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Intensity of grassland management and landscape heterogeneity determine species richness of insects in fragmented hay meadows

Florian Fumy[a,*,1], Cinja Schwarz[a,2], Thomas Fartmann[a,b,3]

[a] Department of Biodiversity and Landscape Ecology, Faculty of Biology and Chemistry, Osnabrück University, Barbarastraße 11, 49076 Osnabrück, Germany

[b] Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, 48157 Münster, Germany

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ABSTRACT

Traditionally managed grasslands rank among the most species-rich ecosystems. However, in agricultural landscapes of Western and Central Europe, their extent has severely decreased. The remaining patches are mostly fragmented and suffer from habitat deterioration. Here, we studied the effects of environmental conditions on species richness of butterflies and grasshoppers in highly fragmented hay meadows. Our study revealed that environmental parameters at the habitat and landscape level influenced species richness of butterflies and grasshoppers in low-intensity hay meadows. In the univariable models, two groups of parameters consistently affected the number of all and threatened species: at the habitat level, species richness was fostered by structural richness, which was indicative of the overall management intensity of the grassland patches. At the landscape level, a higher number of mowing events in the landscape surrounding the hay meadows had a negative effect and higher elevations exhibiting a cooler and wetter climate had a positive effect on species richness. The former reflected the overall intensity of grassland management in the landscape and the later, together with further predictors (cover of forest, habitat connectivity, slope), the landscape heterogeneity. Consequently, the intensity of grassland management at the habitat and landscape level as well as the landscape heterogeneity, which was also related to land-use intensity, determined species richness of butterflies and grasshoppers. Based on these findings, there is an urgent need to enlarge the proportion of grasslands with low land-use intensity in the wider countryside. Additionally, conservation measures should aim at increasing landscape heterogeneity and habitat connectivity.

1. Introduction

Over centuries, humans have created and maintained temperate grasslands by low-intensity management (Bonari et al., 2017; Feurdean et al., 2018). Such traditionally used grasslands rank among the most species-rich ecosystems in Europe. They hold the world record in fine-scale species richness of vascular plants and are hotspots of insect diversity. However, since the industrial revolution and especially after World War II, their extent has severely decreased (Eriksson, 2021; Fartmann, 2023; Schils et al., 2022). This is

* Corresponding author.
E-mail address: florian.fumy@uos.de (F. Fumy).
[1] 0000-0002-0897-4083
[2] 0000-0002-1946-9963
[3] 0000-0002-2050-9221

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particularly true for regions under intensive land use, such as the agricultural landscapes of Western and Central Europe, where the remaining patches of species-rich grasslands are mostly fragmented and suffer from habitat deterioration (Kleijn et al., 2009; Löffler et al., 2023; van Strien et al., 2019; Warren et al., 2021).

In fragmented landscapes, the quality, size and connectivity of habitat patches have been identified as the main drivers of the persistence of grassland insects (Fartmann, 2023). However, the relative importance of each parameter may vary between and within taxonomic groups as well as depending on the landscape configuration (Krämer et al., 2012; Löffler and Fartmann, 2017; Münsch et al., 2019; Poniatowski et al., 2018). Overall, the habitat quality is usually the most important predictor of patch occupancy (Fartmann, 2023; Poniatowski et al., 2018; Tews et al., 2004). Nevertheless, with a rising level of habitat fragmentation, connectivity gains significance (Thomas et al., 2001).

Butterflies and burnet moths (hereinafter termed 'butterflies') and Orthoptera (hereinafter termed 'grasshoppers') are sensitive indicators of environmental conditions in general and land use in particular (Bazelet and Samways, 2012; Fartmann et al., 2013; Fumy et al., 2021; Fumy and Fartmann, 2023; Kőrösi et al., 2022; Marini et al., 2009; Schwarz and Fartmann, 2021). The habitat requirements of both groups are complex. However, the most decisive factors defining habitat quality are vegetation structure and microclimate, which are usually interrelated (García-Barros and Fartmann, 2009; Marini et al., 2009; Poniatowski et al., 2018; Stuhldreher and Fartmann, 2018). In addition, butterflies exhibit a high host-plant specificity (García-Barros and Fartmann, 2009; Munguira et al., 2009). At the landscape level, habitat connectivity and landscape heterogeneity are known to foster species richness of both groups (Fartmann et al., 2021b; Löffler et al., 2023; Marini et al., 2009).

Here, we studied the effects of environmental conditions at the habitat and landscape level on species richness of butterflies and grasshoppers in highly fragmented hay meadows. The investigation was conducted in a grassland-dominated landscape that ranks among the most intensively used grassland areas of Germany, the Günz Valley in southwestern Bavaria (DBU, 2020; Schwieder et al.,

