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Low-intensity land use fosters species richness of threatened butterflies and grasshoppers in mires and grasslands

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A B S T R A C T

Insects are by far the most species-rich branch of the tree of life and fundamental parts of extensive networks of biotic interactions. However, insect populations are declining dramatically and many species are facing extinction in the course of global change. In this study, we investigated species richness of threatened butterflies and grasshoppers in mire and grassland ecosystems in a low-mountain range in SW Germany: the southern Black Forest. Altogether, 84 randomly selected plots (100 m × 100 m) were surveyed. Across a hydrological gradient, each plot belonged to one of the five following habitat types: peat bog, fen, mesic grassland, semi-dry grassland and dry grassland. Our study revealed strong differences in environmental conditions and in assemblage composition of threatened butterfly and grasshopper species in mire and grassland habitats. Species richness and the number of indicator species of both groups peaked in fens and dry grasslands, and to a lesser extent in semi-dry grasslands. All three habitat types were characterized by low to intermediate levels of land use. In line with this, land-use intensity was the key driver of habitat heterogeneity and, hence, of species richness of threatened butterflies and grasshoppers. We recommend a conservation policy that secures the maintenance or re-establishment of low-intensity land use. In particular, we suggest continuous large-scale, low-intensity cattle grazing from spring to autumn, which has been shown to best promote high habitat heterogeneity.

1. Introduction

Large ungulate herbivores have shaped entire biomes for thousands of years, and, accordingly, biodiversity has co-developed with them (Konvička et al., 2021). However, during the late Pleistocene and early Holocene, humans extirpated or at least strongly reduced these megaherbivores on most continents. Subsequently, the livestock of preindustrial farmers and pastoralists took on the role of the wild ungulates in creating species-rich habitats (Hejcman et al., 2013; Konvička et al., 2021). Since the beginning of the industrial era, severe and ever accelerating changes in land use have led to the modern-day agriculture that dominates farmland nowadays and has caused severe biodiversity declines (Fartmann et al., 2021; Hejcman et al., 2013; Stoate et al., 2009). At the same time, traditional land use such as large-scale low-intensity cattle grazing has ceased almost completely. However, remnants of traditional land use have persisted in mountainous landscapes where intensive agriculture is impeded by the pronounced relief and shallow soils (MacDonald et al., 2000; Plieninger et al., 2006).

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Insects are by far the most species-rich branch of the tree of life and fundamental parts of extensive networks of biotic interactions (Cardoso et al., 2020). However, insect populations are declining dramatically and many species are facing extinction in the course of global change. Butterflies and Orthoptera (hereinafter termed 'grasshoppers') can be surveyed applying non-invasive methods, their ecology is well-known and, similar to most other insect groups, both are highly sensitive to changes in climate and habitat configuration. Thus, both are well suited indicator groups to investigate the effects of environmental change in open habitats (Bazelet and Samways, 2012; Fartmann et al., 2013; Poniatowski et al., 2020; Thomas, 2005). This is especially true for threatened species since most of them are habitat specialists and have recently undergone the most severe declines (Bonelli et al., 2021; Poniatowski et al., 2016; Purvis et al., 2000). The habitat requirements of insects in general and butterflies and grasshoppers in particular are highly complex. Particularly, vegetation composition and microclimate, which are often interrelated, define habitat quality (Fartmann et al., 2012; García-Barros and Fartmann, 2009; Gardiner and Dover, 2008; Marini et al., 2009; Poniatowski et al., 2018; Stuhldreher and Fartmann, 2018).

Our study area comprises a low-mountain range in SW Germany: the southern Black Forest. Due to its high share of species-rich mires and grasslands, it is part of one of 30 German biodiversity hotspots (Ackermann and Sachteleben, 2012). In a previous study in the dominant grassland types of the same area, Fumy et al. (2021) identified land-use intensity as the main predictor of grasshopper species richness, especially of threatened species. In this study, we use a similar approach and include a second indicator species group, butterflies. We also extend the focus of this study by adding mires to the list of considered habitat types. Altogether, we surveyed threatened butterfly and grasshopper species in 84 randomly selected plots belonging to one of the five following habitat types: peat bog, fen, mesic grassland, semi-dry grassland and dry grassland. These habitat types, on the one hand, represent a long hydrological gradient and, on the other hand, are likely to differ in land-use intensity.

In order to analyze the drivers of the occurrence of threatened species in a landscape of high conservation value, we (i) assessed differences in land-use intensity, environmental conditions and the number of threatened species between the five habitat types, (ii) related a key property of species-rich habitats (habitat heterogeneity) to an important driver of species richness (land-use intensity) and (iii) analyzed the relationship of numbers of threatened species to land-use intensity and environmental conditions across all habitat types. In order to take into account between-habitat-type variety in land-use intensity, we also (iv) analyzed the effect of land-use intensity on the occurrence of threatened species for each habitat type separately.

Based on the results, we give recommendations for effective strategies for biodiversity conservation in mire and grassland ecosystems, which are expected to foster not only threatened butterflies and grasshoppers but also a wide range of other taxa.

2. Material and methods

2.1. Study area

The study area, the 'Hotzenwald' in the southern Black Forest (federal state of Baden-Württemberg, SW Germany; 47°7′ N/8°1′ E), has an area of about 100 km^2 and covers an elevation gradient of 700–1100 m a.s.l. For Central European conditions, the climate is rather cool and wet, with a mean annual temperature of 6.6 °C and an average annual precipitation of 1650 mm (reference period 1991–2020; German Meteorological Service, 2021). Along the elevation gradient, precipitation increases from about 1470 to 1840 mm/a and mean annual temperature decreases from 7.3° to 5.6°C.

The Hotzenwald is part of the German biodiversity hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann and Sachteleben, 2012). The cultural landscape of the study area is rich in open mire ecosystems and semi-natural grasslands (Fumy and Fartmann, 2021). Most of the mires and grasslands have been managed as commons for centuries (Hermle and Deil, 2002; Regional Office for Environment, 2004). Although a relatively large share of them is still in communal property, management has undergone substantial changes since the 1930 s through administrative interventions and technical innovation (Regional Council Freiburg (Regierungspräsidium Freiburg), 2011). However, traditional rough grazing, in many cases with a local cattle breed called 'Hinterwälder', is still widespread in mires and semi-natural grasslands. (Konold et al., 2014). Due to their high habitat heterogeneity and species richness, these pastures have an outstanding conservation value and, additionally, make a unique contribution to the German cultural heritage (Fumy et al., 2021; Fumy and Fartmann, 2021; Lederbogen et al., 2004). On some of the least productive soils however, irregular management or complete abandonment for over 20 years has resulted in the replacement of formerly species-rich mires and semi-natural grasslands by homogeneous, high-growing vegetation rich in litter and dominated by tall forbs (e.g. *Filipendula ulmaria*), dwarf shrubs (e.g. *Vaccinium myrtillus*, *V. uliginosum*) or grasses (e.g. *Molinia caerulea*, *Nardus stricta*) (Fumy et al., 2021; Geis et al., 2013; own observation).

