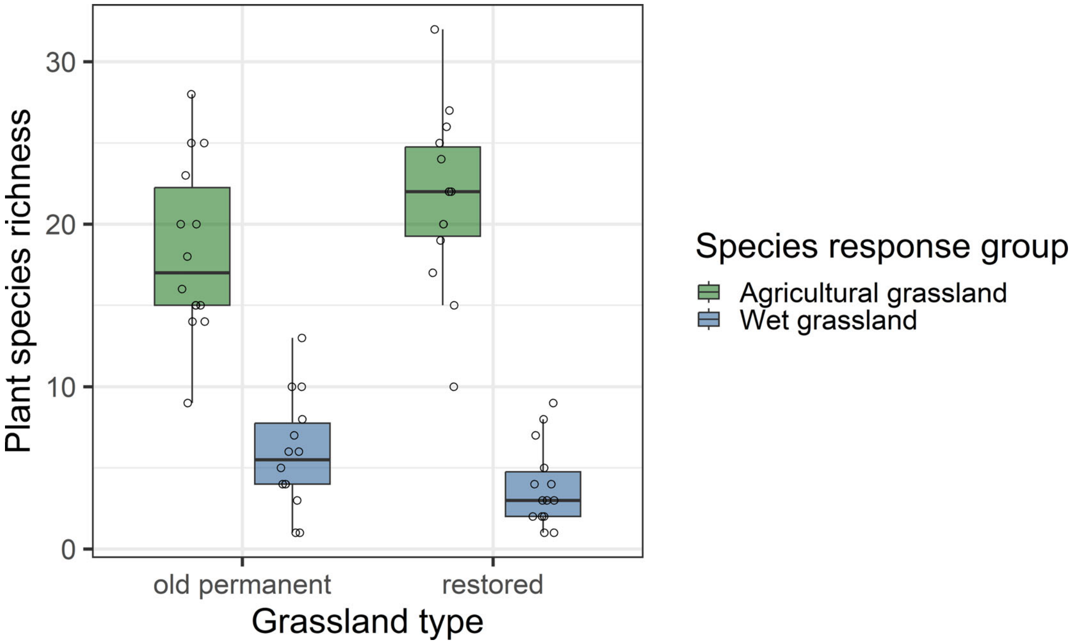


Figure 2. Mean (±SE) Agricultural grassland (green) and wet grassland (blue) species richness on old permanent versus restored grassland (GLM and z-test, $p < 0.05$). The box represents values within the 25th and 75th percentiles, with the median as a thick line. Whiskers extend to the most extreme values within 1.5 times the inter-quartile range from the median. Only significant models of response species groups are displayed.

cover sums, the declines were 52, 74, and 100%. Further, cover sums of flowering forbs were significantly lower under higher $\mathrm{LUI_m}$ (−26% from min. to max. $\mathrm{LUI_m}$), but this was not true for species richness (Table S6; Figs. 3A & S2). Non-sown species richness and cover sums were not significantly affected by $\mathrm{LUI_m}$.

Grassland isolation (distance to old grassland) had effects on species richness of vascular plants, but not on plant cover sums. At the maximum observed distance of study sites from the nearest old grassland (122.5 m), total plant species richness and richness of mesotrophic and non-sown plant species were reduced by 40, 60, and 48%, respectively, compared to sites adjacent to old grassland (Table S6; Fig. 3B). However, we did not find any effects of the cover of old grassland on plants.

The canonical correspondence analysis (CCA) showed that $\mathrm{LUI_m}$ had the strongest influence on plant-community composition, while restored versus old grassland and habitat isolation revealed no significant effects in the permutation tests (Table S8) even though they were significant when fitted to the ordination scores using the function “envfit” from package vegan in R. Most of the wet and mesotrophic grassland plant species were displayed on the right side of the ordination plot as a plant community of intermediate to low $\mathrm{LUI_m}$. The wet grassland plants were largely confined to the upper right part of the ordination biplot, showing them to occur on old grassland sites with low $\mathrm{LUI_m}$ (Fig. 4).