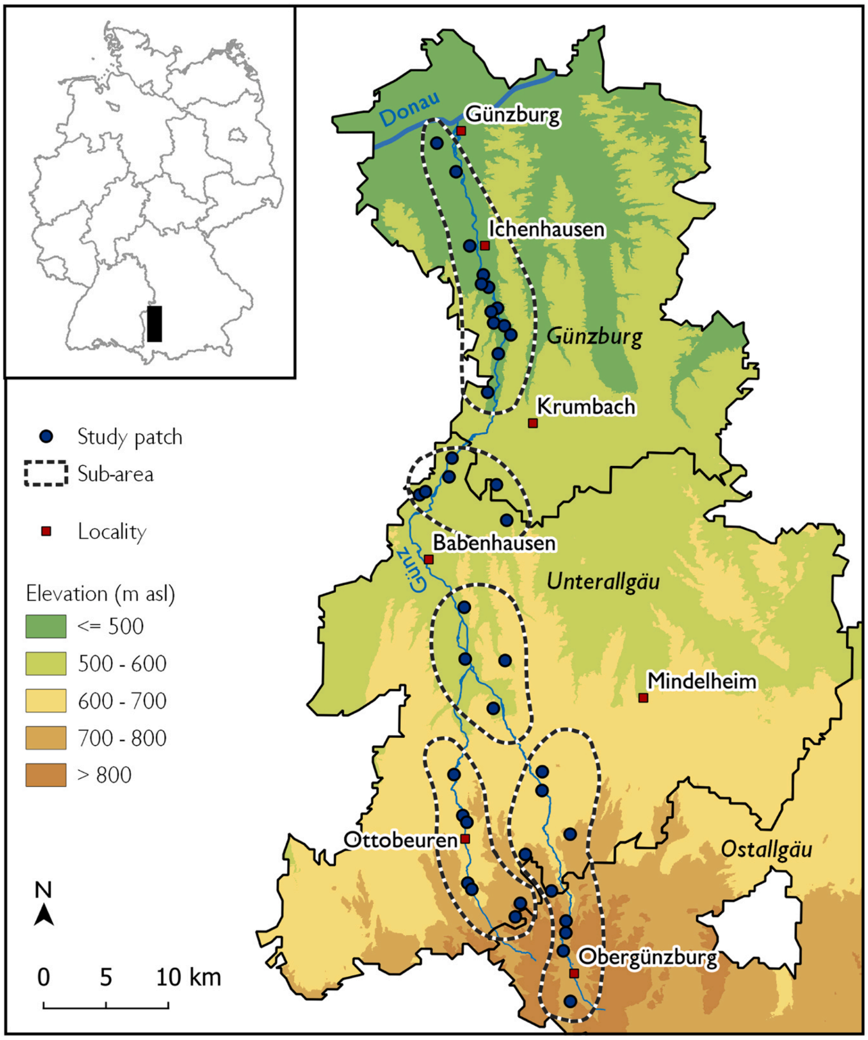

Fig. 1. Location of the study area and study sites in Bavaria, Germany.

2022). The vast majority of the grasslands in the study area are managed intensively and mown four to six times per year for the production of hay, haylage (early baling of part-dry hay) and silage. Species-rich low-intensity hay meadows, however, are rare. Overall, the study area is characterized by a strong climatic and land-use intensity gradient from the submontane south to the colline north. Across this gradient, we sampled species richness of butterflies and grasshoppers at 39 randomly selected patches of low-intensity hay meadows. Relevant environmental predictors of species richness were assessed at the habitat and landscape level. In previous studies of this nature, assessments of the intensity of grassland management were often time-consuming and inaccurate. This is particularly true for evaluations of longer time series or at large spatial scales. A new dataset by Schwieder et al. (2022) that is based on remote sensing data (combined Sentinel-2 and Landsat 8 time series) now provides precise information on the number of annual mowing events at grassland patches in Germany from 2017 on. We used this unique opportunity to integrate these robust data on mowing frequency for both considered spatial scales as potential predictors of species richness. For both insect groups, we considered all and threatened species separately in all analyses. Overall, we hypothesised that environmental variables associated with land-use intensity at the habitat and landscape level would play an important role in explaining species richness in the fragmented hay meadows. Based on the findings of this study, we make recommendations for the conservation management in intensively used agricultural landscapes.

2. Material and methods

2.1. Study area

The study was carried out in the Günz Valley in the southwest of the German Federal State of Bavaria (Fig. 1). Overall, the study area is characterized by a strong environmental gradient from the submontane south to the colline north. The Günz is a small river comprising two main tributaries, the Eastern and the Western Günz, both of which spring at an elevation of 800 m a.s.l. at the foothills of the Bavarian pre-Alps. The Günz flows northward and joins the Danube River in Günzburg at an elevation of 460 m a.s.l. Its water course length is 92 km. The Günz Valley is part of the molasse basin of the northern pre-Alps and comprises a smooth undulating

Table 1
Mean values (± SD) as well as the minimum and maximum of response and predictor variables at the studied low-intensity hay meadows. $N = 39$. If several variables were strongly intercorrelated (Spearman's rank correlation [r_s], $|r_s| > 0.6$), only one was used in the subsequent analysis, which is indicated in the *Used variable*-column. For further information see Section 2.1. ***P < 0.001.

Variable	Mean ± SD	Min.–Max.	r_s	Used variable
Response variables				
Species richness				
Butterflies				
Overall	7.6 ± 3.6	1–16		
Threatened species	2.0 ± 1.6	0–6		
Grasshoppers				
Overall	8.5 ± 2.8	1–16		
Threatened species	1.7 ± 1.1	0–4		
Predictor variables				
Habitat level				
Patch area (ha)	1.5 ± 0.6	0.3–4.2		
Nectar sources	708 ± 403	134–1643		
Number of host-plant species	17.2 ± 5.9	8–27		
Habitat cover (%)				
Bare ground	5.4 ± 6.5	0–30		
Cryptogams	11.3 ± 22.1	0–85		
Herbs	43.0 ± 17.4	10–80		
Grasses	62.3 ± 17.6	15–95		
Structural richness[a]	1.2 ± 0.38	0.3–2.1		
Mowing events/year[b]	2.0 ± 0.4	1.0–3.0		
Landscape level				
Habitat isolation (m)[d]	2213 ± 1875	73–6371		
Slope (°)	2.9 ± 1.66	0.6–6.4		
Elevation (m a.s.l.)	588 ± 103	460–784	1.00	
Temperature (°C)[c]	14.2 ± 0.54	13.2–14.9	–0.98 ***	Elevation
Precipitation (mm)[c]	612 ± 97	450–779	0.98 ***	
Habitat-type cover (%)				
Arable land	15 ± 16	0–58	–0.81 ***	
Forest	24 ± 22	1–74	1.00	Forest
Grassland	57 ± 20	23–95	–0.62 ***	
Mowing events/year	2.7 ± 0.3	1.9–3.3		

[a] Shannon Index (H') of habitat-cover variables.
[b] Mean annual mowing frequency of the period 2018–2019.
[c] Mean summer temperature and precipitation (period: 1991–2020).
[d] Geometric mean of the distance to the three nearest hay meadows with low-intensity management.