In contrast to the pastures on nutrient-poor soils, the grasslands on more productive soils historically were predominantly mown once or twice per year (Regional Office for Environment, 2004) and managed as irrigation meadows that were irrigated in spring in order to foster snow melting and thus to elongate the vegetation period (Leibundgut and Vonderstrass, 2016). However, many of them have recently suffered from land-use intensification, reflected by a regular application of fertilizer and an increasing mowing frequency (Konold et al., 2014). Despite these general changes in land use, some of the meadows in the study area are still characterized by low-intensity land use and species-rich insect assemblages (Fumy et al., 2021, 2020).

2.2. Study design

2.2.1. Study plots

Within the study area, we mapped mire and grassland habitats in the field according to Finck et al. (2017). Altogether, 84 plots

(100 m × 100 m) were surveyed. Each plot was classified as one of the five following habitat types representing a long moisture gradient: peat bog $n = 17$, fen $n = 20$, mesic grassland $n = 15$, semi-dry grassland $n = 18$ and dry grassland $n = 14$. Characteristic plant communities of peat bogs were the *Sphagnetum magellanici* and at higher elevations also the *Eriophoro-Trichophoretum cespitosi*, the *Pino mugo-Sphagnetum* and *Vaccinium-uliginosum* shrubberies. The *Juncetum squarrosi* and communities of the *Scheuchzerio-Caricetea* such as the *Caricion fuscae*, *Caricetum limosae* and *Caricetum rostratae* were typical of fens. *Cynosurion* and *Polygono-Trisetion* communities were characteristic of mesic, the *Polygalo-Nardetum* of semi-dry and the *Festuco-Genistelletum* of dry grasslands (Burkart et al., 2004; Dierschke, 1997; Peppler-Lisbach and Petersen, 2001; Regional Office for Environment, 2004). In order to avoid edge effects from adjacent habitats (Schirmel et al., 2010), each plot had to be surrounded by a buffer of at least 20 m of the focal habitat type. We considered the same study plots as in Fumy et al. (2021) which were chosen randomly using the "random points inside polygons" function in QGIS (QGIS Development Team, 2020), but used a finer habitat-type classification. However, as we included butterflies as a group comprising species with higher mobility, we raised the minimum distance between two plots from 50 m to 100 m, which forced us to randomly remove 20 plots from the previous study that were located too close.

Moreover, we considered peat bogs as a new habitat type and added the 17 respective plots, all of which were chosen applying the same procedure within the respective habitat type.

In order to account for possible spatial autocorrelation, the study area was divided into eight sub-areas considering coherent valley and ridge systems as well as isolation by large forest patches. However, small open habitat patches surrounded by closed forests were added to the respective sub-area exclusively in accordance with the topography (Fig. 1). The sub-area served as a random factor in the statistical analyses (see Section 2.2).

2.2.2. Sampling design

2.2.2.1. Environmental conditions. For each plot, we sampled data on several environmental parameters (Tables 1 and 2). We calculated the mean elevation based on an elevation grid (provided by Sonny, 2020) with a spatial resolution of "1′", which corresponds to a resolution of approx. 20 m × 30 m in the study area. Using the same elevation data, we calculated the mean heatload index (HLI) according to McCune and Keon (2002) as a measure of radiation influx using the 'spatialEco' package by Evans (2019).

We ascertained land-use intensity on an ordinal scale based on Fumy et al. (2021). Within each plot, we mapped the land-use types in the field. Each land-use type in the plots was assigned a land-use intensity value ranging from 0 to 5 (Table 2). The land-use intensity was then calculated for each plot as the weighted mean of the land-use values of all land-use types relative to their cover within the respective plot. Additionally, we calculated a habitat-heterogeneity score from the sum of different habitat layers which we mapped in the field. These habitat layers were: bare ground, stones, litter, dwarf shrubs, shrubs, mosses, dead wood, trees and low (< 5 cm), mid (5–15 cm) and high (> 15 cm) growing tussock grass, other grass and herbs, respectively. We only considered layers with a minimum

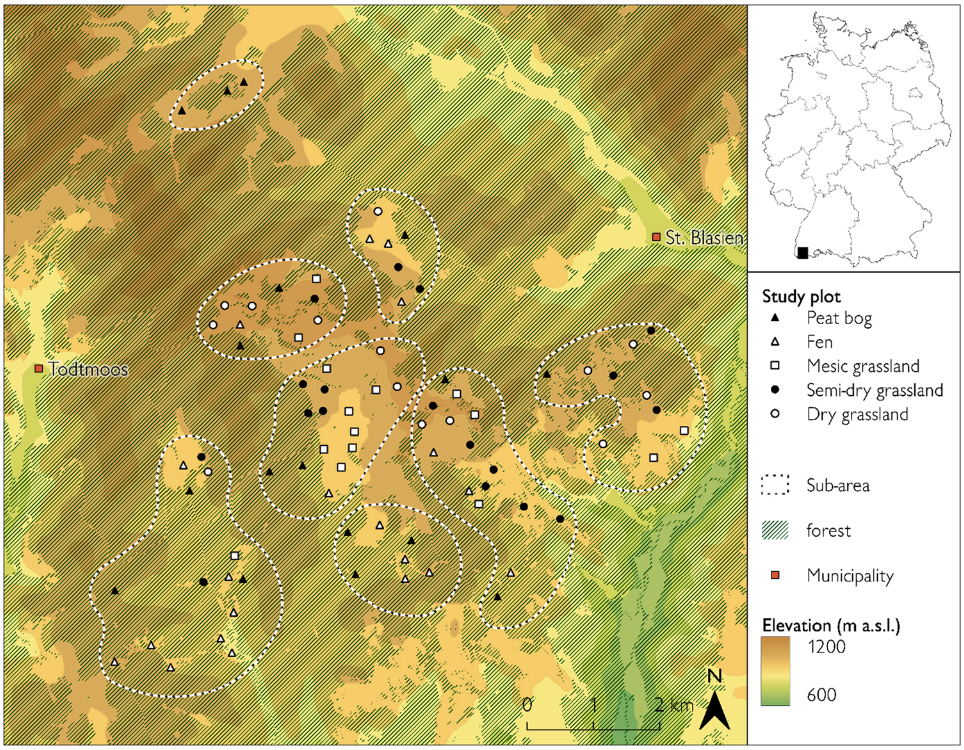

Fig. 1. Location of the study area and plots in the southern Black Forest (SW Germany).

Table 1

Mean (± SE) of environmental parameters at the habitat and landscape level and relationship to butterfly and grasshopper species richness. Low-int. = low-intensity. Species richness was analyzed via GLMM with Poisson error structure. *Sub-area* ($N = 8$) and *habitat type* ($N = 5$) were set up as random factors. All fixed effects were standardized prior to the analyses. P values were obtained from comparison of the respective model with the intercept-only model via an ANOVA. The area under the ROC curve (AUC) is given for all models with P value ≤ 0.05. Across all habitat types, land-use intensity and land-use intensityˆ2 were included together in the models and thus share an AUC value (indicated by "▸"). Additionally, land-use intensity was also analyzed for each habitat type separately (indicated by ": *habitat type*"). Significance levels are indicated as follows: n.s. (not significant) $P > 0.05$, * $P \leq 0.05$, * * $P \leq 0.01$, * ** $P \leq 0.001$.

