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ORIGINAL ARTICLE

Traditional grazing management creates heterogeneous swards and fosters grasshopper densities

Cinja Schwarz and Thomas Fartmann

Department of Biodiversity and Landscape Ecology, Faculty of Biology and Chemistry, Osnabrück University, Osnabrück, Germany

Abstract Common pastures were once the dominant type of land use in many European regions. However, during the past 150 years, they have declined dramatically. Recent studies have shown that they are hotspots for rare plant, butterfly, and bird species in the study area, the Bavarian pre-Alps (southern Germany). However, studies on the value of these pastures for Orthoptera (hereinafter termed "grasshoppers") have been scarce. Here, we studied the effects of traditional summer grazing in common pastures on grasshopper assemblages. Our study revealed that grasshopper species richness did not differ between common pastures ($n = 57$) and controls ($n = 57$). By contrast, density of all and of threatened species varied between common pastures and controls in all plots and within the two vegetation types with the highest grasshopper abundance, grasslands on mineral soil and fens. Two threatened species, *Pseudochorthippus montanus* and *Stethophyma grossum*, were identified as indicators for common pastures; controls had no indicative species. Traditional low-intensity grazing in common pastures has resulted in open and heterogeneous swards with some bare ground, a low cover of litter and an intermediate vegetation height favouring high densities of grasshopper species in general and threatened species in particular. This is especially true for the two most productive vegetation types, grasslands on mineral soil and fens. To promote biodiversity in general and grasshopper densities in particular, we recommend maintaining traditional cattle grazing (stocking capacities: 0.5–2.0 livestock units/ha) in common pastures. Where possible, this grazing regime should also be introduced in the surrounding landscape.

Key words biodiversity conservation; common pasture; habitat heterogeneity; insect abundance; land-use change; mire ecosystem

Introduction

Since the beginning of the industrial era 200 years ago, humans have altered their environment at an unprecedented rate (Foley *et al*., 2005; Rockström *et al*., 2009). As a result, biodiversity is in a steep decline and scientists suspect that we are heading for a 6th mass extinction (Barnosky *et al*., 2011; Dirzo *et al*., 2014). The loss of biodiversity jeopardizes ecosystem functioning and our own well-being (Dirzo *et al*., 2014; Ripple *et al*., 2017; IPBES, 2019; Cardoso *et al*., 2020). Hence, halting the decline is one of the major challenges for humanity in the present time.

Insects are the most species-rich taxonomic group worldwide (Stork, 2018). However, their decline is much stronger than those of plants or vertebrates (Thomas *et al*., 2004; Sánchez-Bayo & Wyckhuys, 2019; Cardoso *et al*., 2020; Wagner, 2020). The loss of insects has cascading effects on various other organisms within ecosystems (Cardoso *et al*., 2020; Wagner, 2020). For example, insect prey abundance directly affects population size of insectivorous species of higher trophical levels (*e.g*., birds) (Fartmann *et al*., 2021). As for biodiversity in general, land-use change has been identified as the main

Correspondence: Cinja Schwarz, Department of Biodiversity and Landscape Ecology, Faculty of Biology and Chemistry, Osnabrück University, Barbarastraße 11, 49076 Osnabrück, Germany. Email: cinja.schwarz@uos.de

driver of the decline of insects (IPBES, 2019; Cardoso *et al*., 2020; Wagner, 2020).

Nutrient-poor, semi-natural grasslands are among the most species-rich ecosystems across Europe (Dengler *et al*., 2014; Chytrý *et al*., 2015; Feurdean *et al*., 2018). However, due to the transition from pre-industrial land use to modern-day agricultural practices, the extent of such grasslands has greatly decreased and the remaining patches have often suffered from habitat deterioration, mainly due to land-use intensification or succession as a consequence of land-use abandonment (Wallis de Vries & Poschlod, 2002; Poschlod & Braun-Reichert, 2017; Fartmann *et al*., 2021). Since 1992, some types of traditionally managed semi-natural grasslands and some of their characteristic species have become protected by the Habitats Directive (EC, 2007). However, still several types of grasslands with high value for insect conservation, for example, wet grasslands on mineral soil or different types of nutrient-poor pastures, have not been covered appropriately by the directive (Gepp, 2001; Plieninger *et al*., 2015). Additionally, among the over 1 000 species protected by the directive, only 70 are insects (Dirzo *et al*., 2014). This bias can at least partly be explained by the limited number of studies on insect declines and the minimal attention paid to the loss of insect diversity at the time.

Until the mid-19th century, common pastures were the dominant type of land use in many European regions and had a high economic value (Lederbogen *et al*., 2004; Brown, 2006; Plieninger *et al*., 2006; Hrvatin & Perko, 2008). However, since then, they have declined dramatically in area and economic importance. The pre-Alps in southern Bavaria (Germany) are one of the last strongholds for common pastures in Central Europe (Lederbogen *et al*., 2004; Thumm *et al*., 2005). Here, the common pastures comprise mosaics of mire ecosystems, grasslands on mineral soil, and light woodlands (Schwarz *et al*., 2018). Recent studies have shown that these pastures are hotspots for rare plant, butterfly, and bird species (Anthes *et al*., 2003; Rosenthal & Lederbogen, 2008; Weking *et al*., 2013; Schwarz *et al*., 2018; Schwarz & Fartmann, 2021). However, studies on the value of these pastures for Orthoptera (hereinafter termed “grasshoppers”) have been scarce. Grasshoppers have a high functional significance in grasslands due to their key role as herbivores and prey (Samways, 2005). Moreover, they rapidly respond to changes in land use (Marini *et al*., 2008; Bazelet & Samways, 2012; Uchida & Ushimaru, 2014; Fumy *et al*., 2021). Hence, they are well-established bioindicators (Samways, 2005; Sliacka *et al*., 2013; Sergeev, 2021).

Here, we studied the effects of traditional summer cattle grazing in common pastures of the Bavarian pre-Alps on grasshopper assemblages. Therefore, we compared environmental conditions and assemblage composition (species richness, density, indicator species) between common pastures ($n = 57$) and surrounding grasslands on mineral soil and open mires as a control ($n = 57$). In particular, we addressed the following research questions:

(i) How do environmental conditions as well as grasshopper species richness, density, and indicator species vary between common pastures and controls?