landscape (BfN, 2012). The climate is relatively cool and humid. In accordance with the elevational gradient, mean annual temperatures increase from 7.7 °C at the headwaters of the Günz in the south to 9.2 °C in the north at the Danube Valley (meteorological stations: Kaufbeuren in the south and Günzburg in the north, respectively; period: 1990–2020; German Meteorological Service, 2023). Along this gradient, mean annual precipitation decreases from 1096–717 mm. In the past, the study area was dominated by fens and wet grasslands, most of which have been drained and converted into arable fields and improved meadows. Today, the study area is dominated by intensive agriculture, with 18% of the total area being managed as intensive meadows (extracted from the data of Schwieder et al., 2022). The few remaining species-rich grasslands cover only a very small fraction of the landscape. Overall, 0.3% of the total area are considered "species-rich grasslands" in the habitat-assessment database of the German Federal State of Bavaria (LFU, 2021), and 0.6% were grasslands that were part of an agri-environment scheme (meadows with earliest mowing date of 15/06 or 01/07 as well as low-intensity pastures) in 2020 (STMUV, 2020). Consequently, species-rich grasslands are highly isolated from each other in the study area. Moreover, their share and number decline along the environmental gradient from the higher elevations in the south, exhibiting a harsher climate, to the lower elevations in the north, providing more favourable climatic conditions for intensive management (BfN, 2012). As a result, the landscape heterogeneity decreases from the south to the north of the study area.

2.2. *Sampling design*

2.2.1. *Study patches*

In 2020, we surveyed 39 patches of low-intensity hay meadows across the study area (Fig. 1). All meadows were either declared "species-rich grassland" in the habitat-assessment database of the German Federal State of Bavaria (LFU, 2021) or part of an agri-environment scheme (STMUV, 2020). Based on these criteria, the study patches were selected randomly (the respective farmers willingness to participate given). In the study year, all meadows were mown twice with the first mowing taking place on June 15th or later. The characteristic plant community of the mesic meadows was the ***Arrhenatherion elatioris,*** but some plants of montane (***Triseto flavescentis-Polygonion bistortae***) and wet (***Molinietalia caeruleae***) meadows were also usually present (for detailed descriptions of the plant communities, see Dierschke, 1997; Mucina et al., 2016). In order to account for possible spatial autocorrelation, the study area was divided into five sub-areas according to the landscape configuration (Fig. 1).

2.2.2. *Sampling of environmental parameters*

2.2.2.1. Habitat level. For each patch, we assessed several environmental parameters in the field once before the first mowing event took place (Table 1). The cover of bare ground, cryptogams, herbs and grasses was estimated at 5% accuracy at three randomly selected plots of 4 m × 4 m size. We calculated the Shannon Index of these coverages as a measure of structural richness. We counted the number of host plants for mono- and oligophagous butterfly species per patch, using Bräu (2013), Ebert (1994) and Ebert and Rennwald (1993a) (1993b) as references. Additionally, we recorded the availability of nectar sources for butterflies by counting all inflorescences within three plots of 4 m × 4 m size per patch. The plots were located in those areas that provided most flowering plants during each butterfly survey (see butterfly sampling; Schwarz and Fartmann, 2021). We weighted nectar abundance by its use by butterflies, which we assessed both with literature data (Ebert, 1994; Ebert and Rennwald, 1993a, 1993b) and field observations. Flowering species which were visited frequently by butterflies received a higher preference class (*PC*) than unpopular ones (for details, see Krämer et al., 2012). If both literature and field observations existed, we used the highest mentioned value. Weighted nectar abundances NA_i were calculated using the following formula of Fartmann et al. (2013).

$$NA_i = na_i \times^i \sum_{j=1}^{k} \frac{PC_{ij}}{NP_j}$$

where na_i is the absolute nectar abundance of the nectar plant species ***i***, ***k*** is the number of butterfly species using plant species ***i*** as a nectar plant, PC_{ij} is the preference class of the butterfly species ***j*** for the nectar plant species ***i*** and ***NP*** is the number of all nectar plant species used by butterfly species ***j***. As a measure of nectar availability, we calculated the mean of the weighted nectar abundances of all visits for each patch (hereinafter termed 'nectar sources').

Moreover, we calculated the average annual mowing frequency within the two years prior to the study year (2018–2019) for each patch. To do so, we used the dataset created by Schwieder et al. (2022).

2.2.2.2. Landscape level. Habitat isolation was calculated for each patch as the mean geometrical distance to the three nearest patches of species-rich grasslands (Kettermann and Fartmann, 2023). Information on the occurrence of such grasslands was derived from the habitat-assessment database of the German Federal State of Bavaria (LFU, 2021). The mean elevation (m a.s.l.) of the patches was calculated based on an elevation grid provided by Sonny (2023) with a spatial resolution of "1′", which corresponds to a resolution of approximately 20 m × 30 m in the study area. Slope as a measure for topographic variability in the landscape surrounding the focal patch (500 m buffer) was calculated from the same elevation grid. For this purpose, we used the 'terrain' function from the 'raster' package by Hijmans (2023) with 'neighbors' set to *8* ("*queen case*") and 'unit' to *degrees*. Characteristics of the local climate of each patch (mean summer [April–September] precipitation and temperature) were derived from 1-km^2 grid datasets (30-year mean: 1991–2020; German Meteorological Service, 2023) (Table 1). We calculated the proportion of the land-cover types arable land, forest and grassland within a radius of 500 m around each patch from ATKIS data (Authorative Topographic-Cartographic Information System; AdV, 2018 Table 1). As a measure of grassland-management intensity at the landscape level, we calculated the mean number of annual mowing events of all meadows within a radius of 500 m around the focal patch, again using the dataset of Schwieder et al. (2022). All calculations were performed in R statistical environment (R Core Team, 2023). All raster-to-polygon extractions used the 'extract' function in the 'raster' package by Robert & Hijmans (2019).

2.2.3. Sampling of insects

2.2.3.1. Butterflies. Butterfly species were recorded at four times between May and August with at least three weeks between two visits and not within an embargo period of two weeks after any mowing event (BfN, 2021; Löffler et al., 2020). Butterflies were surveyed by walking through each patch in a loop-like manner for 120 min, excluding time taken for species determination. Species were identified visually or using net catches and released after identification. Butterfly sampling only took place between 10 a.m. and 17 p.m. CEST and was only conducted under favourable weather conditions (temperature > 13 °C [sunshine] or > 17 °C [cloud cover 40–80%] and low wind speed [maximum: 4 bft.]; BfN, 2021) In contrast to grasshoppers, the Central European butterfly fauna exhibits several migratory species than can regularly be observed outside their breeding habitats (Fartmann et al., 2013; Löffler et al., 2023). Hence, we focused on resident species and did not record migratory ones according to the classification of Eitschberger et al. (1991). The scientific nomenclature follows Reinhardt et al. (2020).