Butterflies

The models for butterflies showed that species richness and abundance mainly depend on local factors, but restored versus old grassland history did not have a significant effect (Table S7). Cover percentage of flowering forbs, as a measure of habitat quality, had a positive effect on both richness and abundance of all butterfly groups, with the exception of abundance of red-list butterflies (Table S7; Figs. 5A & S3A). We found one third of the transects to be without flower cover, and only on 21% of the transects did we find between 10 to 32% flower cover. According to the statistical model, an increase of cover percentages of flowering forbs from 1 to 10% would result in an increase of species richness by 50%.

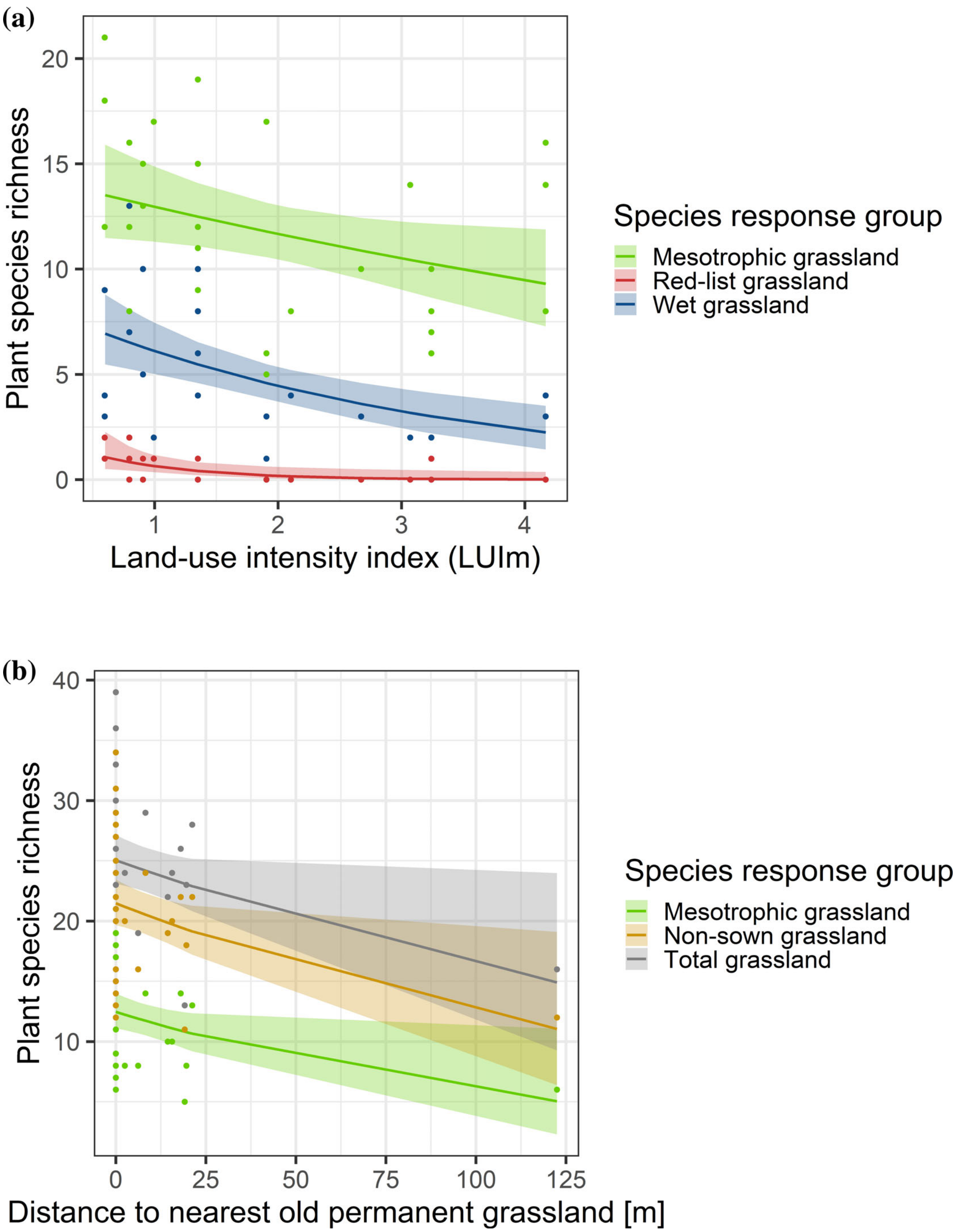
Land use intensity negatively affected species richness and abundance of all butterfly groups (Table S7; Figs. 5B & S3B). However, $\mathrm{LUI_m}$ was only significant in models that excluded the cover percentage of flowering forbs, which may be due to the fact that $\mathrm{LUI_m}$ and flowering forbs were negatively correlated ($r = -0.46$) and may indicate that the effect of $\mathrm{LUI_m}$ is an indirect effect mediated through the reduction of flowering forbs through frequent mowing or fertilization.