(ii) What are the drivers of grasshopper assemblage composition?

(iii) Which implications for grasshopper conservation can be drawn from our findings?

Materials and methods

Study area

The study area (hereafter referred to as pre-Alps) is located at the northern foothills of the Alps (750–900 m a.s.l.) in the south of the German Federal State of Bavaria. The landscape was formed by the last glaciation and is characterized by a heterogeneous young moraine relief (Bayerisches Geologisches Landesamt, 1996). Due to a rather cool and wet climate (mean annual temperature: 7.7 °C; mean annual precipitation: 1 336 mm; meteorological station Bad Kohlgrub [742 m a.s.l.]; period: 1992–2019; DWD, 2020), numerous mires developed in the valleys and hollows (Succow & Jeschke, 1990; Bayerisches Geologisches Landesamt, 1996). Today, the study area contains one of the largest networks of mire ecosystems in Central Europe with an outstanding value for biodiversity conservation and, hence, belongs to one of the German biodiversity hotspots (Ackermann *et al*., 2012; BfN, 2012).

Grasslands, mainly used for dairy farming, are the dominant type of land use in the pre-Alps (BfN, 2012). However, besides large areas of improved grasslands, traditionally managed grasslands such as common pastures, litter meadows (meadows mown in autumn to obtain bedding for livestock), and hay meadows have remained due to the geographical, climatical, and economical marginalization of the study area (Lederbogen *et al*., 2004; Brown, 2006; Schwarz & Fartmann, 2021).

Sampling design

Plots We studied seven randomly selected common pastures, which are traditionally managed by rural

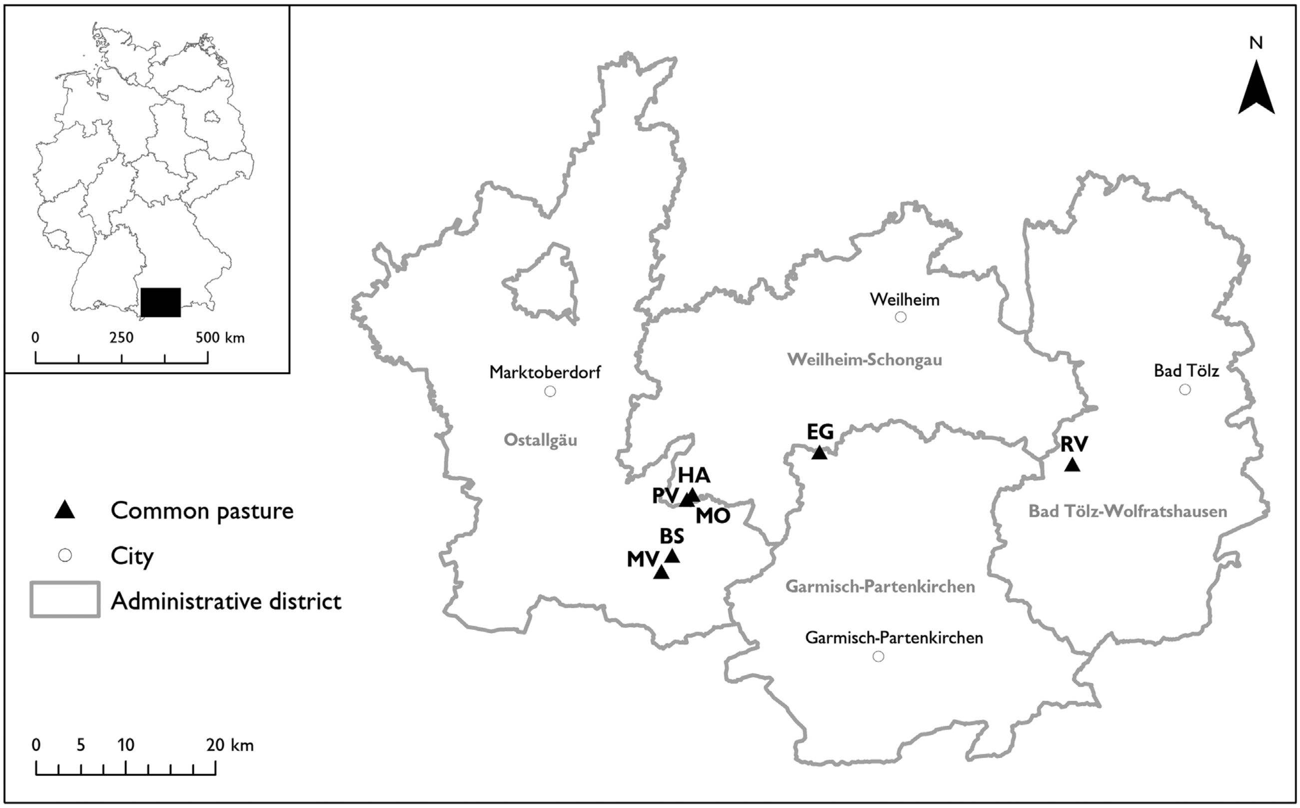

Fig. 1 Location of the study area and common pastures in Upper Bavaria (southern Germany). Common pasture: BS = Berghofer Söldner; EG = Echelsbach Gschwend; HA = Hachegger Viehweide; MO = Moosreitener Viehweide; MV = Mühlenberger Viehweide; PV = Premer Viehweide; RV = Rieder Viehweide.

communities, and their adjacent grasslands and mires (Fig. 1). Each common pasture with its adjacent grasslands and mires is hereafter referred to as a "subarea." Common pastures had a size of 5–121 ha (mean ± SE: 57 ± 15). Grazing was performed with brown dairy cattle in low stocking capacities (0.5–2.0 livestock units [LSU]/ha) from May to October (Lederbogen *et al*., 2004; Thumm *et al*., 2005, own observation). Overall, common pastures were characterized by a high heterogeneity of habitat types. In addition to large areas of grasslands on mineral soil, the pastures comprised mosaics of grazed fens, transition mires, and raised bogs (Schwarz *et al*., 2018). In all seven common pastures, low-intensity grazing has been conducted for centuries. Except grasslands on mineral soils, the common pastures have largely never been fertilized (Lederbogen *et al*., 2004).