2.2.3.2. Grasshoppers. We sampled grasshopper species twice between mid-July and late-August when most of the species are adult. Additionally, we searched for *Gryllus campestris* and *Tetrix* spp. during the butterfly surveys in May and June (BfN, 2021; Detzel, 1998; Schlumprecht and Waeber, 2003). All grasshopper surveys were performed under suitable weather conditions (temperature > 15 °C, cloud cover < 50%) and not within an embargo period of two weeks after any mowing event (BfN, 2021; Fischer et al., 2020). All available habitat structures were surveyed for the occurrence of grasshopper species using acoustic and visual detection as well as sweep netting (Fumy et al., 2020; Löffler et al., 2020); all individuals were released after identification. Per patch, each survey took 60 min. The scientific nomenclature follows Fischer et al. (2020).

2.3. Statistical analysis

All statistical analyses were performed using R statistical environment (R Core Team, 2023). To assess the effects of the recorded environmental parameters on overall species richness and richness of threatened species of butterflies and grasshoppers, we conducted univariable and multivariable Generalized Linear Mixed-effects Models (GLMM) with Poisson (butterflies) and negative-binomial (grasshoppers) error structures. Threat status in Bavaria was derived from Voith et al. (2016b) for butterflies and from Voith et al. (2016a) for grasshoppers. In addition to threatened species, we also considered near-threatened species to be 'threatened' (Fumy and Fartmann, 2023). Prior to the multivariable analyses, we assessed multicollinearity for all predictor variables and excluded inter-correlated variables ($|r_s| > 0.6$, VIF < 2) (see Graham, 2003; Zuur et al., 2010). Possible spatial autocorrelation was taken into account by adding sub-area as a random intercept in all models. All fixed effects were centred and scaled. In order to increase the robustness of models with multiple predictors and to identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach including the top-ranked models within $\Delta AIC_C < 2$ (Burnham and Anderson, 2010; Grueber et al., 2011). We used the 'lme4′ package of Bates et al. (2021) for all GLMM analyses and the 'dredge' and the 'model.avg' functions in the R package 'MuMIn' by Bartoń (2023) for model averaging. We evaluated the explanatory power of the models by calculating marginal (variance explained by fixed effects) and conditional (variance explained by both fixed and random effects) R^2 (Nakagawa et al., 2017).

3. Results

3.1. Environmental conditions

The hay-meadow patches had a mean size (± SD) of 1.5 ± 0.6 ha (Table 1). They were usually characterised by closed and homogeneous swards dominated by grasses but also many herbs. The overall availability of nectar sources and host plants was mostly high. As in the study year, the hay meadows were typically mown twice annually over the preceding two years (maximum: three mowing events). The patches were mostly located in a gently rolling landscape with intensively used grasslands (mean [± SD] number of mowing events per year: 2.7 ± 0.3), some forests and a few arable fields. Cover of forests in the surrounding of the patches was negatively correlated with the cover of grasslands. Overall, the patches of hay meadows were strongly isolated from other patches of species-rich grasslands. On average (± SD), the patches were located at an elevation of 588 ± 103 m a.s.l. Accordingly, summers were relatively cool (mean ± SD: 14.2 ± 0.5 °C) and very wet (612 ± 97 mm). Temperature and the share of arable land in the surrounding of the patches were negatively and precipitation positively correlated with elevation.

3.2. Species richness

In total, we recorded 35 resident butterfly species on the 39 patches, 14 of which were considered threatened (Table A1). On average (± SD), we detected 8.5 ± 2.8 species in total and 2.0 ± 0.3 threatened species per patch (Table 1). The most common ones were *Polyommatus icarus* (occurring in 95% of the patches), *Aphantopus hyperantus* (80%) and *Cyaniris semiargus* (74%) (Table A2). The latter was considered threatened.

Overall, we observed 21 grasshopper species on the 39 patches; among them were 6 threatened ones (Table A2). On average (± SD), we detected 8.5 ± 2.8 species in total and 1.7 ± 1.1 threatened species per patch (Table 1). The most widespread ones were *Pseudochorthippus parallelus* and *Roeseliana roeselii* (both occurred in 97% of the patches), *Chorthippus dorsatus* (85%) and *Chorthippus biguttulus* (82%) (Table A2). *Chorthippus dorsatus* was considered threatened.

3.3. Environmental drivers of species richness

In the studied low-intensity hay meadows, several environmental parameters at the habitat and the landscape level influenced species richness of butterflies and grasshoppers (Table 2). At the habitat level, structural richness was the most important predictor. It had a positive effect on species richness of all and threatened species in butterflies and grasshoppers. In butterflies, moreover, the number of host plant species had a positive and the number of mowing events per year during the two years prior to the study had a negative effect on species richness of all and threatened species.

Table 2

Results of univariable GLMMs: Relationship between environmental parameters and butterfly species richness as well as grasshopper species richness. Sub-area was set up as a random factor (see Fig. 1). For further information see Table 1. $N = 39$. R^2_m = variance explained by fixed effects, R^2_c = variance explained by both fixed and random effects (Nakagawa et al., 2017). Statistical significances are indicated as follows: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. = not significant.