Surprisingly, we found significant negative effects of cover of old grassland on species richness and abundance of all butterfly groups, except for total species richness (Table S7; Figs. 5C & S3C). The CCA revealed no significant differences in the butterfly community composition (Table S8).

Discussion

Restoration Success of Vascular Plants

In contrast to our overall expectations, total species richness of plants did not differ between restored and old grassland. Thus, re-colonization of vascular plants over 30 years was possible.



Figures 3. (A, B) Relationship of GLM regression models between mesotrophic (green), red-list (red) and wet (blue) grassland species richness and land-use intensity index LUI$_m$ (A) and mesotrophic, non-sown (orange) and total (gray) grassland species richness and distance to nearest old permanent grassland (B); *z*-test, $p < 0.05$. Only significant models of response species groups are displayed and fitted with predicted values of species richness.

Directly after restoration, no seed bank of grassland plants was available due to former arable land use, and, thus, species richness could only increase through colonization due to dispersal from the surrounding landscape. Obviously, colonization of the restored sites by non-sown vascular plant species, in addition to the seven sown species, was high enough to reach typical levels of species richness of the old grassland sites. However, the low total species richness (median of 24 species) of the old grassland sites in our study region suggests that they are ecologically degraded compared to their potential (Roscher et al. 2004; Vahle 2015; Tischew et al. 2018) just as in other regions of northern Germany (Oelmann et al. 2009; Oppermann