To compare common pastures with ungrazed surrounding grasslands on mineral soil and open mires, we used a paired design. Therefore, we randomly selected 57 plots with a size of 500 m^2 (20 m × 25 m) in common pastures. To contrast data from the common pastures with those of the adjacent grasslands on mineral soil and open mires, 57 control plots with the same size were randomly chosen. Each plot had a distance between 20 and 25 m to the fence of the respective common pasture to avoid edge effects (Schirmel *et al*., 2010). Altogether, we divided the plots into the following four vegetation types using character plant species according to Oberdorfer (1992) and Dierßen & Dierßen (2008): (i) grasslands on mineral soil, (ii) fens, (iii) transition mires, and (iv) raised bogs (Table 1) (Schwarz & Fartmann, 2021). Additionally, land use of control plots was differentiated into the three land-use types: (i) fallow, (ii) mown once, and (iii) mown twice or more (Table 1).

Habitat quality To assess habitat quality, we sampled several environmental variables once per plot in August 2015 (Table 2). Cover of different vegetation layers was estimated for a randomly selected subplot of 9 m^2 (3 m × 3 m), except the cover of shrubs, which was estimated

Table 1 Absolute and relative frequencies of the four vegetation types in common pastures ($n = 57$) and controls ($n = 57$) as well as of the three land-use types in controls (abandoned: $n = 28$; mown once: $n = 24$; mown twice or more often: $n = 5$). Differences in absolute frequencies were tested using Chi-squared test. Common pastures vs. control: not significant; land-use types of the control plots: $P \leq 0.001$.

					Control					
	Common pasture		Control		Abandoned		Mown once		Mown ≥ twice	
Vegetation type	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Grassland on mineral soil	14	25	13	23	1	4	7	29	5	100
Fen	9	16	12	21	4	14	8	33	0	0
Transition mire	17	30	15	26	6	21	9	38	0	0
Raised bog	17	30	17	30	17	61	0	0	0	0

for the whole plot. Vegetation density was determined in 0–5 cm, 10–15 cm and 25–30 cm height from ground using a wire-frame box of 30 cm depth and 50 cm width (Poniatowski & Fartmann, 2008; Löffler & Fartmann, 2017). Vegetation height was measured at three random points in each plot and averaged for further analysis. We measured the potential sunshine duration (accuracy 0.5 h) using a horizontoscope after Tonne (Scherer *et al*., 2021) for the month of August in the center of each plot. Cow droppings were counted in every pasture plot on a randomly selected subplot of 100 m^2 (10 m × 10 m) as a proxy for grazing intensity.

Grasshopper assemblages We sampled grasshopper assemblages in August 2015, when nearly all species are adult (Schlumprecht & Waeber, 2003). Grasshopper densities were investigated once for each plot using a box quadrat (1.41 × 1.41 m) (Gardiner *et al*., 2005). The quadrat was placed randomly 10 times per plot (total area = 20 m^2), and individuals of each species within the quadrat were counted (Fartmann *et al*., 2008; Poniatowski & Fartmann, 2010; Helbing *et al*., 2014). Grasshoppers were determined using Bellmann (2006) and nomenclature follows Fischer *et al*. (2020). For further analysis, we classified species as either threatened (including near-threatened species) or non-threatened according to the current red data book of Bavaria (Voith *et al*., 2016).

Statistical analysis

We performed a Chi-squared test to examine differences in the nominal variables vegetation type between common pastures and land-use type within controls (Table 1). Differences in all metric environmental variables, species richness, and density of grasshoppers (response variables) between common pastures and controls (predictor variable) were tested using a generalized linear mixed-effects model (GLMM) with "subarea" as a random factor and an observation-level random intercept nested in "subarea" in case of overdispersion (error structure: binomial, negative binomial, Poisson, or Gaussian, respectively) (Table 2 and Fig. 2). All pairwise comparisons between land-use types were made using the function "glht()" in the multcomp package (Hothorn *et al*., 2008). Moreover, we conducted an indicator species analysis (ISA) (Dufrêne & Legendre, 1997) to identify species indicative for common pastures and controls in general and within each of the four vegetation types (Table 3).

To ascertain those environmental variables (predictor variables) that explain grasshopper species richness and density (response variables) in common pastures best, further GLMMs with "subarea" as a random factor were conducted. Model averaging based on an information-theoretic approach was used to increase model robustness and identify the most important variables (Burnham & Anderson, 2002; Grueber *et al*., 2011). We applied the "dredge" function (R package MuMIn, Bartón, 2016) and only included top-ranked models within $\Delta AIC_C < 3$ for model averaging (*cf*. Grueber *et al*., 2011). Ranges of marginal and conditional R^2 values were calculated as measures of the explanatory power of the top-ranked models (Nakagawa & Schielzeth, 2013; Nakagawa *et al*., 2017). We calculate the variance inflation factor (VIF) and used only variables with VIF ≤ 5 in the GLMMs to avoid multicollinearity (Sheather, 2009). Statistical analysis was performed using R 3.4.3.

Table 2 Mean values (± standard errors) of environmental variables in common pastures ($n = 57$) and controls ($n = 57$) in general and within the four vegetation types (grassland on mineral soil: $n = 27$; fen: $n = 21$; transition mire: $n = 32$; raised bog: $n = 34$). Differences were tested using Generalized Linear Mixed-Effects Models (GLMM). In all models, 'subarea' was set up as random factor. In the case of overdispersion, an observation level random effect was used. Bold values: Variable differs significantly. Error structures were marked with superscripted letters after P values: b = binomial, nb = negative binomial, p = Poisson, g = Gaussian. n.s. = not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