Parameter	Mean ± SE	Butterflies			Grasshoppers		
		Estimate ± SE	*P*	AUC	Estimate ± SE	*P*	AUC
Habitat level							
Elevation (m a.s.l.)	972 ± 6	–0.04 ± 0.07	n.s.	.	0.13 ± 0.07	n.s.	.
Heat-load index (HLI)	0.68 ± 0.01	–0.01 ± 0.06	n.s.	.	0.03 ± 0.06	n.s.	.
Land-use intensity (LUI)	1.71 ± 0.16	–0.13 ± 0.12	n.s.	▸0.84	0.11 ± 0.14	n.s.	▸0.89
LUIˆ2	.	–0.46 ± 0.11	* **		–0.42 ± 0.1	* **	
LUI: peat bog	0.14 ± 0.05	3.27 ± 0.99	* **	0.83	5.59 ± 1.75	* *	0.9
LUI: fen	1.22 ± 0.19	-0.18 ± 0.17	n.s.	.	-0.01 ± 0.18	n.s.	.
LUI: mesic grassland	3.9 ± 0.31	-1.05 ± 0.25	* **	0.86	-0.62 ± 0.15	* **	0.93
LUI: semi-dry grassland	2.21 ± 0.23	-0.12 ± 0.21	n.s.	.	-0.41 ± 0.18	*	0.92
LUI: dry grassland	1.31 ± 0.23	-0.49 ± 0.34	n.s.	.	-0.31 ± 0.25	n.s.	.
Habitat heterogeneity	9.01 ± 0.55	0.19 ± 0.07	* *	0.70	0.29 ± 0.05	* *	0.85
Landscape level							
Open habitat	49 ± 3	–0.13 ± 0.07	n.s.	.	0.11 ± 0.06	n.s.	.
Low-int. open habitat	20 ± 2	0.19 ± 0.08	*	0.72	0.32 ± 0.05	* **	0.84

Table 2

Land-use types in the plots and their assigned land-use intensity values. Land-use intensity ranges from 0 (no land use) to 5 (very high land-use intensity).

Land-use intensity	Value	Description
No land use	0	Abandoned open mire and semi-natural grassland
Very low	0.5	Open mire and semi-natural grassland: sporadically grazed, at most two to four weeks per year
Low	1	Open mire and semi-natural grassland: meadows mown once or pastures with low stocking rates
Moderate	2	Improved grassland: meadows mown twice or pastures with intermediate stocking rates
Moderate/high	3	Improved grassland: meadows mown thrice or pastures with strip grazing (rotation cycle of two to four weeks)
High	4	Improved grassland with liquid-manure fertilization: meadows mown thrice or highly intensive strip grazing (rotation cycle of two to five days)
Very high	5	Improved grassland with liquid-manure fertilization: meadows mown four times

cover of 5 %. Minimum and maximum values of the habitat-heterogeneity score were 1 (only one type of habitat layer was present) and 17 (all possible habitat layers were present), respectively. Additionally, we considered the configuration of open habitats in the surrounding of the study plots (hereinafter termed "landscape scale") and mapped the proportion of open habitats in general and with low-intensity land use (land-use values: 0–2; see Table 2) in a buffer of 100 m around each plot in the field. All sampled environmental parameters were expected to potentially affect the occurrence of threatened butterfly and grasshopper species.

2.2.2.2. Butterfly and grasshopper assemblages. In 2018, we surveyed threatened butterfly and grasshopper species (including near-threatened species) according to the red data books of Baden-Württemberg (grasshoppers: Detzel et al., 2021; butterflies: Ebert et al., 2005) 1. Threatened butterfly species were sampled on each plot at four times between May and August with at least three weeks between each visit. Butterflies were surveyed by walking each plot in a loop-like manner for 30 min, excluding time taken for species determination. Species were identified visually or using net catches and released after identification. Butterfly sampling 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, 2019; Settele et al., 2015). The scientific nomenclature follows Settele et al. (2015).

Threatened grasshopper species were sampled at three times between June and August, which includes the phenology peak of all species (Fartmann et al., 2022), with at least three weeks between each visit. In each plot, all available habitat structures were surveyed for the occurrence of grasshopper species under favourable weather conditions (temperature > 15 °C, cloud cover < 50 %) using acoustic and visual detection as well as sweep netting; all individuals were released after identification (Fischer et al., 2016; Samways, 2019). Arbusticolous and arboricolous species that rarely occur in open habitats were excluded from all analyses as our sampling techniques do not produce reliable data for these species. To improve the detection of quiet or high-frequency stridulating species, such as *Conocephalus fuscus* and *Metrioptera brachyptera*, a bat detector was used. The scientific nomenclature follows Fischer et al. (2016).

2.3. Statistical analysis

All statistical analyses were performed using R statistical environment (R Core Team, 2020). Differences in environmental parameters between the five studied habitat types were analyzed using the Kruskal-Wallis *H* test and Dunn's test as a post-hoc test using