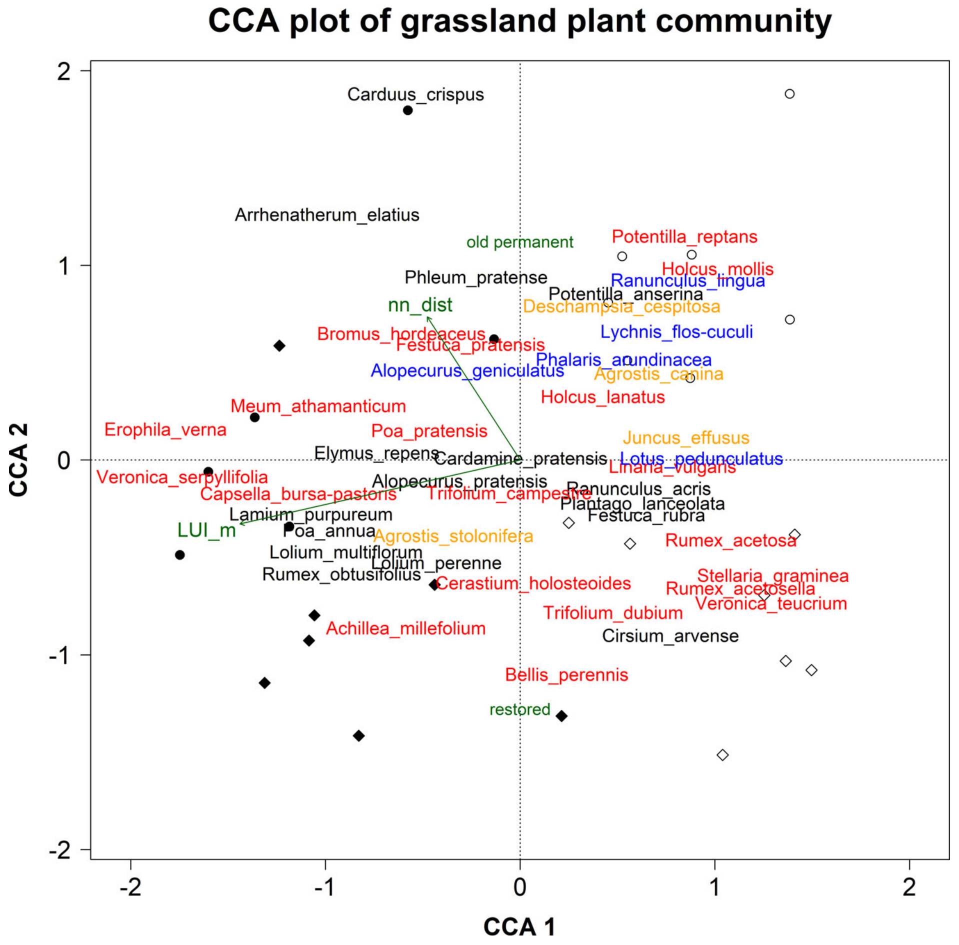


Figure 4. Biplot of canonical correspondence analysis (CCA) ordination for all plant species. Wet grassland species (blue), mesotrophic grassland species (red), both groups (orange), all others (black). Displayed are the first two axes of the ordination, with CCA Axis 1 at the *x*-axis and CCA Axis 2 at the *y*-axis, respectively. Sites: dots indicate old, rectangles indicate restored grassland; open symbols indicate low, closed symbols indicate intermediate land-use intensity. Explanatory variables in green indicate the direction of the effects.

et al. 2009; Wesche et al. 2012). Hence, the restoration interventions in our study area were only partially successful to the effect that they helped to restore levels of species richness of impoverished agricultural grasslands, but not particularly species-rich grassland.

A clear enrichment due to restoration was shown for agricultural grassland species, but contrastingly, the richness of wet grassland species was higher on old grassland. This was also reflected in the analysis of community composition as there was a clear tendency of a separate wet grassland plant community on old grassland with low land-use intensity ($\mathrm{LUI}_{\mathrm{m}}$) characterized by species such as *Lychnis flos-cuculi* (Ragged robin), *Juncus effusus* (Common rush), and *Lotus pedunculatus* (Marsh bird's foot trefoil). There are three possible explanations for this strong difference in restoration success between the overarching group of agricultural grassland species on the one hand and wet grassland species on the other hand. First, only drier grassland was turned into arable land, while the old grassland may also include sites that were too wet for arable land use. Thus, site conditions, particularly the water regime, may be less suitable for wet grassland species on restored sites. Further, possible differences in wetness might also be due to drainage pipes that were still present at restored sites. Second, the restored sites had smoothed surfaces due to arable land use, whereas old grassland study sites typically had structurally rich and heterogeneous surfaces, mostly characterized by moist ground depressions, often with an aspect of *J. effusus* and *L. flos-cuculi*. Hence, the lack of suitable microsites may explain the lower colonization success of wet grassland species on restored sites. Third, the distances between restored sites and patches of wet-grassland species on suitable microsites within old grasslands may have been larger than the distance of grassland parcels to the nearest neighboring old grassland. In that case, dispersal limitation may have played a stronger role for the wet-grassland species compared to agricultural grassland species that are more evenly distributed.

Similar effects were found by Kiss et al. 2021, where abandoned cropland was sown with low-diversity grass mixtures in 2005, and the establishment of target grassland species was restricted by propagule and microsite limitation. Thus,