				Grassland on mineral soil			Fen			Transition mire			Raised bog		
Variable	Pasture	Control	*P*	Pasture	Control	*P*	Pasture	Control	*P*	Pasture	Control	*P*	Pasture	Control	*P*
Cover (%) of															
Shrubs	6.6 ± 1.4	7.4 ± 1.6	n.s.^{b}	0.4 ± 0.4	0.0 ± 0.0	n.s.^{b}	1.1 ± 0.7	4.2 ± 2.5	n.s.^{b}	**7.9 ± 3.2**	**2.7 ± 1.9**	**^{b}	13.2 ± 2.5	19.6 ± 3.4	n.s.^{b}
Poaceae	19.8 ± 2.5	23.1 ± 3.0	n.s.^{b}	37.9 ± 4.2	41.5 ± 6.6	n.s.^{b}	18.3 ± 5.5	24.4 ± 6.3	n.s.^{b}	21.6 ± 4.6	28.0 ± 4.7	n.s.^{b}	4.0 ± 0.6	3.7 ± 0.4	n.s.^{b}
Cyperaceae	52.8 ± 2.3	48.8 ± 2.8	n.s.^{b}	42.9 ± 3.8	30.8 ± 6.7	n.s.^{b}	**68.9 ± 6.0**	**54.6 ± 6.9**	*^{b}	52.9 ± 4.8	55.0 ± 3.9	n.s.^{b}	52.4 ± 2.9	52.9 ± 3.4	n.s.^{b}
Litter	16.1 ± 1.7	15.0 ± 1.9	n.s.^{b}	10.4 ± 2.5	8.8 ± 1.3	n.s.^{b}	14.4 ± 3.9	10.4 ± 2.2	n.s.^{b}	16.8 ± 3.1	16.8 ± 5.9	n.s.^{b}	21.2 ± 3.4	21.2 ± 2.9	n.s.^{b}
Mosses	61.6 ± ± 3.8	55.3 ± 4.3	n.s.^{b}	36.3 ± 7.5	31.7 ± 8.5	n.s.^{b}	68.3 ± 7.5	51.7 ± 7.2	n.s.^{b}	58.2 ± 4.9	45.0 ± 8.2	n.s.^{b}	82.4 ± 5.5	84.9 ± 3.6	n.s.^{b}
Open soil	**5.3 ± 0.7**	**2.4 ± 0.5**	***^{b}	**5.5 ± 1.3**	**2.1 ± 0.8**	*^{b}	3.1 ± 1.1	2.7 ± 1.4	n.s.^{b}	**8.4 ± 1.9**	**4.7 ± 0.9**	***^{b}	**3.1 ± 0.7**	**0.4 ± 0.2**	***^{b}
Vegetation height (cm)	21.8 ± 1.4	23.1 ± 2.1	n.s.^{nb}	23.5 ± 3.9	22.0 ± 3.8	n.s.^{nb}	**24.8 ± 2.7**	**22.5 ± 3.6**	**^{g}	**24.1 ± 2.5**	**23.6 ± 2.4**	***^{nb}	16.5 ± 0.9	24.0 ± 5.8	n.s.^{nb}
Vegetation density (%)															
0–5 cm height	91.4 ± 1.7	93.7 ± 1.2	n.s.^{b}	96.3 ± 2.2	98.7 ± 0.8	n.s.^{b}	97.8 ± 0.9	94.2 ± 2.0	n.s.^{b}	95.9 ± 1.5	96.0 ± 1.6	n.s.^{b}	**79.4 ± 3.7**	**87.6 ± 3.0**	**^{b}
25–30 cm height	6.5 ± 1.1	11.4 ± 2.7	n.s.^{b}	**5.9 ± 1.3**	**15.2 ± 7.8**	***^{b}	4.7 ± 1.7	8.5 ± 3.8	n.s.^{b}	9.4 ± 3.1	16.8 ± 6.6	n.s.^{b}	5.0 ± 1.5	5.6 ± 2.1	n.s.^{b}
Sunshine duration (h)	11.5 ± 0.3	11.6 ± 0.2	n.s.^{p}	11.4 ± 0.6	11.0 ± 0.6	n.s.^{nb}	10.8 ± 0.8	12.1 ± 0.3	n.s.^{nb}	11.0 ± 0.7	11.9 ± 0.3	n.s.^{nb}	12.3 ± 0.2	11.5 ± 0.4	n.s.^{n}