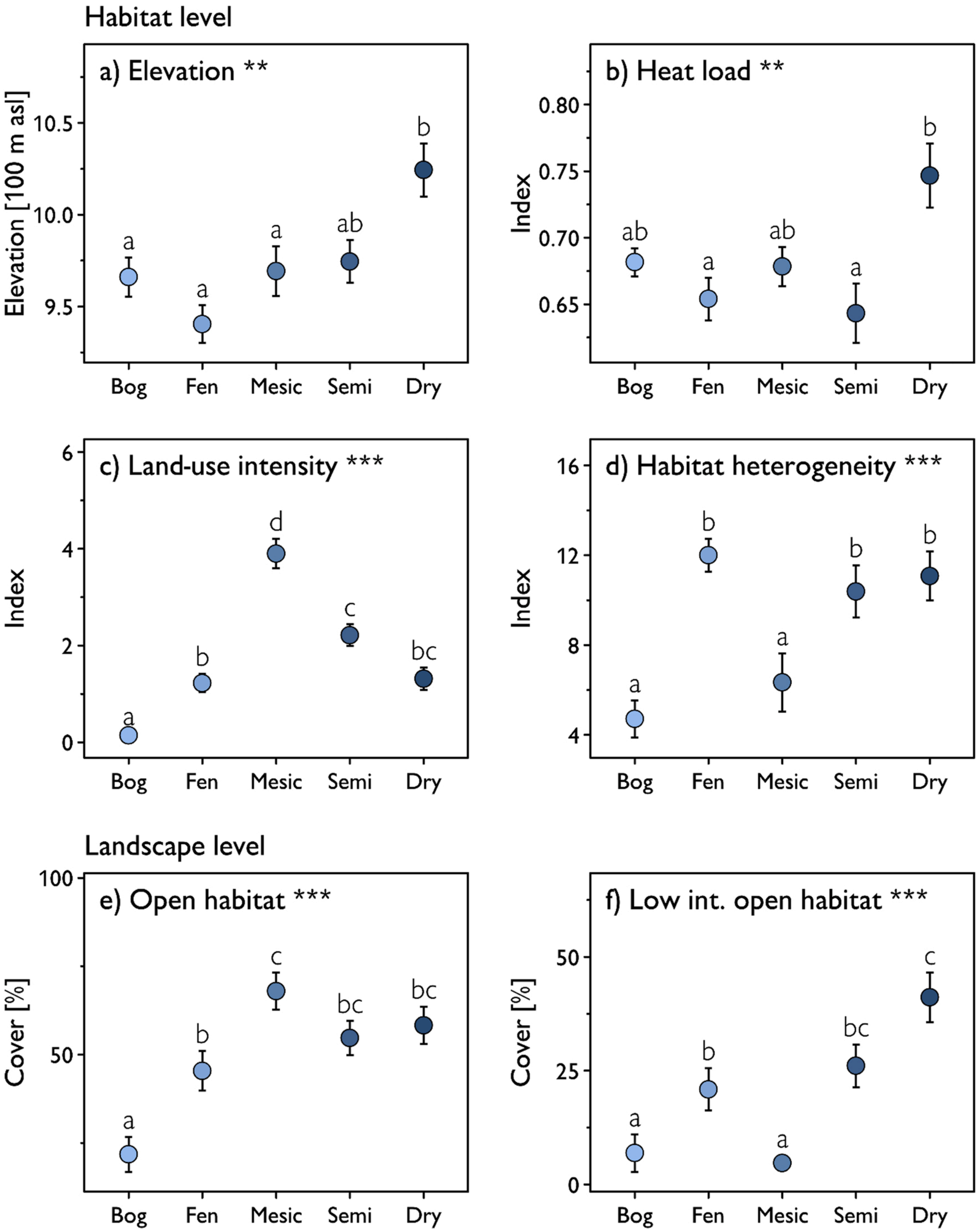

Fig. 2. Mean (± SE) elevation [$Chi^2 = 17.7$] (a), heat load [$Chi^2 = 14.6$] (b), land-use intensity [$Chi^2 = 59.7$] (c), habitat heterogeneity [$Chi^2 = 28.7$] (d), open habitat [$Chi^2 = 35.3$] (e) and low-intensity open habitat [$Chi^2 = 35.3$] (f) in the five studied habitat types. Peat bog ($n = 17$), fen ($n = 20$), mesic grassland ($n = 15$), semi-dry grassland ($n = 18$) and dry grassland ($n = 14$). Differences were tested using the Kruskal-Wallis *H* test and Dunn's test as a post-hoc test. Different letters indicate significant differences between grassland types ($P \leq 0.05$).

the 'dunn.test' package (Dinno, 2017). We chose this nonparametric approach because Generalized Linear Mixed-effects Models (GLMM) could not be applied due to overdispersion.

Differences in the numbers of threatened butterfly and grasshopper species between the five studied habitat types were analyzed using GLMMs with Poisson error structure, *habitat type* as a categorical predictor and *sub-area* as a random factor. Pairwise comparisons between the habitat types were made using the 'glht' function in the 'multcomp' package by Hothorn et al. (2008), with the Tukey test as a post-hoc test (homogeneity of variance was given).

To assess the effect of land-use intensity on habitat heterogeneity, we conducted a GLMM with *habitat heterogeneity* as the response variable and *land-use intensity* (centred and scaled values) as a fixed effect with negative binomial error structure. Graphical inspection of the data suggested an unimodal rather than a linear relationship between the response and predictor variable, so centred, scaled and squared values of the predictor were additionally entered in the model. The variables *sub-area* and *habitat type* served as random factors. The model was compared to the respective intercept-only model via ANOVA.

To identify species indicative for the five studied habitat types, we conducted an indicator species analysis using the 'multipatt' function in the R package 'indicspecies' by Cáceres, de, Legendre (2009). We considered indicator relationships of single species with single and combined habitat types and used the 'IndVal.g′ association index according to Cáceres et al. (2010). The statistical significance of this indicator value was tested using a permutation test; the number of permutations was set to 999 (for further details see Cáceres, de, Legendre (2009).

To assess the effects of the environmental parameters on species richness of threatened butterflies and grasshoppers, we conducted uni- and multivariable GLMMs with Poisson error structure. Multicollinearity was low for all predictors in all models ($|r_s| < 0.5$, VIF < 2) (see Graham, 2003; Zuur et al., 2010). Since habitat heterogeneity significantly depended on land-use intensity (unimodal relationship; see Section 3.1 Environmental conditions), it was not included in the multivariable GLMMs. Possible autocorrelation in space and within the considered habitat types was taken into account by adding *sub-area* and *habitat type* as random factors. All fixed effects were centred and scaled. Graphical inspection suggested a unimodal rather than linear relationship between both response variables and land-use intensity, so we additionally added centred, scaled and squared values of land-use intensity to all models. Additionally, we conducted univariable models for each habitat type separately using *land-use intensity* as a fixed effect and *sub-area* as a random factor. In order to increase the robustness of models with multiple predictors and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach including the top-ranked models within $\Delta AIC_C < 1$ (Burnham and Anderson, 2010; Grueber et al., 2011). We used the 'lme4′ package of Bates et al. (2015) for all GLMM analyses and the 'dredge' and the 'model.avg' functions in the R package 'MuMIn' by Bartoń (2017) for model averaging.

3. Results

3.1. Environmental conditions

Environmental conditions differed strongly between the habitat types. At the plot level, dry grasslands were situated at the highest elevations and had the highest heat-load-index values. Land-use intensity peaked in mesic grasslands and decreased towards both ends

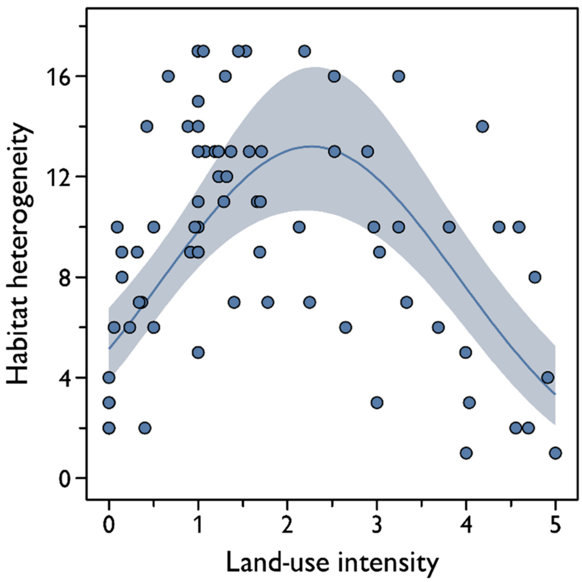

Fig. 3. Relationship between land-use intensity and habitat heterogeneity within the plots analyzed via GLMM with negative binomial error structure. *Sub-area* ($N = 8$) and *habitat type* ($N = 5$) were set up as random factors. All fixed effects were standardized prior to the analyses. The full model was compared to the intercept-only model via an ANOVA: * ** $P \leq 0.001$.

of the studied hydrological gradient. Peat bogs were characterized by the lowest land-use intensity; most of them were even abandoned. Habitat heterogeneity was highest in fens, dry grasslands and semi-dry grasslands differing from mesic grasslands and peat bogs (Fig. 2).