Parameter	Butterflies						Grasshoppers					
	All species			Threatened species			All species			Threatened species		
	Est. ± SE	P	R^2_m/R^2_c	Est. ± SE	P	R^2_m/R^2_c	Est. ± SE	P	R^2_m/R^2_c	Est. ± SE	P	R^2_m/R^2_c
Habitat level												
Patch area	0.04 ± 0.06	n.s.	.	-0.04 ± 0.23	n.s.	.	0.05 ± 0.06	n.s.	.	0.06 ± 0.12	n.s.	.
Nectar sources	0.06 ± 0.07	n.s.	.	0.16 ± 0.24	n.s.	.	.	.	.	.	.	.
No. host-plant species	**0.28 ± 0.06**	***	**0.39/0.39**	**0.73 ± 0.26**	**	**0.21/0.37**	.	.	.	.	.	.
Structural richness	**0.19 ± 0.07**	**	**0.21/0.28**	**0.53 ± 0.23**	*	**0.11/0.33**	**0.12 ± 0.06**	*	**0.11/0.11**	**0.36 ± 0.12**	**	**0.22/0.22**
Mowing events/year	**–0.20 ± 0.07**	**	**0.20/0.39**	**–0.54 ± 0.20**	**	**0.11/0.44**	–0.08 ± 0.06	n.s.	.	–0.15 ± 0.13	n.s.	.
Landscape level												
Habitat isolation	**–0.13 ± 0.06**	*	**0.09/0.31**	**–0.54 ± 0.23**	*	**0.1/0.46**	–0.05 ± 0.06	n.s.	.	**–0.31 ± 0.14**	*	**0.15/0.27**
Slope	**0.22 ± 0.07**	**	**0.27/0.29**	0.46 ± 0.24	n.s.	0.09/0.29	**0.12 ± 0.05**	*	**0.12/0.12**	**0.24 ± 0.12**	*	**0.11/0.11**
Elevation	**0.22 ± 0.06**	**	**0.29/0.29**	**0.81 ± 0.34**	*	**0.24/0.38**	**0.13 ± 0.05**	*	**0.14/0.14**	**0.27 ± 0.12**	*	**0.14/0.14**
Temperature	**–0.22 ± 0.06**	**	**0.29/0.29**	**–0.87 ± 0.31**	**	**0.28/0.41**	**–0.15 ± 0.05**	**	**0.17/0.17**	**–0.30 ± 0.12**	*	**0.16/0.16**
Precipitation	**0.24 ± 0.06**	**	**0.31/0.31**	**0.96 ± 0.30**	**	**0.34/0.42**	**0.14 ± 0.06**	*	**0.14/0.14**	**0.31 ± 0.12**	*	**0.18/0.18**
Arable land	–0.07 ± 0.10	n.s.	0.04/0.16	–0.23 ± 0.29	n.s.	0.02/0.27	–0.08 ± 0.06	n.s.	.	–0.21 ± 0.14	n.s.	.
Forest	**0.14 ± 0.06**	*	**0.12/0.21**	**0.56 ± 0.23**	*	**0.13/0.32**	0.08 ± 0.06	n.s.	.	0.22 ± 0.12	n.s.	.
Grassland	–0.09 ± 0.06	n.s.	0.05/0.28	–0.44 ± 0.23	n.s.	0.07/0.41	–0.03 ± 0.06	n.s.	.	–0.10 ± 0.13	n.s.	.
Mowing events/year	**–0.15 ± 0.06**	**	**0.12/0.34**	**–0.81 ± 0.19**	***	**0.23/0.58**	**–0.14 ± 0.05**	*	**0.14/0.23**	**–0.22 ± 0.09**	*	**0.08/0.20**

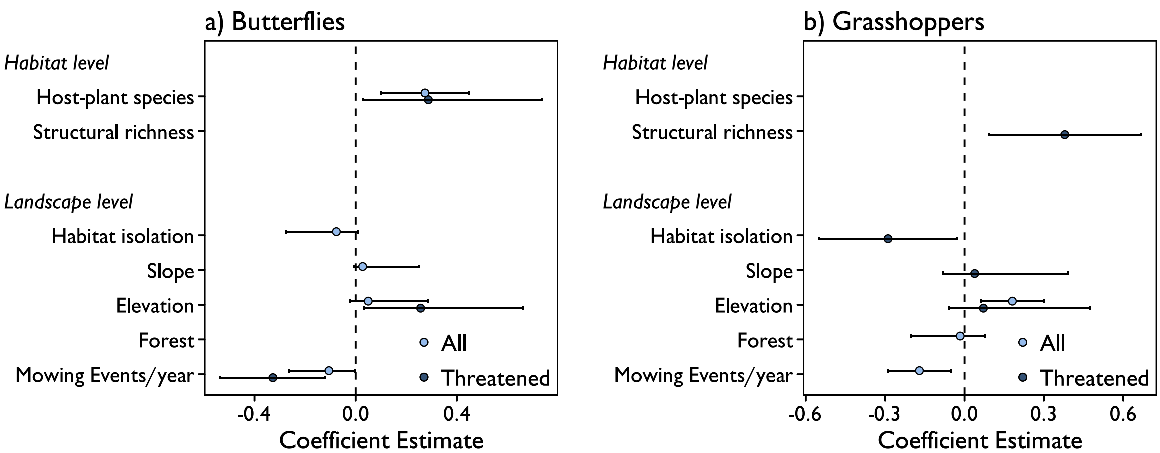

Fig. 2. Results of multivariable GLMMs: Relationship between environmental parameters and butterfly species richness as well as grasshopper species richness. Sub-area was set up as a random factor (see Fig. 1). Model-averaged coefficients (standardized estimates ± 95% confidence intervals [CI]) derived from top-ranked models ($\Delta AIC_C < 2$) are shown. CI of significant predictors ($P < 0.05$) do not cross x = 0. For further information see Table A3 and Section 2.1. $N = 39$.

