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Land-use intensity determines grassland Orthoptera assemblage composition across a moisture gradient

Florian Fumy [a,*], Steffen Kämpfer [a], Thomas Fartmann [a,b]

[a] Department of Biodiversity and Landscape Ecology, 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

Two of the main principles of global and national conservation strategies consist in focusing on the most species-rich and most vulnerable ecosystems. In this study, we investigated the Orthoptera species assemblages of species-rich grasslands in the southern Black Forest, one of 30 German biodiversity hotspots. Across a moisture gradient, we considered the three dominant grassland types within the study area: (i) dry, (ii) mesic and (iii) wet grasslands. In order to analyze the drivers of biodiversity in a landscape of high conservation value, we related (i) differences in Orthoptera assemblage composition between the three grassland types and (ii) the relationship of Orthoptera assemblage composition within each grassland type to environmental conditions. In our study, we detected considerable variation in land-use intensity which dropped from high in mesic to low in dry and again to near-zero in wet grasslands. Land-use intensity was the only predictor of Orthoptera species richness in the multivariable Generalized Linear Mixed-effects Models. The mean number of both all and threatened species was highest in the grassland type with low land-use intensity, dry grasslands, differing from those of mesic (high land-use intensity) and wet (mostly abandoned) grasslands. Additionally, dry grasslands had the highest number of all, threatened and exclusive indicator species. Both (i) intensive land use in mesic grasslands and (ii) abandonment of land use in wet grasslands led to a homogenization of the habitat structures and the species assemblages. In contrast, dry grasslands with low land-use intensity and high habitat heterogeneity were hotspots of Orthoptera species richness.

1. Introduction

The loss of biodiversity ranks among the most appalling natural crises in human history (Cardoso et al., 2020; IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services), 2019). The conservation of biodiversity from the local to the global scale is, thus, one of the most urgent challenges for humankind (Dirzo and Raven, 2003; Mittermeier et al., 2011; Samways et al., 2020). In order to protect biodiversity, conservation efforts should be guided systematically. Two of the main principles of global and national conservation strategies consist in focusing on the most species-rich and most vulnerable ecosystems (Brooks et al., 2006). Accordingly, biodiversity hotspots have been designated on global (see for example Mittermeier et al., 2011) and national scales. These hotspots harbor outstandingly species-rich ecosystems and high shares of endangered species. In Germany, one fundamental aspect of the national strategy for biodiversity conservation is the realization of conservation measures in national biodiversity hotspots (Ackermann and Sachteleben, 2012).

Many of the European biodiversity hotspots exhibit high shares of grasslands, which are among the most species-rich ecosystems in Europe and cover >20% of the EU-28 land surface (EC (European Commission), 2019; Feurdean et al., 2018; Wilson et al., 2012). Most of the European grasslands have been shaped by human agricultural practice (Feurdean et al., 2018; Veen et al., 2009). However, due to the transition from pre-industrial land use to industrial agriculture, the extent of semi-natural grasslands of high conservation value has dramatically decreased, mainly driven by agricultural intensification, but also by land-use abandonment (Dengler et al., 2014; MacDonald et al., 2000; Wallis de Vries et al., 2002). As a result, the biodiversity of European grassland ecosystems has become increasingly threatened.

Because of the significant role Orthoptera play both as herbivores and prey, they are of great functional importance in grassland ecosystems (Samways, 2005). Furthermore, they are among the most suitable indicator groups to investigate the effects of land-use change (e.g.

* Corresponding author.
E-mail address: florian.fumy@uos.de (F. Fumy).