At the landscape level, the cover of open habitats was highest in dry and semi-dry grasslands and lowest in peat bogs. Fens had an intermediate position differing from both peat bogs and the three grassland types. The cover of open habitats with low land-use intensity in the surrounding of the plots decreased from dry and semi-dry grasslands to fens to peat bogs and mesic grasslands. Land-use intensity predicted habitat heterogeneity within the plots and was highest at low to intermediate levels of land use and lowest in abandoned and intensively used plots (Fig. 3).

3.2. Species assemblages

In total, we recorded 26 threatened butterfly and 19 threatened grasshopper species. The most widespread butterfly species were *Argynnis aglaja*, *Melitaea athalia* and *Argynnis adippe*, which were present in 49 %, 48 % and 38 % of the plots, respectively. The most common grasshopper species were *Euthystira brachyptera*, *Stenobothrus lineatus* and *Tettigonia cantans*, occurring in 62 %, 56 % and 49 % of the plots, respectively. Species richness differed between the five habitat types. The number of butterfly species was highest in fens followed by dry grasslands and lowest in mesic grasslands; semi-dry grasslands and peat bogs had an intermediate position. Species richness of grasshoppers was highest in dry grasslands, intermediate in fens, semi-dry and mesic grasslands and lowest in peat bogs (Fig. 4; see Appendix A1 for the model output tables).

Altogether, 13 butterfly and 14 grasshopper species were indicative for one or more habitat types (Table 3). The two habitat types with the highest overall species richness, dry grasslands and fens, also had the highest number of indicator species in general (19 and 14 species, respectively) and exclusive indicator species (7 and 3 species, respectively). Semi-dry grasslands (10 species), peat bogs (8 species, among them one exclusive species) and mesic grasslands (6 species) had clearly lower numbers of indicative species.

Threatened butterfly and grasshopper species richness were determined by the same drivers. The univariable GLMMs revealed (i) humpback-shaped responses of species richness to land-use intensity, where species richness was positively related to land-use intensity in the peat bogs and negatively in the mesic and in the semi-dry (the latter only for grasshoppers) grasslands, (ii) an increase in species numbers with habitat heterogeneity and (iii) positive relationships of species numbers with the cover of low-intensity open habitats in the surrounding of the plots (Table 1).

In the multivariable GLMMs, land-use intensity was the only predictor of species richness (Table 4, Fig. 5, see Appendix A2 for the model selection table). Threatened butterfly and grasshopper species richness both showed a unimodal response to this variable, peaking at low to intermediate land-use intensity. The explanatory power of all models was high with AUC values ranging from 0.70 to 0.89.

4. Discussion

Our study revealed strong differences in environmental conditions and in species numbers of threatened butterflies and grasshoppers in mire and grassland habitats. Species richness and the number of indicator species of both insect groups peaked in fens and

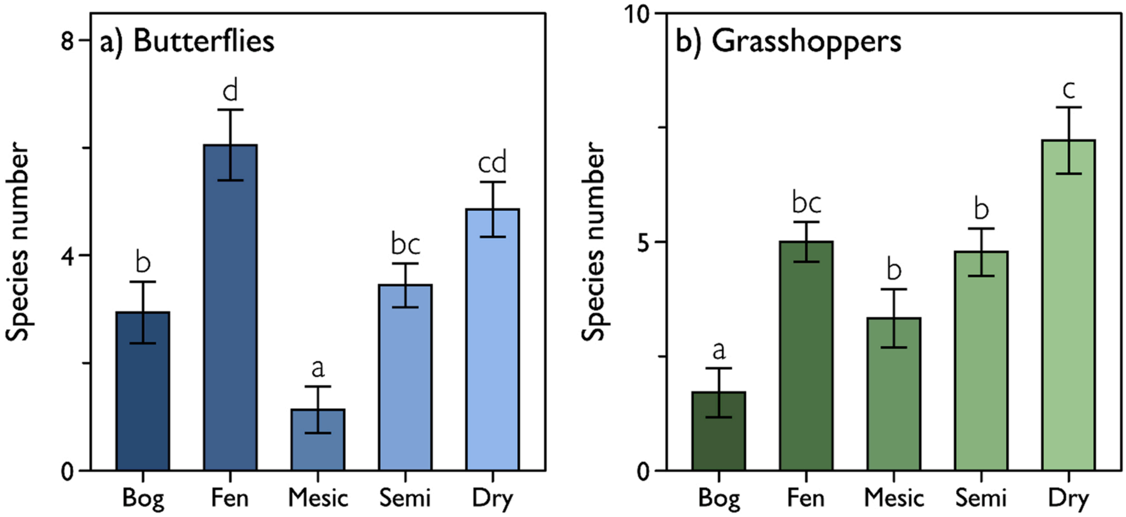

Fig. 4. Mean species richness (± SE) of threatened butterfly (a) and grasshopper (b) species in the five studied habitat types. Peat bog ($N = 17$), fen ($N = 20$), mesic grassland ($N = 15$), semi-dry grassland ($N = 18$) and dry grassland ($N = 14$). Differences between the habitat types were tested using Generalized Mixed-effects Models (GLMM) with *sub-area* ($N = 8$) as a random factor. Different letters indicate significant differences between habitat types ($P \leq 0.05$). See Appendix A1 for the model output tables.

Table 3
Indicator species for the five studied habitat types. Taxon: B = butterfly, G = grasshopper. Specificity (Spec) indicates the degree of habitat-type restriction of the species (0 = species occurred exclusively in other habitat types; 1 = species occurred in no other habitat type). Sensitivity (Sens) indicates the fidelity of the species to the considered habitat type (0 = species did not occur in any plot of the focal habitat type; 1 = species occurred in all plots of the focal habitat type). The indicator value (IV) indicates the association of the species with the respective habitat type, considering both specificity and sensitivity (0 = species not associated with the focal habitat type; 1 = species perfectly associated with the focal habitat type). Significance levels are indicated as follows: n.s. (not significant) $P > 0.05$, * $P \leq 0.05$, * * $P \leq 0.01$, * ** $P \leq 0.001$.