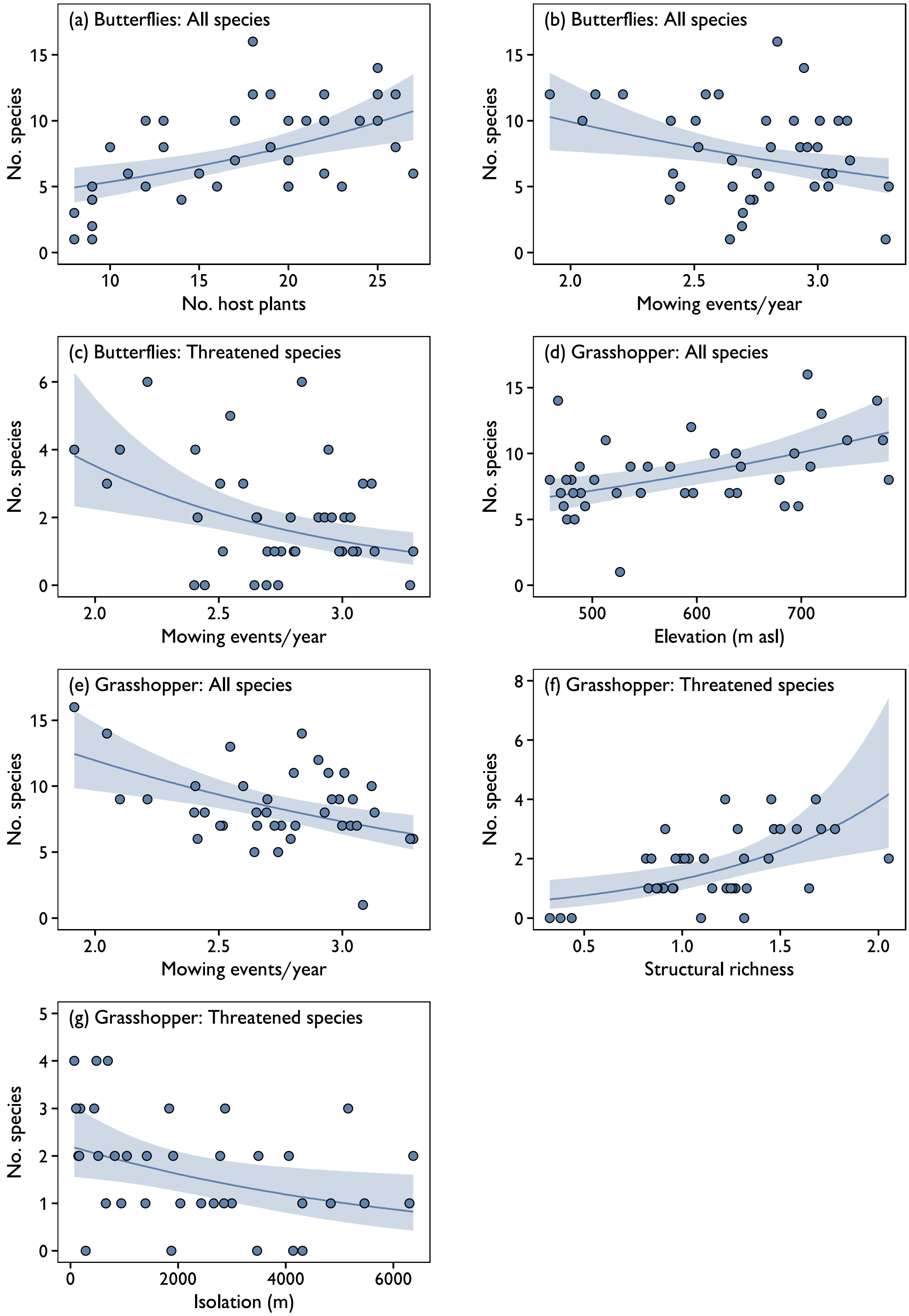

Fig. 3. Results of multivariable GLMMs: Relationship between significant environmental parameters and butterfly species richness (a–c) as well as grasshopper species richness (d–g). The regression slopes and 95% confidence intervals (blue bands) were fitted using the respective first-ranked model from model dredging with the ggpredict function from the ggeffects package (Lüdecke, 2018). See Table A3 for detailed model statistics.

At the landscape level, four predictors consistently affected species richness of all and threatened species in butterflies and grasshoppers (Table 2). Species richness increased with elevation and precipitation but decreased with temperature and the number of mowing events in grasslands around the focal patch of hay meadow. Except mowing events per year, all variables were inter-correlated (see Section 3.1). In butterflies, additionally, the habitat isolation had a negative and the forest cover around the focal patch of hay meadow had a positive effect on species richness of all and threatened species. Moreover, slope fostered overall species richness. In grasshoppers, slope also had a positive effect on overall species richness and additionally on the number of threatened species. Furthermore, richness of threatened species decreased with habitat isolation.

In the multivariable GLMM, the most important predictor was the mean number of annual mowing events of all meadows within a radius of 500 m around the focal patch of hay meadow (Fig. 2, Table A3). It was indicative of the overall intensity of grassland management at the landscape level and had a negative effect on all and threatened butterfly species as well as on all grasshopper species. Moreover, overall species richness of butterflies increased with the number of host plants. For grasshoppers, structural richness, habitat isolation and elevation were further predictors of species richness. The total number of species increased with elevation, and the number of threatened species was fostered by structural richness but declined with habitat isolation. Fig. 3.

4. Discussion

Our study revealed that in a landscape with intensive agriculture, environmental parameters at the habitat and landscape level influenced species richness of butterflies and grasshoppers in fragmented low-intensity hay meadows. In the univariable models, three groups of parameters consistently affected the number of all and threatened species in both taxa: at the habitat level, species richness was fostered by structural richness. At the landscape level, a higher number of mowing events in the landscape surrounding the hay meadows had a negative effect and higher elevations exhibiting a cooler and wetter climate had a positive effect on species richness. However, there were also some differences in the drivers of species richness in butterflies and grasshoppers and among all and threatened species. Despite these differences, all predictors in the univariable and multivariable models had in common the fact that they were to some degree related to the intensity of land use.

Recent studies have shown that habitat quality is the main driver of the persistence of insect species in landscapes with well-connected semi-natural grasslands (Krämer et al., 2012; Löffler and Fartmann, 2017; Münsch et al., 2019; Poniatowski et al., 2018). However, in our study, conducted in a landscape with intensive grassland management and highly fragmented low-intensity hay meadows, predictors at both the habitat and the landscape level determined species richness of butterflies and grasshoppers. At the habitat level, the structural richness of the hay meadows was a key driver of species number. It promoted species richness of all four response variables in the univariable models and, additionally, of threatened grasshoppers in the multivariable model. Structural richness is accompanied by a high availability of different microhabitats and, therefore, is known to generally increase the number of species in a patch (Steinmann et al., 2011; Tews et al., 2004). This has also been documented for butterflies and grasshoppers (Fumy et al., 2021; Fumy and Fartmann, 2023; Kruess and Tscharntke, 2002; Löffler and Fartmann, 2017; Marini et al., 2009).