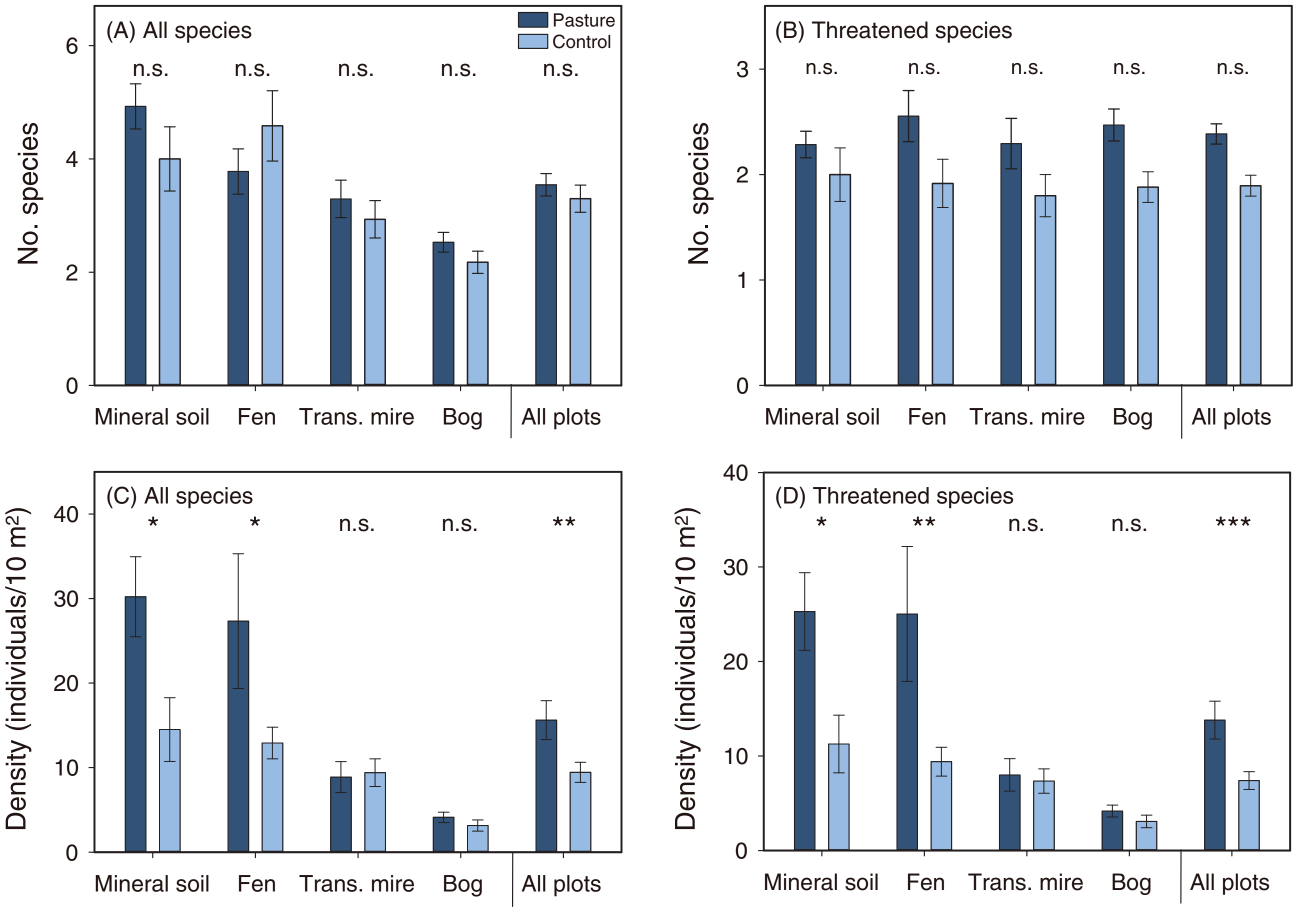

Fig. 2 Mean values (± standard error) of the number of all species (A), number of threatened species (B), density of all species (C), and density of threatened species (D) in common pastures ($n = 57$) and controls ($n = 57$). Differences were tested using GLMM. In all models, "subarea" was set up as random factor. In the case of overdispersion, an observation level random effect was used. n.s. = not significant, $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$.

Results

Plots

The composition of vegetation types did not differ between common pastures and controls (Table 1). Grasslands on mineral soil, fens, transition mires and raised bogs always accounted for a share of around one quarter of the plots. By contrast, land use clearly varied between common pastures and controls. All common pastures were grazed ($n = 57$) (*cf.* Section Sampling design) whereas one half of the controls was abandoned, two fifths were mown once (usually used as litter meadows) and the remaining tenth comprised grasslands mown twice or more (Table 1). Within the controls, land-use intensity decreased from grasslands on mineral soil to fens/transition mires to raised bogs.

Land use had a clear effect on environmental conditions on the plots (Table 2). Grazing intensity in common pastures, indicated by the density of cow droppings, decreased in the following order: grasslands on mineral soil (mean no. of cow droppings/100 m^2 ± SE: 14.1 ± 2.3), fens (6.8 ± 1.8), transition mires (3.2 ± 0.8), and raised bogs (1.6 ± 0.6). Cow-dropping density differed statistically between grasslands on mineral soil and those of the three other vegetation types (GLMM, $P \leq 0.05$). Cattle grazing in common pastures compared to controls resulted in a higher cover of open soil (all plots as well as plots of grasslands on mineral soil, transition mires, and raised bogs) and a lower vegetation density (plots of grasslands on mineral soil and raised bogs). Additionally, within fens, common pastures had a higher cover of Cyperaceae and a taller vegetation than controls. Moreover, within transition mires used as common

Table 3 Results of ISA (Dufrêne & Legendre, 1997) for common pastures and controls in general and within the four vegetation types. Threat status (TS): threatened species in Bavaria (Voith *et al*., 2016). Values hatched in grey: species that are indicator species for this land-use type. ab = relative abundance, fr = frequency, n.s. = not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

Species	TS	*P*	Pasture		Control		*P*	Mineral soil				Fen				Transition mire				Raised bog			
								Pasture		Control		Pasture		Control		Pasture		Control		Pasture		Control	
			ab	fr	ab	fr		ab	fr	ab	fr	ab	fr	ab	fr	ab	fr	ab	fr	ab	fr	ab	fr
Ch. albo-marginatus	.	n.s.	43	11	57	9	*	35	29	**51**	**31**	0	0	9	8	5	12	0	0	0	0	0	0
Ch. brunneus	.	n.s.	0	0	100	2	n.s.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	6
Ch. dorsatus	x	n.s.	78	47	22	46	***	**53**	**100**	18	92	24	78	2	67	1	29	1	33	0	6	0	6
Chr. dispar	.	n.s.	0	0	100	2	n.s.	0	0	0	0	0	0	0	0	0	0	100	7	0	0	0	0
C. fuscus	.	n.s.	49	42	51	46	*	23	64	16	54	18	67	**25**	**92**	8	53	10	53	0	0	0	0
D. verrucivorus	x	n.s.	0	0	100	4	*	0	0	0	0	0	0	**100**	**17**	0	0	0	0	0	0	0	0
E. brachyptera	.	n.s.	33	12	67	23	n.s.	25	29	17	23	10	22	11	42	1	6	37	33	0	0	0	0
M. brachyptera	x	n.s.	40	53	60	39	***	1	7	7	8	12	56	5	17	9	53	8	27	20	88	**39**	**88**
O. viridulus	x	n.s.	36	5	64	9	n.s.	14	7	45	23	0	0	24	17	17	12	0	0	0	0	0	0
P. montanus	x	**	**61**	**98**	39	89	***	17	100	9	77	**30**	**100**	14	100	11	94	11	100	5	100	3	82
P. parallelus	.	n.s.	65	9	35	5	*	**60**	**29**	37	23	0	0	0	0	4	6	0	0	0	0	0	0
R. roeselii	.	n.s.	53	14	47	14	*	**46**	**43**	19	23	5	11	21	25	1	6	8	13	0	0	0	0
S. grossum	x	*	**67**	**40**	33	16	n.s.	15	21	22	23	2	22	8	8	25	53	7	20	20	53	1	12
T. subulata	.	n.s.	61	18	39	12	**	**49**	**57**	16	23	11	22	21	25	0	0	0	0	0	0	3	6
T. undulata	.	n.s.	0	0	100	7	n.s.	0	0	0	0	0	0	53	17	0	0	0	0	0	0	47	12
T. cantans	.	n.s.	36	5	64	9	n.s.	9	7	0	0	0	0	43	25	15	6	17	7	8	6	8	6