Indicator species	Taxon	Habitat type					Spec	Sens	IV	*P*
		Bog	Fen	Mesic	Semi	Dry				
Plebejus optilete	B	✓	.	.	.	.	0.88	0.35	0.56	* **
Pseudochorthippus montanus	G	✓	✓	.	.	.	0.79	0.73	0.76	* **
Colias palaeno	B	✓	✓	.	.	.	1.00	0.46	0.68	* **
Boloria aquilonaris	B	✓	✓	.	.	.	0.82	0.46	0.62	* *
Melitaea athalia	B	✓	✓	.	✓	✓	0.97	0.57	0.74	* **
Argynnis adippe	B	✓	✓	.	✓	✓	0.96	0.45	0.66	* *
Metrioptera brachyptera	G	✓	✓	.	.	✓	0.88	0.57	0.71	* **
Boloria selene	B	✓	✓	.	.	✓	0.89	0.35	0.56	*
Aporia crataegi	B	.	✓	.	.	.	0.70	0.45	0.56	* *
Boloria titania	B	.	✓	.	.	.	0.63	0.50	0.56	* **
Miramella alpina	G	.	✓	.	.	.	0.71	0.30	0.46	*
Boloria eunomia	B	.	✓	✓	.	.	1.00	0.26	0.51	* **
Euthystira brachyptera	G	.	✓	✓	✓	✓	0.91	0.70	0.80	* *
Omocestus viridulus	G	.	✓	✓	✓	✓	0.94	0.46	0.66	*
Argynnis aglaja	B	.	✓	.	✓	✓	0.84	0.67	0.75	* **
Stenobothrus lineatus	G	.	.	✓	✓	✓	0.88	0.85	0.87	* **
Stenobothrus stigmaticus	G	.	.	✓	✓	✓	0.95	0.57	0.74	* **
Stauroderus scalaris	G	.	.	✓	✓	✓	0.87	0.43	0.61	* *
Decticus verrucivorus	G	.	.	.	✓	✓	0.74	0.69	0.71	* **
Hesperia comma	B	.	.	.	✓	✓	0.79	0.44	0.59	* *
Argynnis niobe	B	.	.	.	.	✓	0.62	0.71	0.67	* **
Erebia medusa	B	.	.	.	.	✓	0.61	0.71	0.66	* **
Psophus stridulus	G	.	.	.	.	✓	1.00	0.29	0.54	* *
Tetrix bipunctata	G	.	.	.	.	✓	0.75	0.36	0.52	* *
Myrmeleotettix maculatus	G	.	.	.	.	✓	0.68	0.36	0.49	* *
Platycleis albopunctata	G	.	.	.	.	✓	1.00	0.21	0.46	* *
Bicolorana bicolor	G	.	.	.	.	✓	0.72	0.29	0.45	*
No. species		**8**	**14**	**6**	**10**	**19**				
No. exclusive species		**1**	**3**	**.**	**.**	**7**				

Table 4
Multivariable GLMM (Poisson error structure): Relationship of threatened butterfly and grasshopper species richness with environmental parameters. *Sub-area* ($N = 8$) and *grassland type* ($N = 5$) were set up as random factors. All fixed effects were standardized prior to the analyses. Presented are the averaged models (full average) from the top-ranked models ($\Delta AIC_C < 1$). The area under the ROC curve (AUC) is given. Significance levels are indicated as follows: n.s. (not significant) $P > 0.05$, * $P \leq 0.05$, * * $P \leq 0.01$, * ** $P \leq 0.001$.

Parameter	Butterflies (AUC = 0.85)			Grasshoppers (AUC = 0.89)		
	Estimate ± SE	*Z*	*P*	Estimate ± SE	*Z*	*P*
Intercept	1.58 ± 0.14	11.2	* **	1.72 ± 0.17	9.94	* **
Elevation	–0.08 ± 0.08	0.97	n.s.	.	.	.
Land-use intensity	–0.14 ± 0.11	1.24	n.s.	0.13 ± 0.14	0.92	n.s.
Land-use intensity^2	–0.46 ± 0.11	3.94	* **	–0.40 ± 0.10	3.92	* **
Low-intensity open habitat	0.04 ± 0.07	0.52	n.s.	0.07 ± 0.08	0.88	n.s.

dry grasslands and to a lesser extent in semi-dry grasslands. All three habitat types were characterized by low to intermediate levels of land use. In line with this, land-use intensity was the main predictor of species richness across the five studied habitat types. Additionally, land-use intensity positively affected species richness in the habitat type with the lowest and negatively in that with the highest average land-use intensity, peat bog and mesic grassland, respectively. Grasshoppers were also affected negatively in the semi-dry grasslands, which ranged from low to intermediate land-use intensity.

Such as many other insect species, threatened Central European butterfly and grasshopper species are usually habitat specialists that rely on very specific habitat characteristics (Bräu, 2013; Poniatowski et al., 2016; Schlumprecht and Waeber, 2003). The main parameters determining habitat quality for both groups are (i) a favourable microclimate, which is interrelated with vegetation structure, (ii) adequate oviposition sites (including the occurrence of suitable host plants for butterflies), (iii) sufficient food and (iv) shelter against predators or extreme weather (Erhardt and Mevi-Schütz, 2009; García-Barros and Fartmann, 2009; Gardiner and Dover, 2008; Stuhldreher and Fartmann, 2018; Willott and Hassall, 1998; Wünsch et al., 2012). These complex requirements are often best fulfilled in heterogeneous habitats (Fartmann et al., 2012; Helbing et al., 2014; Kruess and Tscharntke, 2002; Löffler and Fartmann,