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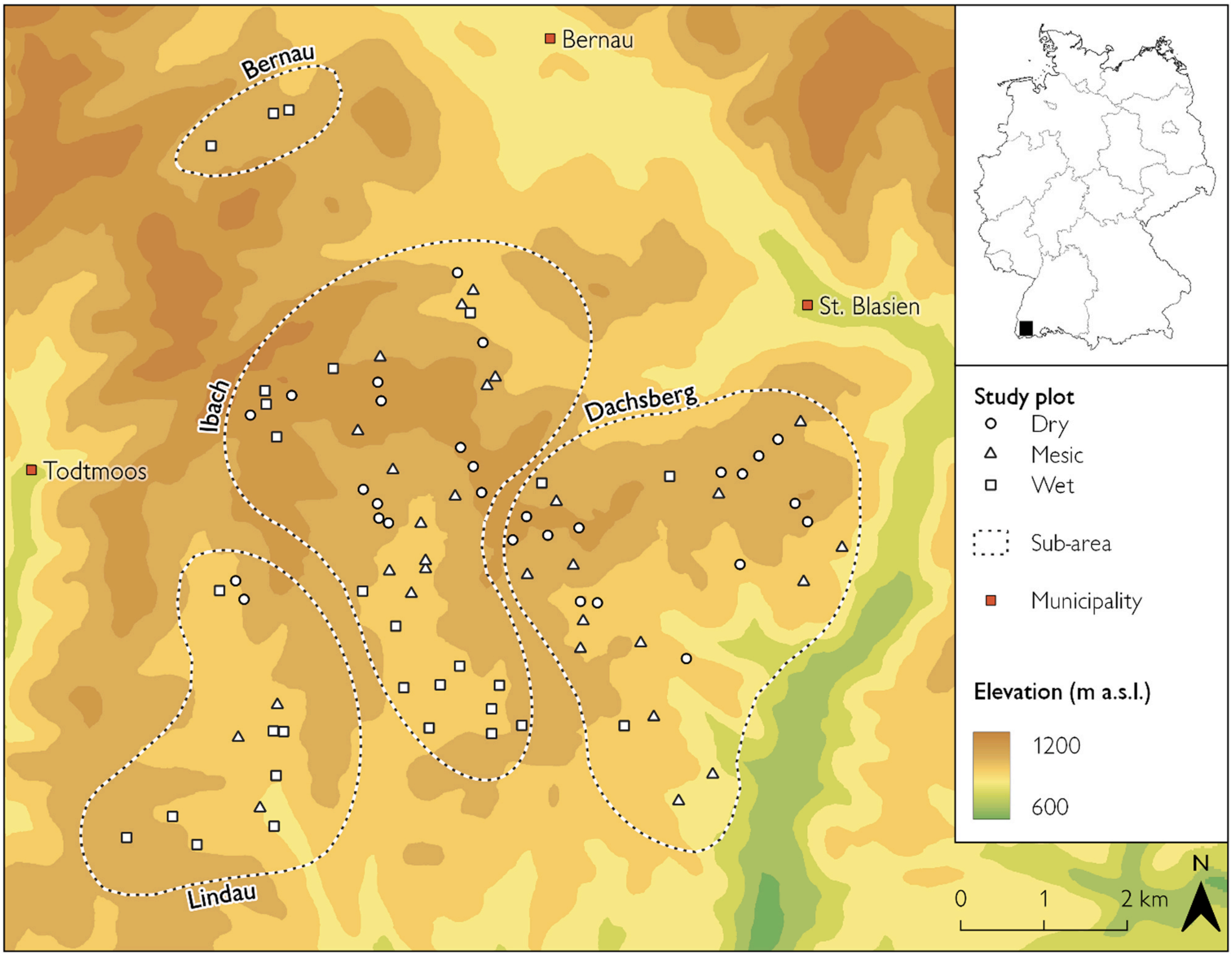

Fig. 1. Location of the study area and plots in the southern Black Forest (SW Germany).

Bazelet and Samways, 2012; Fartmann et al., 2012; Löffler et al., 2019). The habitat requirements of Orthoptera are complex. Particularly, the often interrelated parameters of vegetation structure (Fartmann et al., 2012; Poniatowski and Fartmann, 2008) and microclimate (Gardiner and Dover, 2008) define habitat quality.

In this study, we investigated the Orthoptera species assemblages of semi-natural grasslands in the southern Black Forest (SW Germany). Due to the high share of species-rich grasslands, the study area is part of one of 30 German biodiversity hotspots (Ackermann and Sachteleben, 2012). Species richness of Orthoptera has been shown to be very high in the study area and includes a large number of specialized and threatened species (Detzel, 1997; Fumy et al., 2020). Across a moisture gradient, we considered the three dominant grassland types within the study area: (i) dry, (ii) mesic and (iii) wet grasslands. In order to analyze the drivers of biodiversity in a landscape of high conservation value, we related (i) differences in Orthoptera assemblage compositions between the three grassland types and (ii) the relationship of Orthoptera assemblage compositions within each grassland type to environmental conditions. Based on the results, we give recommendations for effective strategies for biodiversity conservation in temperate grassland ecosystems, which are expected to foster Orthoptera 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), occupies about 100 km^2, ranging from 700 to 1100 m a.s.l. For Central Europe, the climate is rather cool and wet, with a mean annual temperature of 6.3 °C and an average annual precipitation of 1700 mm (reference period 1981–2010; German Meteorological Service, 2021). Along the elevation gradient, precipitation increases from about 1600 to 1900 mm/a and mean annual temperature decreases from 6.8° to 5.7 °C (German Meteorological Service, 2021).