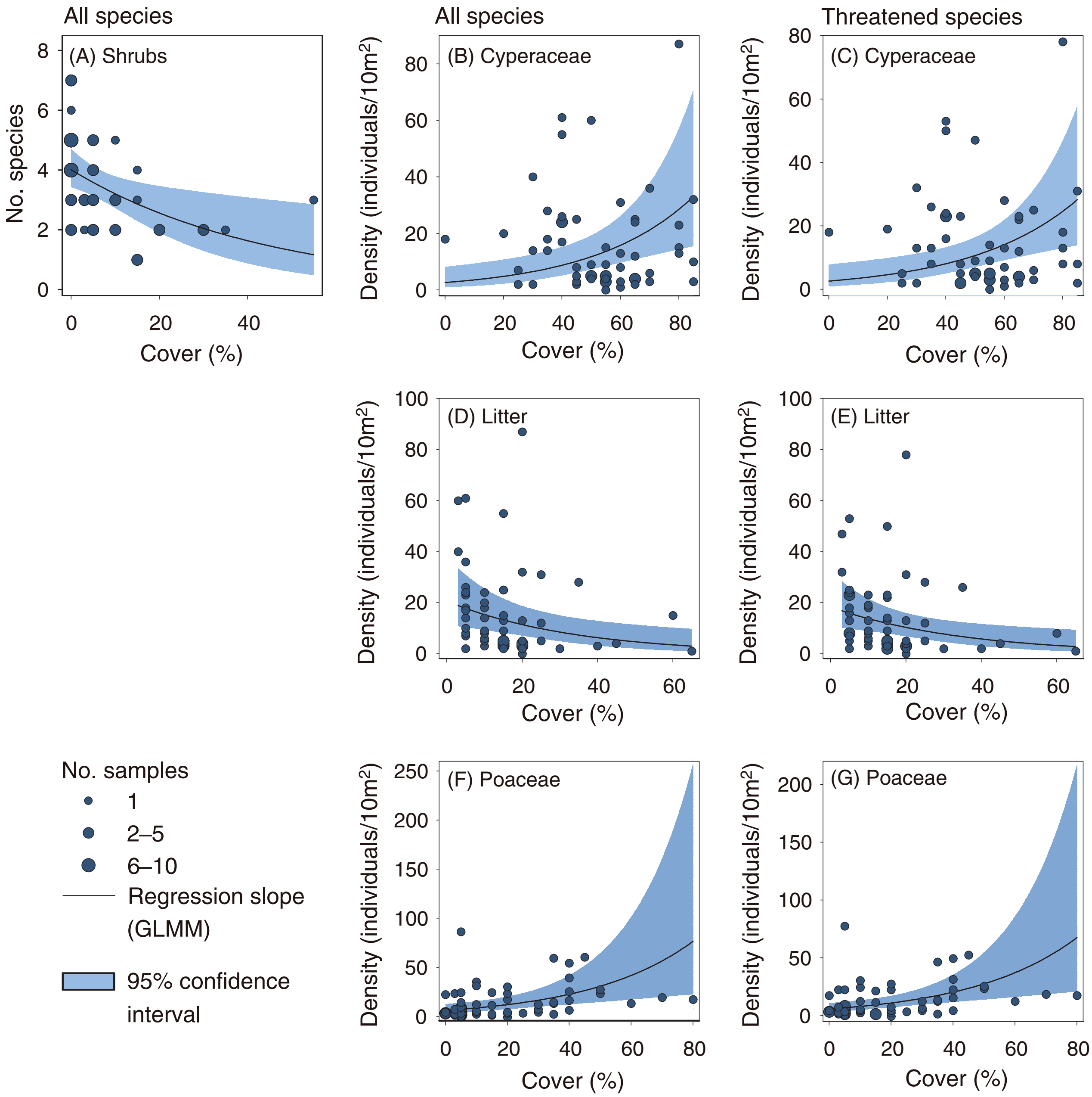

Fig. 3 Relationship between the number of all species (mean ± SE: 3.5 ± 0.2), density of all species (15.9 ± 2.3), and density of threatened species (14.0 ± 2.0) and environmental variables in common pastures (see Table 4 for detailed GLMM statistics).

pastures, the cover of shrubs and the vegetation height were higher.

Grasshopper assemblages and response to environmental conditions

Overall, we recorded 2 891 grasshopper individuals belonging to 16 species (Table 3). Five of these species are considered threatened. Species richness of all and of threatened species did not differ between common pastures and controls (all plots and within all four vegetation types; Fig. 2A and B). By contrast, density of all and of threatened species varied in all plots and within the 2 vegetation types with the highest grasshopper abundance, grasslands on mineral soil and fens, between common pastures and controls (Fig. 2C and D).

Table 4 Model-averaging results (GLMM) of the relationship between the response variables number of all species (Poisson) (A), number of threatened species (Poisson) (B), density of all species (negative binomial) (C), and density of threatened species (negative binomial) (D) and environmental variables (predictor variables) in common pastures. Differences were tested using Generalized Linear Mixed-Effects Models (GLMM). In all models, 'subarea' was set up as random factor. Predictor variables tested in all models were cover of shrubs, Cyperaceae, Poaceae, herbs, litter, mosses, open soil, vegetation height, vegetation density (25–30 cm height) and sunshine duration. For all models, model-averaged coefficients (full average) were derived from the top-ranked model (Δ AICc < 3). The explanatory power of the models is shown by ranges of marginal and conditional R2 values (Nakagawa & Schielzeth, 2013; Nakagawa *et al*., 2017) of the top-ranked models (Δ AICc < 3). n.s. = not significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