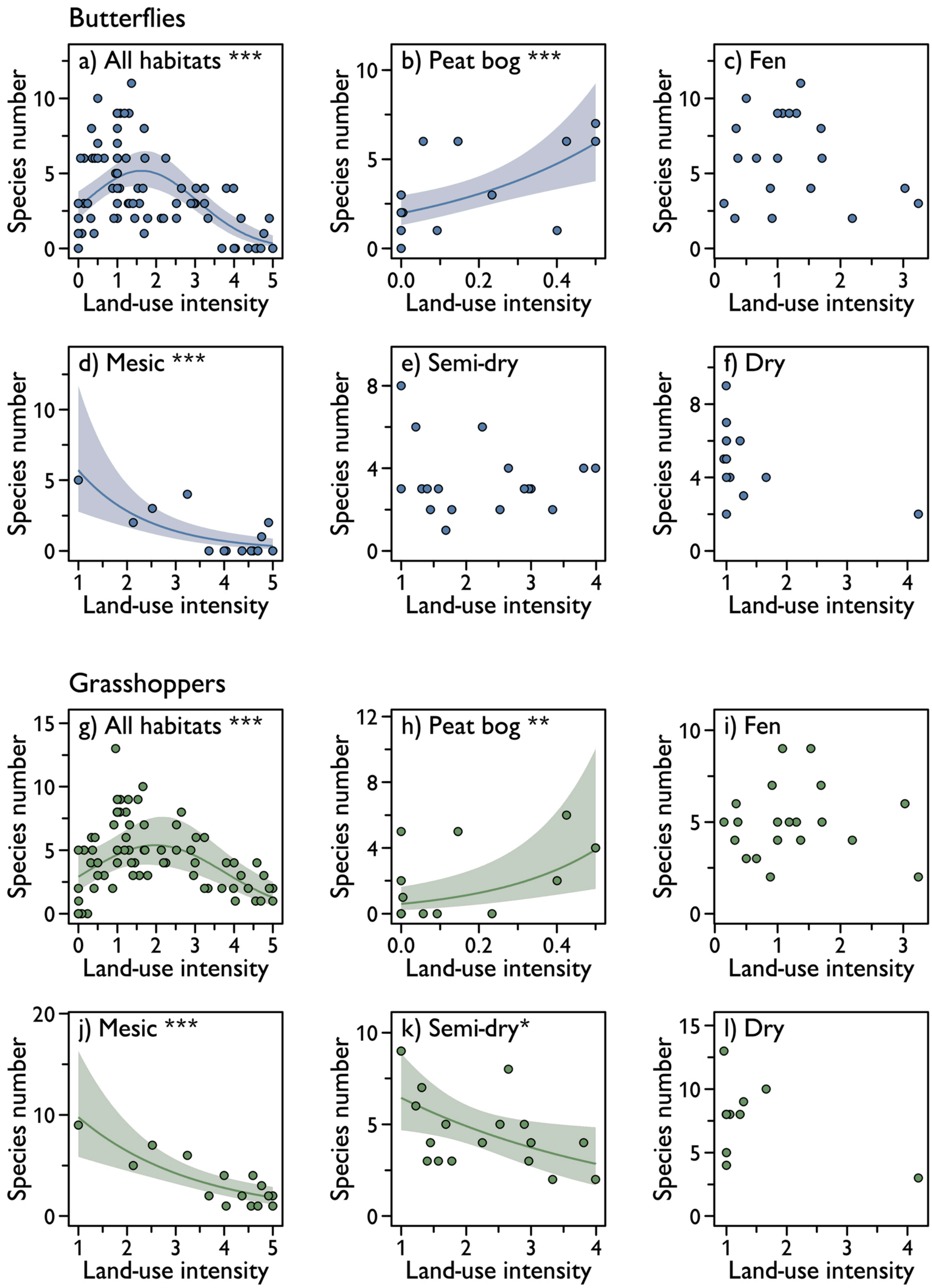

Fig. 5. Relationship of threatened butterfly (a–f) and grasshopper (g–l) species richness to land-use intensity across all habitat types as the only significant parameter from the multivariable GLMM and for each habitat type separately (univariable GLMM). Curves and intervals were calculated using the ggeffects-package in R (Lüdecke, 2018). Significance levels are indicated as follows: $P > 0.05$, * $P \leq 0.05$, * * $P \leq 0.01$, * ** $P \leq 0.001$. For model details see Tables 1 and 4.

2017; Marini et al., 2009; Schirmel et al., 2010).

Our GLMM analysis showed that the habitat heterogeneity within the plots depended in a humpback-shaped pattern on land-use intensity. Fens, dry and semi-dry grasslands had the highest habitat heterogeneity. Most of them were managed by large-scale low-intensity cattle grazing (own observation). Such pastures generally feature high habitat heterogeneity with spatial mosaics of patches with bare ground, short grazing lawns and taller vegetation (Bogenrieder, 2012; Fumy et al., 2021; Gardiner, 2018; Schwarz et al., 2018; Török et al., 2014) and thus fulfil most of the aforementioned conditions that are necessary for species-rich assemblages of specialized butterflies and grasshoppers. As a result, all three habitat types were characterized by high levels of insect-species richness. It is noteworthy that other studies found diversity of insect species to benefit much more from low-intensity, "traditional" hay meadow management than from low-intensity grazing (e.g. Bonari et al., 2017; Löffler and Fartmann, 2017). However, the effects of grazing with sheep, which were analyzed in these studies, and of continuous grazing on large areas with low cattle stocking rates might differ largely. Since both types can be termed "low-intensity grazing", we want to emphasize that we ascribe the observed positive effect of low-intensity grazing on threatened butterfly and grasshopper species richness to the habitat properties created by the latter.

Mesic grasslands and peat bogs were located at the two ends of the land-use intensity gradient. Mesic grasslands exhibited an intensive management, especially mowing thrice or more and regular liquid manure application, and a species-poor, homogeneous vegetation (Fumy et al., 2021; own observation). In the vast majority of the peat bogs, the land had not been in use for more than two decades (cf. Section 2.1 Study area). Additionally, all bogs had been affected by historic drainage and, hence, most of them were dominated by a monotonous vegetation with low plant-species richness due to encroachment of grasses (*Molinia caerulea*), dwarf shrubs (*Vaccinium myrtillus*, *V. uliginosum*) or shrubs (Fumy et al., 2021; Geis et al., 2013; own observation). As a consequence, and by contrast with fens, dry and semi-dry grasslands, both mesic grasslands and peat bogs featured very low levels of habitat heterogeneity and insect species richness. In addition, land-use intensity had a significant effect on species richness in the habitat-type-specific models for both habitat types: Deviations from the typical management (abandonment and high-intensity management, respectively) fostered species richness. Thus, species richness was highest under land-use-intensity levels that are associated with higher habitat heterogeneity in both types.

The explanatory power of land-use intensity for species richness was higher than that of habitat heterogeneity in the univariable GLMMs. Accordingly, further parameters that depend upon land-use intensity may add to the observed biodiversity patterns. This seems to be especially true for plots with intensive land use. We assume that additional effects of fertilization and mowing also contributed to the observed low species richness in these plots. This assumption is in line with the results of Humbert et al. (2021) who found that local above-ground temperatures at high-productive sites are significantly lower than at unfertilized sites with low productivity, which affects the occurrence of grasshoppers. The vast majority of insects, especially of habitat specialists, is dependent on nutrient-poor environments and suffers from excessive nitrogen in their food resources (Wallis De Vries, 2014). In line with this, it has been observed that fertilization alters plant quality, with negative effects on butterfly and grasshopper species (Kurze et al., 2018; Nijssen et al., 2017). Moreover, each mowing event causes direct mortality of insects and results in higher predation rates through insectivorous vertebrates (e.g. birds) as a consequence of the removal of all protective vegetation (Buri et al., 2013; van Klink et al., 2019; Wünsch et al., 2012).

Besides the species richness, we used the results of an indicator species analyses as a second measure for the conservation value of the five mire and grassland types. Habitat types that host many indicator species, especially exclusive ones, can be considered most important for biodiversity conservation, since the respective species are unlikely to thrive in other habitats. In our study, the mire and grassland types associated with high habitat heterogeneity and intermediate land-use intensity, dry grassland and fens, had the highest numbers of indicator species (19 and 14, respectively) and exclusive indicator species (7 and 3, respectively). Thus, these habitat types are of prime conservation interest.

Our study highlights the prime importance of high habitat quality for species-rich assemblages of threatened butterflies and grasshoppers, which is driven by land-use intensity and the interrelated habitat heterogeneity. This is in accordance with previous research from other landscapes with high habitat availability and connectivity (Fartmann et al., 2012; Klein et al., 2020; Löffler and Fartmann, 2017; Maes and Bonte, 2006; Münsch et al., 2019; Poniatowski et al., 2020; Uchida and Ushimaru, 2014). However, many of the studied species have high area requirements (Salz and Fartmann, 2009) and depend on dense habitat networks for long-term survival since they build metapopulations (Poniatowski et al., 2018). Therefore, the landscape configuration should have an effect on species richness, even in landscapes of high conservation value such as the study area (Cappellari and Marini, 2021). Indeed, the number of threatened butterfly and grasshopper species increased with the cover of open habitats with low land-use intensity in the surroundings of the study plots.