The mowing frequency can be an important predictor of structural richness in grasslands. Usually, the structural richness decreases with a higher number of mowing events per year (Cizek et al., 2012; Fumy et al., 2021; Fumy and Fartmann, 2023). However, in our study, (i) the variability in mowing frequency was very low, (ii) both variables were not intercorrelated and (iii) the effects of structural richness on species richness were much stronger than those of the mowing frequency. Consequently, other parameters than the number of mowing events per year were more important for differences in structural richness within the studied patches. Further measures that are regularly associated with intensive grassland management, such as drainage, flattening of the micro relief, intensive fertilisation or reseeding, also result in homogeneous swards (Fartmann et al., 2021a; Humbert et al., 2021; Settele et al., 2009). We are not able to disentangle the genuine effect of each of these measures on the loss in structural richness. Nevertheless, we believe that structural richness reflects overall intensity of grassland management at the patches in our study quite well.

Many butterfly species exhibit highly specialized host-plant preferences and are mono- or oligophagous (García-Barros and Fartmann, 2009; Munguira et al., 2009). Accordingly, the availability of sufficient host plants is an important predictor of species richness in butterflies (Fartmann et al., 2013; Krämer et al., 2012). In line with this, the number of host-plant species fostered the richness of all and threatened butterfly species in the univariable models and also of all butterfly species in the multivariable model. Phytodiversity in hay meadows is usually also strongly affected by land-use intensity (Ellenberg and Leuschner, 2010; Fartmann et al., 2021a). In particular, intensive fertilisation and reseeding can strongly reduce species richness of vascular plants in grasslands.

Butterflies belong to those insects that are known to be very sensitive to the mowing frequency and changes in the mowing regime (Börschig et al., 2013; Bruppacher et al., 2016; Settele et al., 2009). Even one additional mowing event in a certain year can already lead to local extinctions of butterfly species. In highly fragmented patches, such as the hay meadows of the study area, such losses can often hardly be compensated due to the lack of potential source populations and low habitat connectivity (Poniatowski et al., 2018; Poniatowski et al., 2016). In line with this, the species richness of all and threatened butterfly species declined with increasing mowing frequency in the univariable models.

At the landscape level, the number of mowing events in the landscape surrounding the studied hay meadows had a negative effect and higher elevations exhibiting a cooler and wetter climate had a positive effect on the number of butterfly and grasshopper species in the univariable as well as some of the multivariable models. Due to the strong effect of the number of mowing events per year on species richness, we assume that this parameter is a good indicator for the overall intensity of grassland management in the landscape. Previous studies have already shown that landscapes which are dominated by intensively-used grasslands generally exhibit low species richness, in particular with respect to butterflies but also grasshoppers (Fartmann et al., 2021b; Löffler et al., 2023). This is usually also true for the few remaining protected or well-managed grasslands in such landscapes.

Species richness of butterflies and especially of grasshoppers in Central Europe is usually highest in regions with warm summers (Fischer et al., 2020; Reinhardt et al., 2020). By contrast, in our study, higher elevations exhibiting a cooler and wetter climate fostered species richness of all and threatened species of both taxa in the univariable models as well as overall species richness of grasshoppers in the multivariable model. In the study area, however, it is not only the harsher climate that is associated with increasing elevation but also a lower overall land-use intensity and higher landscape heterogeneity (see Section 2.1). In line with this, the cover of arable land in the surrounding of the hay meadows was negatively correlated with elevation. Arable land ranks among the most hostile habitats for insects in modern-day agricultural landscapes (Ekroos et al., 2010). Accordingly, we assume that the lower overall land-use intensity and the higher landscape heterogeneity were responsible for the greater species richness at higher elevations. Only recently, Löffler et al. (2023) highlighted the prime importance of uplands for insect conservation since they suffered less from land-use intensification compared to the lowlands.

Further predictors of species richness were slope, habitat connectivity and cover of forest. The overall number of butterfly species as well as the number of all and threatened species increased with slope in the univariable models. It is a measure for the topographic variability in the surroundings of the hay meadows and, hence, a further aspect of landscape heterogeneity (Larkin et al., 2016; see also above).

Particularly in highly fragmented landscapes, it is assumed that habitat connectivity plays a crucial role for patch occupancy, species richness and long-term survival of insects (Fartmann, 2023; Maes and Bonte, 2006; Poniatowski et al., 2018). Our study corroborates this. We found a negative effect of habitat isolation on overall species richness of butterflies as well as on the number of threatened butterfly and grasshopper species in the univariable models. Additionally, the number of threatened grasshopper species decreased with habitat isolation in the univariable models.

Light forests and forest fringes are usually nutrient-poor and can be important habitats for many grassland butterfly species (Löffler et al., 2023; Ram et al., 2020). Hence, especially in landscapes with a low share of species-rich grasslands, they can enhance species richness of grassland butterflies at the landscape level. Indeed, the cover of forests, which was negatively correlated with the cover of grasslands, had a positive effect on the number of all and threatened butterfly species in the univariable models.

In conclusion, at the habitat level, the structural richness of hay meadows was an indicator for the overall intensity of grassland management and a key driver of butterfly and grasshopper species richness. At the landscape level, the number of mowing events in the landscape surrounding the studied hay meadows had a negative effect and higher elevations exhibiting a cooler and wetter climate had a positive effect on species richness. The former reflected the overall intensity of grassland management in the landscape and the later, together with further predictors (cover of forest, habitat connectivity, slope), the landscape heterogeneity. Consequently, the intensity of grassland management at the habitat and landscape level as well as the landscape heterogeneity, which was also related to land-use intensity, determined species richness of butterflies and grasshoppers in highly fragmented hay meadows.