All species					Threatened species				
Variable	Est.	SE	Z	*P*	Variable	Est.	SE	Z	*P*
(A) No. species					(B) No. species				
(Intercept)	1.39	0.08	16.92	***	(Intercept)	–	–	–	–
Shrubs	–0.02	0.01	–2.51	*	Shrubs	–	–	–	–
$R^2_M = 0.16$, $R^2_C = 0.16$									
(C) Density					(D) Density				
(Intercept)	2.14	0.15	14.54	***	(Intercept)	2.13	0.49	4.30	***
Cyperaceae	0.03	0.01	6.31	***	Cyperaceae	0.03	0.01	3.90	***
Litter	–0.04	0.01	3.56	***	Litter	–0.04	0.01	2.75	**
Poaceae	0.03	0.01	5.74	***	Poaceae	0.03	0.01	4.08	***
Shrubs	–0.01	0.01	0.83	n.s.	Shrubs	–0.01	0.01	0.67	n.s.
$R^2_M = 0.33–0.38$, $R^2_C = 0.57–0.67$					$R^2_M = 0.36–0.40$, $R^2_C = 0.51–0.61$				

Considering all plots, two threatened species, *Pseudochorthippus montanus* and *Stethophyma grossum*, were identified as indicators of common pastures (Table 3). By contrast, controls had no indicative species. Within three of the four vegetation types, further indicator species were detected. In grasslands on mineral soil, *Chorthippus dorsatus*, *Pseudochorthippus parallelus*, *Roeseliana roeselii*, and *Tetrix subulata* were ascertained as indicator species of common pastures. The former is a threatened species. By contrast, within this vegetation type, *Chorthippus albomarginatus* was indicative for controls. In fens, the threatened species *P. montanus* was an indicator for common pastures and *Conocephalus fuscus* and the threatened species *Decticus verrucivorus* were characteristic for controls. Additionally, in raised bogs, *Metrioptera brachyptera* was identified as an indicator species of controls.

The GLMM analysis revealed that a higher cover of shrubs had negative effects on overall species richness in common pastures (Fig. 3A, Table 4). The cover of shrubs was negatively correlated with the number of cow droppings and vegetation density in 0–5 cm height (Table S1). The GLMM analysis for the number of threatened species failed to identify environmental predictors (Table 4). By contrast, GLMM analyses on the drivers of density of all and of threatened species in common pastures produced very similar results and had a high explanatory power (Fig. 3B–G, Table 4). Grasshopper density increased with the cover of grasses (Poaceae and Cyperaceae) but decreased with the cover of litter and shrubs. The cover of Poaceae was positively correlated with the number of cow droppings and vegetation density in 0–5 cm height (Table S1). Values of marginal R^2 ranged between 0.33 and 0.40.

Discussion

Our study revealed that grasshopper species richness did not differ between common pastures and controls in the Bavarian pre-Alps. However, density of all and of threatened species varied between common pastures and controls in all plots and within the two vegetation types with the highest grasshopper abundance, grasslands on mineral soil and fens. Two threatened species, *P. montanus* and *S. grossum*, were identified as indicators for common pastures. By contrast, controls had no indicative species.

Usually, changes in abundance of species reflect alterations in environmental conditions much earlier than shifts in species richness (Wettstein & Schmid, 1999; Fartmann *et al*., 2012; Löffler & Fartmann, 2017) since declines in the latter can only be detected if a population has completely disappeared (Thomas *et al*., 2006; Dirzo *et al*., 2014). Composition of vegetation types was very similar between common pastures and controls; solely land use varied. Hence, we observed differences in grasshopper density but not in species richness between common pastures and controls.

The key variables determining habitat quality for grasshoppers are (i) a suitable (warm) microclimate, (ii) enough food resources, (iii) appropriate oviposition sites, and (iv) refuges against predators or adverse weather (Gardiner & Dover, 2008; Wünsch *et al.*, 2012). Such diverse requirements are usually only fulfilled in habitats that are shaped by some kind of low-intensity land use (Kruess & Tscharntke, 2002; Löffler & Fartmann, 2017; Fumy *et al.*, 2021). Low-intensity grazing in common pastures has led to open and heterogeneous vegetation with some bare ground, a low cover of litter and an intermediate vegetation height favouring high densities of grasshoppers in general and threatened species in particular. The two threatened indicator species of common pastures, *P. montanus* and *S. grossum*, are also known to achieve their highest abundance in open wet grasslands and mires with low management intensity (Schlumprecht & Waeber, 2003).

Grasshopper species richness within common pastures was favored by a low cover of shrubs. Shrub cover reflected grazing intensity within the pastures since it was negatively correlated with the density of cow droppings. Grazing intensity in turn was related to the productivity of the vegetation types (*cf.* Lederbogen *et al.*, 2004; Ellenberg & Leuschner, 2010) and, hence, decreased in the order: grasslands on mineral soil, fens, transition mires, and raised bogs. Undergrazing favors the establishment of shrubs and taller vegetation rich in litter (Löffler *et al.*, 2019; Fumy *et al.*, 2021). As a result, patches of sunlit bare ground, vital for soil-breeding species, disappear and microclimatic conditions become cooler (Stoutjesdijk & Barkman, 1992), with negative effects on grasshopper species (Marini *et al.*, 2008; Helbing *et al.*, 2014). By contrast, for the number of threatened species within common pastures, the GLMM failed to identify environmental predictors, which we attribute to the relatively constant number of threatened species across the environmental gradient.

However, the GLMM analyses on the drivers of density of all and of threatened species in common pastures produced consistent results and had a high explanatory power. Density of both groups increased with the cover of grasses (Poaceae and Cyperaceae) but decreased with the cover of litter and shrubs. The majority of grasshopper species feed on grasses (Ingrisch & Köhler, 1998). Recent studies have shown that the food supply may limit grasshopper densities in habitats with a sparse vegetation (Helbing *et al.*, 2014; Löffler *et al.*, 2016). In the common pastures, this seems to be especially true for raised bogs where the cover of grasses was much lower than in grasslands on mineral soil or in fens. Additionally, undergrazing, indicated by a higher cover of litter and shrubs, had not only negative effects on species richness but also on density of grasshoppers.