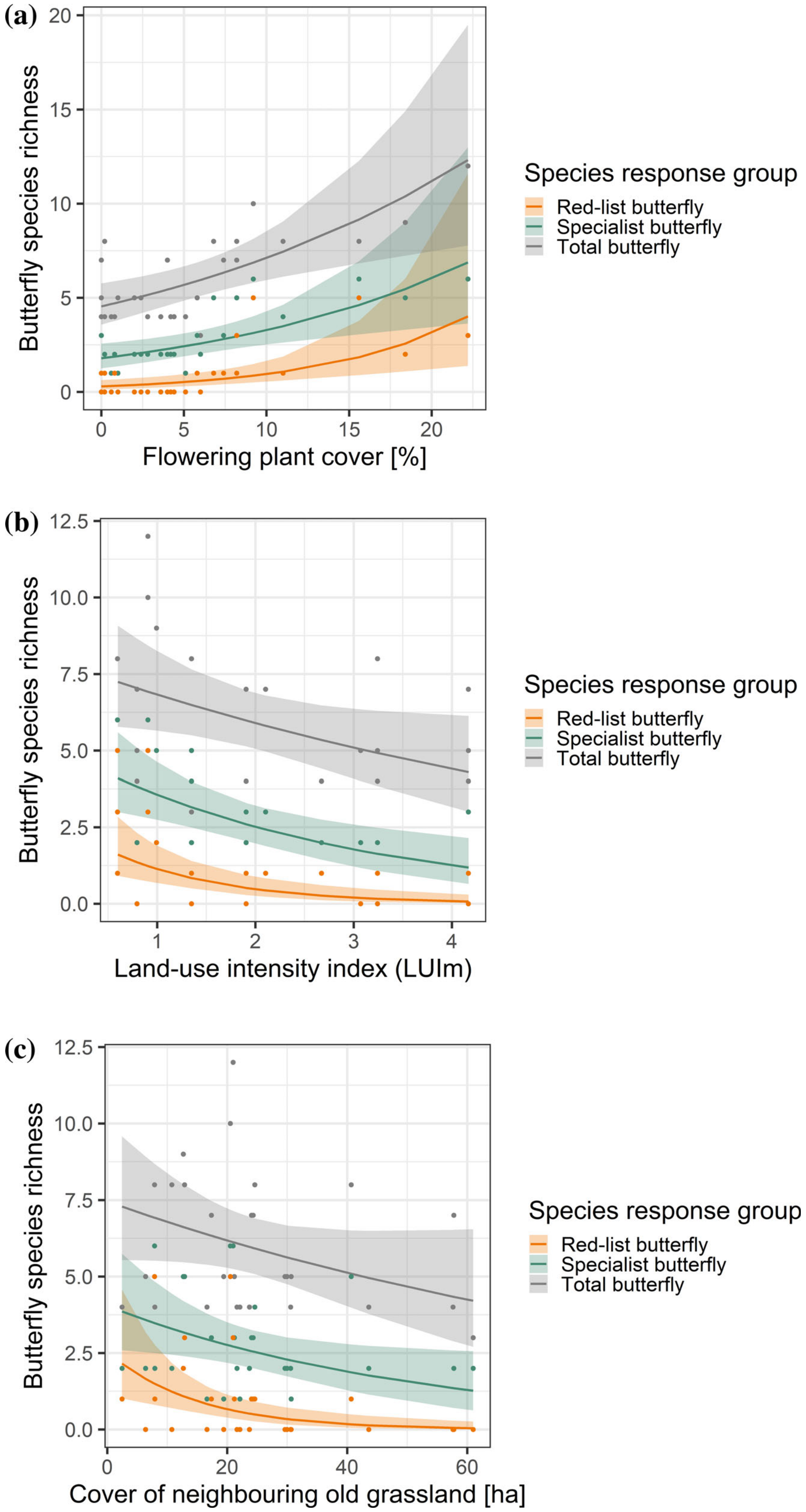


Figure 5. (A–C) Relationship of GLM regression models between red-list (red), specialist (green) and total (gray) butterfly species richness and flowering plant cover (A), land-use intensity index LUI$_m$ (B), and cover of neighboring old grassland (C); *z*-test, $p < 0.05$. Only significant models of response species groups are displayed and fitted with predicted values of species richness.

restoration of grassland plant communities can be modulated by local environmental conditions and microsites, and, further, by dispersal-related effects, such as propagule pressure and species pool (Conradi & Kollmann 2016). Here, the main target groups of restoration, that is, wet grassland species, apparently were restricted by such factors, while the group of agricultural grassland species was able to establish well in the restored grassland, probably as a consequence of its wide range of species' habitat requirements, including species of intensified grassland.

With respect to $\mathrm{LUI_m}$, we found contrasting effects on plant groups. As hypothesized, low $\mathrm{LUI_m}$ promoted high species richness and cover sums of target restoration and nature conservation species groups, that is, mesotrophic, wet grassland, flowering, and red-list plant groups. Contrastingly, total species richness and richness of agricultural grassland species were unaffected, and their cover sums even increased with increasing $\mathrm{LUI_m}$. This is consistent with observations by Conradi et al. (2017) who found stochastic immigration and extinction with low nutrient availability, whereas nutrient enrichment caused a niche-based selection of few species having a greater competitive ability for light, such as many productive grass species and forbs among the agricultural grassland species. These competitive species can attain particularly high cover at high nutrient supply, as also observed in our study.