Summing up, our study showed that low to intermediate levels of land use, such as cattle grazing with low stocking rates, promoted habitat heterogeneity and fostered species richness of specialized butterflies and grasshoppers in open mires and grasslands. By contrast, both abandonment and intensive land use resulted in monotonous swards that featured little diversity and hence led to biotic homogenization.

5. Implications for conservation

In our study, land-use intensity was the key driver of habitat heterogeneity and, hence, species richness of threatened butterflies and grasshoppers. Accordingly, we recommend a conservation policy that secures the maintenance or re-establishment of low-intensity land use. In particular, we suggest large-scale low-intensity cattle grazing during the whole vegetation period, in the study area preferably with the local cattle breed 'Hinterwälder'. It has been shown that such a grazing regime most effectively promotes high habitat heterogeneity and biodiversity in general, especially in landscapes where (cattle) grazing was widespread in historical land-use practice (Adler et al., 2001; Bucher et al., 2016; Bussan, 2022; Hall and Bunce, 2019; Schwarz et al., 2018; Schwarz and Fartmann, 2022; Torma et al., 2019). Where grazing is not an option, mowing once or twice per year while annually leaving about 10 % of the meadow area uncut in a rotational manner can offer an alternative (Buri et al., 2013; Humbert et al., 2012). In order to reduce the productivity and foster habitat heterogeneity in the more intensively managed habitats, the application of liquid manure and chemical fertilizers should cease completely (see also Humbert et al., 2021). Solid manure could be an alternative but must be applied with caution and only on grasslands on more nutrient-rich soils. Abandoned mires and grasslands suffer from advanced succession, so that shrubs and trees have to be cleared prior to the re-introduction of regular management (Geis et al., 2013). In drained mires, it is also necessary to block the drainage ditches in order to stabilize the water level (Geis et al., 2013; Tanneberger et al., 2017).

Our results suggest that the loss of habitat heterogeneity due to the ongoing processes of land-use intensification and abandonment still poses a severe threat to insect diversity in Europe, especially in landscapes of high conservation value rich in remnants of traditional land use. In contrast to low-intensity land use, modern, revenue-oriented farming does not fulfil the role of wild ungulates in creating species-rich habitats, a role that was taken on by the livestock of preindustrial farmers and pastoralists thousands of years ago (Hejcman et al., 2013; Konvička et al., 2021). Consequently, we are confident that the maintenance and re-introduction of continuous low-intensity large-scale cattle grazing from spring to autumn is one of the most effective strategies for the conservation of threatened insect species and biodiversity in general in mire and grassland ecosystems across Europe.

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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

A data table is added as supplementary material.

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Appendix A

Appendix A1: Differences in the numbers of threatened butterfly and grasshopper species between the five studied habitat types analyzed using GLMMs with Poisson error structure, *habitat type* (N = 5) as a categorical predictor and *sub-area* (N = 8) as a random factor. Shown are the results of the Tukey Honest Significant Difference post-hoc test.

Habitat type comparison		Estimate	Std. Error	Z	*P*
Butterflies					
	fen - upland moor	0.72	0.17	4.29	< 0.001
	mesic - upland moor	-0.95	0.28	-3.40	0.006
	semi-dry - upland moor	0.16	0.19	0.83	0.917
	dry - upland moor	0.50	0.19	2.69	0.051
	mesic - fen	-1.67	0.26	-6.47	< 0.001
	semi-dry - fen	-0.56	0.16	-3.61	0.003
	dry - fen	-0.22	0.15	-1.45	0.583
	semi-dry - mesic	1.11	0.27	4.06	< 0.001
	dry - mesic	1.46	0.27	5.37	< 0.001
	dry - semi-dry	0.34	0.18	1.96	0.276
Grasshoppers					
	fen - upland moor	0.87	0.13	6.61	< 0.001
	mesic - upland moor	-0.04	0.17	-0.24	0.999
	semi-dry - upland moor	0.57	0.14	4.10	< 0.001

(*continued on next page*)

(*continued*)

Habitat type comparison	Estimate	Std. Error	Z	*P*
dry - upland moor	0.95	0.14	7.00	< 0.001
mesic - fen	-0.91	0.14	-6.50	< 0.001
semi-dry - fen	-0.30	0.11	-2.78	0.041
dry - fen	0.09	0.10	0.87	0.907
semi-dry - mesic	0.61	0.15	4.14	< 0.001
dry - mesic	0.99	0.14	6.89	< 0.001
dry - semi-dry	0.38	0.11	3.41	0.006

Appendix A2: Effect of environmental parameters on threatened butterfly and grasshopper species richness: Model selection table for model averaging in multivariable GLMMs (= dredge output). Model averaging included the top-ranked models within ΔAICC <1. Parameter abbreviations: Ele = elevation, L-i hab = low-intensity open habitat (proportion in 100 m buffer around study plots), HLI = heat load index, LUI = land-use intensity.

Intercept	Ele	L-i hab	HLI	LUI	LUIˆ2	df	logLik	AICc	delta	weight
Butterflies										
1.60	-0.10			-0.14	-0.48	6.00	-171.22	355.5	0.00	0.23
1.58				-0.13	-0.46	5.00	-172.44	355.6	0.12	0.22
1.55	-0.15	0.12		-0.15	-0.44	7.00	-170.13	355.7	0.21	0.21
1.54		0.07		-0.12	-0.43	6.00	-172.02	357.1	1.61	0.10
1.58			-0.06	-0.15	-0.46	6.00	-172.02	357.1	1.61	0.10
1.60	-0.09		-0.05	-0.15	-0.48	7.00	-170.85	357.2	1.65	0.10
1.55		0.06	-0.06	-0.15	-0.43	7.00	-171.70	358.9	3.34	0.04
1.15	-0.16	0.20		-0.36		6.00	-177.04	367.2	11.65	0.00
1.16		0.14		-0.33		5.00	-178.90	368.6	13.05	0.00
1.16	-0.15	0.19	-0.05	-0.38		7.00	-176.76	369.0	13.47	0.00
Grasshoppers										
1.72		0.12		0.15	-0.40	6.00	-176.86	366.8	0.00	0.33
1.75				0.11	-0.42	5.00	-178.36	367.5	0.68	0.23
1.73	0.04	0.11		0.17	-0.40	7.00	-176.70	368.9	2.06	0.12
1.75	0.07			0.14	-0.42	6.00	-177.91	368.9	2.10	0.11
1.73		0.12	0.01	0.16	-0.40	7.00	-176.84	369.2	2.34	0.10
1.75			0.01	0.12	-0.42	6.00	-178.35	369.8	2.97	0.07
1.75	0.07		0.02	0.16	-0.42	7.00	-177.88	371.2	4.41	0.04
1.35		0.15		-0.26		5.00	-184.41	379.6	12.77	0.00
1.35	0.03	0.14		-0.25		6.00	-184.34	381.8	14.95	0.00
1.36		0.15	-0.02	-0.26		6.00	-184.38	381.8	15.03	0.00

Appendix B. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02357.

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