In contrast to common pastures, only two fifths of the control plots were characterized by low-intensity management, that is, meadows mown once, usually used as litter meadows. One half of the controls were abandoned and the remaining tenth comprised grasslands mown twice or more. Both abandonment and intensive land use have negative impacts on grasshoppers (Fumy *et al.*, 2021). Abandonment results in the same but stronger effects as described above for undergrazing (Löffler *et al.*, 2019; Fumy *et al.*, 2020). Intensive grassland management also leads to homogeneous and dense swards. In such stands, key microhabitats for oviposition (bare ground or taller vegetation that remains during winter) as well as shelter against predators and adverse weather (taller vegetation) are usually lacking (Fumy *et al.*, 2021). Moreover, each mowing event causes direct mortality of grasshopper individuals and, subsequently, facilitates predation through insectivorous vertebrates, since sheltered vegetation has been removed (Wünsch *et al.*, 2012; Buri *et al.*, 2013). Hence, we explain the lower grasshopper densities in general and of threatened species in controls in particular by the high share of abandoned and intensively used plots, respectively. Additionally, we attribute the lack of indicator species of controls in general by the wide gradient in land-use intensity and, hence, strong differences in habitat structure (unpublished data; see also Löffler *et al.*, 2019; Fumy *et al.*, 2020, 2021) although averaged values were often comparable to those of common pastures.

The density of all and of threatened grasshopper species was higher in common pastures compared to control for two vegetation types: grasslands on mineral soil and fens. Both vegetation types occurred on the most productive soils across the studied environmental gradient and were characterized by the highest grazing intensity. By contrast, in controls, only one half and two thirds of the plots, respectively, had a low land-use intensity (mowing once). The remaining plots were either intensively managed (especially in grasslands on mineral soil) or abandoned (particularly in fens). These findings highlight that consistent low-intensity grazing on productive soils favors a high abundance of grasshoppers in general and threatened species in particular. This type of traditional grazing even promotes coexistence of species with very different habitat requirements due to the creation of heterogeneous swards. In grasslands on mineral soil, the threatened species *C. dorsatus* as well as *P. parallelus*, *R. roeselii*, and *T. subulata* were identified as indicator species of common pastures. *C. dorsatus* is a characteristic of wet grasslands with low land-use intensity; *P. parallelus* occurs in a wide range of different grassland types; *R. roeselii* depends on dense grassland vegetation with an intermediate height, and *T. subulata* colonizes open and wet habitats rich in bare ground (Schlumprecht & Waeber, 2003). By contrast, *C. albomarginatus* was ascertained as the only indicator species of controls, which we attribute to the high share of intensively managed plots in grasslands on mineral soil. Indeed, *C. albomarginatus* is known to belong to the very few grasshopper species that tolerate intensive grassland management (Schlumprecht & Waeber, 2003). In fens, the threatened species *P. montanus* was detected as an indicator species of common pastures; additionally, *C. fuscus* and the threatened species *D. verrucivorus* were indicative for controls. *P. montanus* is a specialized species of wet grasslands and fens that requires a low intensity of land use to establish strong populations (Schlumprecht & Waeber, 2003). By contrast, *C. fuscus* and *D. verrucivorus* depend on taller vegetation, at least in some parts of their habitat (Schlumprecht & Waeber, 2003; Schirmel *et al*., 2010; Wünsch *et al*., 2012). Consequently, we explain the occurrence of these two species by the high proportion of abandoned fens in controls.

In contrast to the two more productive vegetation types, in transition mires and raised bogs, the differences in species composition between common pastures and controls were only weak. We attribute this finding to the very slight differences in land use (very low grazing pressure [common pastures] *vs*. abandonment [control]) and the generally low successional speed within both vegetation types (*cf*. Ellenberg & Leuschner, 2010). Nevertheless, we identified at least one indicator species: the threatened species *M. brachyptera* was indicative for raised bogs in controls. Within raised bogs, the species prefers dense vegetation (Schlumprecht & Waeber, 2003). Indeed, vegetation density near the ground in this vegetation type was higher in controls compared to common pastures. We assume that the abandonment of all control plots and at least weak grazing effects at common pastures were responsible for this difference.

In conclusion, land use had a clear effect on the density of all and of threatened grasshopper species. Traditional low-intensity grazing in common pastures has resulted in open and heterogeneous swards with some bare ground, a low cover of litter and an intermediate vegetation height favoring a high abundance of species in general and threatened species in particular. This is especially true for the two most productive vegetation types, grasslands on mineral soil and fens.

Implications for conservation

Recent studies have shown that traditionally grazed common pastures in southern Bavarian are hotspots of plant and insect diversity, including many rare species (Anthes *et al*., 2003; Lederbogen *et al*., 2004; Rosenthal & Lederbogen, 2008; Streitberger *et al*., 2012; Weking *et al*., 2013; Helbing *et al*., 2014; Schwarz & Fartmann, 2021). Our study now highlights that traditional summer cattle grazing in grasslands on mineral soil and fens also enhances grasshopper density in general and density of threatened species in particular.

Grasshoppers are of great functional importance in grassland ecosystems due to their key role as prey for species of higher trophical levels such as insectivorous birds (Samways, 2005; Fartmann *et al*., 2021). Schwarz *et al*. (2018) showed that the insectivorous Tree Pipit (*Anthus trivialis*) preferred the common pastures in the pre-Alps for breeding. In part, they explained this preference by a higher availability of arthropod food resources in comparison to the surrounding landscape. Our study now provides hard field data that support this assumption.

To promote biodiversity in general and grasshopper densities in particular, we recommend maintaining traditional cattle grazing (stocking capacities: 0.5–2.0 LSU/ha) from May to October in common pastures. Where possible, this grazing regime should also be introduced in the surrounding landscape – however, not at the expense of traditionally managed litter meadows since they are also characterized by highly diverse plant and animal assemblages that are adapted to late mowing (Anthes *et al*., 2003; Settele *et al*., 2009; Schwarz & Fartmann, 2021).

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Research involving human and animal rights

No grasshoppers were harmed during the course of this project.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Results of Spearman rank correlations (rs) of environmental variables.