Our analysis of community composition confirmed the results of the regression models in that wet grassland and mesotrophic plant species were largely confined to plant communities under lower $\mathrm{LUI_m}$. These results concur with previous studies that documented the importance of nutrient inputs, mowing frequency, and, connected to this, prevented seed maturation and dispersal limitation (Dierschke & Briemle 2008; Oelmann et al. 2009). In a case study during a 50-year time period examining five floodplain regions in northern Germany (Wesche et al. 2012), increasing fertilizer input was the key driver of species loss of *Molinietalia*, that is, wet grassland species with high moisture and low nutrient Ellenberg indicator values and of flowering, insect-pollinated, and red-list species. Likewise, long-term experiments in the Netherlands found that fertilizer treatments decreased the initial species number of unfertilized grasslands by 25% (Berendse et al. 1992). In our study, target grassland species groups, that is, mesotrophic, wet grassland, flowering, and red-list plant groups were highest at low to intermediate levels of disturbance by human land use and thus, support the Intermediate Disturbance Hypothesis (Mcintyre & Martin 2001; Yuan et al. 2016). These plant communities are dependent on low-intensity agricultural land use to avoid, on the one hand, riparian forest succession (no land use) and, on the other, degradation toward species-poor agricultural grassland (too high land-use intensity).

Consistent with our hypothesis, we found a negative relationship between the distance to old grassland and the species richness of total, mesotrophic, and non-sown species groups. Hence, the colonization of these species groups into our grassland sites appears to be improved by high connectivity to old grassland. However, there was one extreme datapoint of >100 m distance in our analysis, while all other sites had distances <25 m to old grasslands. Ignoring the extreme datapoint led to a non-significant effect. Hence, we cannot be sure about the significance of the effect of distance to old grassland. Nevertheless, the result suggests that the adjacency of source habitats for desired species to restored sites is important, as grassland plants mostly have limited dispersal capacities.

Many other studies found that the connectivity of grasslands increased plant species richness (Brückmann et al. 2010; Öckinger et al. 2012; Kormann et al. 2015; Löffler et al. 2020). In addition to natural dispersal abilities by wind or seed-eating birds, anthropogenic transport media for seeds, such as mowing machines moving from one grassland to a neighboring grassland, were found to play an important role in propagating plant seeds (Bullock et al. 2003), but this is as rarely studied as the propagation by cattle (Kiviniemi & Eriksson 1999; Hooftman et al. 2021).

Altogether, the results of our study suggest that colonization of grassland restoration sites by target species, such as mesotrophic and wet grassland plants as well as red-list and flowering plants, is limited by microsite conditions and high land-use intensity that prevents seed maturation and entails competitive exclusion by fast-growing, and often re-sown, grass species. To promote mesotrophic and wet grassland plants, we suggest a $\mathrm{LUI_m}$ up to 1.4. This means mowing two times and, correlated with this, a total organic nitrogen input of around 30 kg per ha and year. Correspondingly, for red-list plants, a $\mathrm{LUI_m}$ lower than 1 means a mowing frequency of between one and two times and a total organic nitrogen input of 0–6 kg per ha and year. Furthermore, smaller distances to old species-rich grassland might promote successful colonization of mesotrophic and non-sown plant species richness, and we suggest these as source habitats, but also create new source habitats by sowing target plant communities and restoring moist site conditions.

Restoration Success of Butterflies

The results of our study only partly confirm our hypotheses for butterflies. Contrary to our hypothesis, we did not find significant differences in species richness and abundance between old and restored grassland for butterfly species. Likewise, the community composition of butterflies did not show significant patterns. Hence, restoration was generally successful for butterflies, albeit the overall diversity of butterflies was low in our study region.

We can confirm that grassland restoration success for butterflies strongly depends on habitat quality. We found a pronounced positive effect of cover percentage of flowering forbs on species richness and abundance of all butterfly groups, except for the abundance of red-list species. Dennis et al. (2006) emphasize a resource-based thinking of habitats for butterfly conservation. Butterflies depend directly on the existence and abundance of host, food, and nectar plants. Therefore, increasing the cover of flowering forbs generally means higher provisioning of resources for less specialized (polyphagous) butterfly species at least.