5. Implications for conservation

Halting the recent insect decline is one of the greatest challenges for nature conservation today (Cardoso et al., 2020; Samways et al., 2020). This is especially true for fragmented landscapes since even protected areas suffer from rapid species losses in such landscapes (Cooke et al., 2023; Rada et al., 2019). Although the overall numbers of detected grassland butterfly and grasshopper species in the studied low-intensity grasslands were high, including several threatened species, many species only occurred rarely. Our study thus highlights (i) the prime importance of low-intensity land use and landscape heterogeneity for the conservation of grassland biodiversity in highly fragmented agricultural landscapes and (ii) the urgent need to increase the proportion of grasslands with low land-use intensity in the wider countryside (see also Löffler et al., 2023). Species-rich grasslands covered only 0,3% of the total land surface (which corresponds to 1.4% of the total grassland area) in the study area, which is typical of intensively-used agricultural landscapes. That is far from the goals set out in the EU Biodiversity Strategy for 2030, stating that at least 10% of the agricultural area should be under high-diversity landscape features and 25% of agricultural land should be under organic farming (EC, 2020).

The study area forms a grassland-dominated corridor between two regions that are rich in grasslands of high conservation value, the foothills of the Alps in the south and the Danube Valley in the north (see Section 2.1). Accordingly, an improvement of habitat connectivity within the study area should also facilitate the exchange of individuals between these two local biodiversity hotspots. Beyond butterflies and grasshoppers, there are many other taxa (e.g. other groups of insects, plants or birds) that are known to generally benefit from the recommended conservation measures (Brüggeshemke et al., 2022; Fartmann et al., 2021a; Samways et al., 2020).

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Declaration of Competing Interest

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

Data Availability

The authors are unable or have chosen not to specify which data has been used.

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Appendix

Table A1
Patch occupancy (%) and threat status of all butterfly and burnet moth species detected in this study. Threat status: · = least concern, x = threatened (near threatened or threatened in Bavaria; Voith et al., 2016b).

Species	Threat status	Occupancy (%)
Adscita statices	·	5
Anthocharis cardamines	·	8
Aphantopus hyperantus	·	79
Aporia crataegi	·	23
Araschnia levana	·	36
Argynnis paphia	·	44
Boloria eunomia	x	10
Boloria selene	x	13
Brenthis ino	x	36
Carcharodus alceae	·	5
Carterocephalus palaemon	x	15
Coenonympha arcania	·	3
Coenonympha pamphilus	·	28
Cupido minimus	x	5
Cyaniris semiargus	x	74
Erebia aethiops	x	3
Erebia medusa	x	5
Eumedonia eumedon	x	13
Fabriciana adippe	x	3
Leptidea sinapis/juvernica	·	3
Limenitis camilla	·	3
Lopinga achine	x	3
Maniola jurtina	·	10
Melanargia galathea	·	49
Melitaea diamina	x	8
Minois dryas	x	3
Ochlodes sylvanus	·	46
Papilio machaon	·	10
Pararge aegeria	·	3
Polygonia c-album	·	15
Polyommatus icarus	·	95
Pyrgus malvae	x	10
Thymelicus lineola	·	59
Thymelicus sylvestris	·	36
Zygaena filipendulae	·	3

Table A2
Patch occupancy (%) and threat status of all grasshopper species detected in this study. Threat status: · = least concern, x = threatened (near threatened or threatened in Bavaria; Voith et al., 2016a).

Species	Threat status	Occupancy (%)
Chorthippus albomarginatus	·	56
Chorthippus biguttulus	·	82
Chorthippus brunneus	·	15

(*continued on next page*)

Table A2 (*continued*)

Species	Threat status	Occupancy (%)
Chorthippus dorsatus	x	85
Chrysochraon dispar	·	3
Conocephalus dorsalis	x	3
Conocephalus fuscus	·	44
Euthystira brachyptera	·	36
Gomphocerippus rufus	·	38
Gryllus campestris	x	44
Omocestus viridulus	x	8
Phaneroptera falcata	·	10
Pholidoptera griseoaptera	·	54
Pseudochorthippus montanus	x	10
Pseudochorthippus parallelus	·	97
Roeseliana roeselii	·	97
Stethophyma grossum	x	26
Tetrix subulata	·	41
Tetrix undulata	·	28
Tettigonia cantans	·	36
Tettigonia viridissima	·	38

Table A3
Detailed results of multivariable GLMMs: Relationship between environmental parameters and butterfly species richness as well as grasshopper species richness. Sub-area was set up as a random factor (see Fig. 1). For further information see Table 1 and Section 2.1. $N = 39$. $R^2{}_m$ = variance explained by fixed effects, $R^2{}_c$ = variance explained by both fixed and random effects (Nakagawa et al., 2017). Presented are the averaged models calculated from the best-ranked models of model dredging, respectively, within delta < 2. Statistical significances are indicated as follows: n.s. $P \geq 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Butterflies				Grasshoppers			
	All species		Threatened species		All species		Threatened species	
	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*	Est. ± SE	*P*
(Intercept)	1.98 ± 0.06	***	0.54 ± 0.13	***	2.12 ± 0.06	***	0.44 ± 0.14	**
Habitat quality								
No. host-plant species	0.27 ± 0.09	**	0.29 ± 0.22	n.s.	.	.	.	.
Structural richness	.	.	.	.	.	.	0.38 ± 0.14	**
Landscape quality								
Habitat isolation	−0.08 ± 0.08	n.s.	.	.	.	.	−0.29 ± 0.13	*
Slope	0.03 ± 0.06	n.s.	.	.	.	.	0.04 ± 0.09	n.s.
Elevation	0.05 ± 0.08	n.s.	0.26 ± 0.2 0	n.s.	0.18 ± 0.06	**	0.07 ± 0.13	n.s.
Forest	.	.	.	.	−0.02 ± 0.04	n.s.	.	.
Mowing events/year	−0.13 ± 0.08	*	−0.33 ± 0.10	**	−0.17 ± 0.06	**	.	.
R^2_m/R^2_c	**0.48/0.48**		**0.35–0.43/0.35–0.43**		**0.26–0.28/0.26–0.28**		**0.33/0.33–0.36**	

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