The lack of effect of cover of flowering plants on the abundance of red-list butterfly species is probably due to the fact that red-list species have more specific habitat requirements, particularly regarding host-plant specificity and, possibly also, that they occurred in very low numbers in this study. For example, *Lycaena virgaureae* (Scarce copper) and *Adscita statices* (Green forester) need *Rumex acetosa* (Common sorrel) or *Rumex acetosella* (Sheep sorrel) as host plants for larvae and also imagoes feed on a very narrow plant range (Settele et al. 2015). More generally, Turlure et al. (2013) stress the importance of local adaptations of butterfly populations and the specific requirements of larvae regarding host-plant quality for successfully reaching adult stages. Hence, for the return of rare and red-list grassland butterflies, it is not sufficient to achieve high abundances of flowers, but it is necessary to establish a diversity of grassland forbs and legumes, especially, the host, food, and nectar plants of specialist and red-list butterflies (Krauss et al. 2005; Krämer et al. 2012).

In accordance with our hypothesis, we constantly found negative relationships of $\mathrm{LUI_m}$ with species richness and abundance of all butterfly groups. Red-list butterflies had the most pronounced negative effect by higher values of $\mathrm{LUI_m}$. These results concur with previous studies (WallisDeVries & van Swaay 2013; Roth et al. 2021; Meier et al. 2022). Especially, the diversity of specialist butterfly species decreases with increasing agricultural intensity (Ekroos et al. 2010). Both increasing mowing frequency and fertilizer input have a negative impact on host plants for larvae and nectar plants for adult butterflies (Tscharntke et al. 2003; Dover & Settele 2009). Thus, $\mathrm{LUI_m}$ is an important determinant of habitat quality of grasslands for many butterfly species (Szabó et al. 2022). Therefore, the statistical effect of $\mathrm{LUI_m}$ on species richness and abundance of butterflies may largely be indirect and due to its impact on host and nectar plants. Additionally, intensively used grasslands are often characterized by a high, dense, and closed vegetation layer which negatively affects the microclimate for adult and larval stages of butterflies (García-Barros & Fartmann 2009; Wickmann 2009).

In contrast to our hypothesis, increasing cover of old grassland in the surrounding landscape had negative effects on species richness and abundance of specialist grassland and red-list butterflies, as well as on total butterfly abundance. However, a closer look at the grasslands in our study region might explain this unexpected result. First, we mostly observed very low cover percentages of flowering plants at the study sites during the surveys, also on old grassland. Probably, the poor food and nectar resources caused a dilution effect of the generally small butterfly populations when old-grassland cover in the surroundings of the study sites was high. Further, grassland edges may have higher habitat quality than both the grasslands and the margins of arable fields, which may amplify the dilution effect in the grassland-dominated landscape sections (Kasiske et al. 2024). Similarly, Valdés and Ehrlén (2019) found reduced densities of butterflies when the neighboring landscape offered higher abundance of host plants. Nevertheless, other studies found that local species assemblages of flower-visiting insects were positively affected by nearby semi-natural grasslands (Ekroos et al. 2013) and that habitat connectivity at larger scales had a positive effect, especially on specialist and endangered grassland butterfly species (Binzenhöfer et al. 2008; Brückmann et al. 2010; Pérez-Sánchez et al. 2020; Loos et al. 2021).

Altogether, we recommend further restoration measures promoting flowering forbs, including specifically selected host plants, especially for grassland specialists and red-list species under a land-use intensity where seed maturation is feasible.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Site table.
Table S2. Plant groups.
Table S3. Butterfly groups.
Table S4. Data plants.
Table S5. Data butterflies.
Table S6. Plant species richness and cover sums of regression models.
Table S7. Butterfly species richness and abundance of regression models.
Table S8. CCA results.
Figure S1. Mean (±SEM) total (gray) and wet grassland (blue) cover sum (%) on old permanent versus restored grassland (GLM and *z*-test, $p < 0.05$).
Figure S2. Relationship of GLM regression models between flowering forbs (yellow), mesotrophic (green), agricultural (dark green) red-list (red), total (gray), and wet (blue) grassland plant cover (%) and land-use intensity index LUI_m (*z*-test, $p < 0.05$).
Figure S3. (A–C) Relationship of GLM regression models between red-list (red), specialist (green), and total (gray) butterfly abundance and flowering plant cover (A), land-use intensity index LUI_m (B), and cover of neighboring old grassland (C) (*z*-test, $p < 0.05$).

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