The Hotzenwald is part of the German biodiversity hotspot 'Hochschwarzwald mit Alb-Wutach-Gebiet' (Ackermann and Sachteleben, 2012). Large parts of the cultural landscape in the study area are dominated by semi-natural grasslands which are of major importance for biodiversity conservation in Europe (Feurdean et al., 2018; Veen et al., 2009). In accordance with their soil moisture, these grasslands can be classified into three types: (i) dry, (ii) mesic and (iii) wet grasslands.

Most of the dry grasslands have been managed as commons for centuries (Eggers, 1957; Hermle and Deil, 2002). Although a relatively large share of the grasslands is still in communal property, the management of the common pastures has undergone substantial changes since the 1930s through administrative interventions and technical innovation, such as the introduction of electric fences (MEBW, 2016). However, traditional rough grazing, in many cases with a local cattle breed called 'Hinterwälder', is still widespread (Konold et al., 2014). Due to their high habitat diversity and species richness, these heterogeneous pasture ecosystems have an outstanding conservation value and, additionally, make a unique contribution to German cultural heritage (Lederbogen et al., 2004; Regional Council Freiburg

(Regierungspräsidium Freiburg), 2011).

Historically, the mesic grasslands were predominantly mown once or twice per year (Regional Office for Environment (Landesanstalt für-Umweltschutz Baden-Württemberg), 2004) and managed as irrigation meadows (Borcherdt, 1985; Leibundgut and Vonderstrass, 2016; Schellberg, 2005). However, many of these grasslands have recently suffered from land-use intensification, reflected by a regular application of fertilizer and an increasing mowing frequency (Konold et al., 2014; Nowak and Schulz, 2002). Ditch irrigation systems for the former irrigation meadows have been abandoned completely (Schellberg, 2005). Despite these general changes in land use, some of the mesic grasslands are still characterized by low land-use intensity and species-rich insect assemblages (Fumy et al., 2020).

The wet grasslands in the study area were traditionally mown once or twice a year, or grazed by cattle at low stocking rates (Geis et al., 2013; Regional Council Freiburg (Regierungspräsidium Freiburg), 2011). However, as a consequence of irregular management or complete abandonment for over 20 years, many of these formerly species-rich wet grasslands are now homogeneous, high-growing, rich in litter and dominated by tall forbs (e.g. *Filipendula ulmaria*) or grasses (e.g. *Molinia caerulea*) (own observation). Although some sites suffered from drainage, the study area still features an extensive network of hydrologically intact wet grasslands.

2.2. Study design

2.2.1. Study plots

We compared Orthoptera species assemblages of the three dominant grassland types in the study area: (i) dry, (ii) mesic and (iii) wet grasslands. Prior to the plot selection, we mapped habitat types in the field according to Finck et al. (2017) and classified the grasslands according to the EUNIS (EEA (European Environment Agency)) habitat classification (E1 = dry, E2 = mesic, D2 = wet grasslands). Characteristic plant communities were the Polygalo-Nardetum and Festuco-Genistelletum in dry, Cynosurion and Polygono-Trisetion communities in mesic and Calthion communities as well as the Caricion fuscae and Juncetum squarrosi in wet grasslands (Burkart et al., 2004; Dierschke, 1997; Köppler, 2004; Peppler-Lisbach and Petersen, 2001).

Orthoptera occurrence was surveyed in 87 plots, each having a size of 100 m × 100 m. Per grassland type, we randomly selected 29 plots with homogeneous vegetation structure (stratified random sampling). The minimum distance between plots was set to 50 m. To avoid edge effects from adjacent habitat types (Schirmel et al., 2010), each plot had to be surrounded by a buffer of at least 20 m of the focal grassland type (dry, mesic or wet). In order to account for possible spatial autocorrelation, the study area was divided into four sub-areas according to aggregations of the study plots (Fig. 1).

2.2.2. Sampling design

2.2.2.1. Environmental conditions. For each plot, 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 (i) the heatload index (HLI) according to McCune and Keon (2002) as a measure of radiation influx and (ii) the topographic position index (TPI)—with a search radius of two elevation grid cells—according to Weiss (2001) as a measure of topographic variety. Both the HLI and the TPI were calculated using the ‘spatialEco’ package by Evans (2019). For both variables, we used the range per plot as an explanatory variable in our models. The HLI and TPI ranges reflect the difference between the elevation grid cells with the highest and lowest radiation or prominence values—within each plot—respectively. Both indicate topographic diversity of the study plots.

Table 1
Land-use types in the study plots and their assigned land-use intensity values. Land-use intensity ranges from 0 (no land use) to 5 (very high land-use intensity). For each plot, land-use intensity was calculated as the weighted mean intensity of the land-use types present in the respective plot.

Land-use intensity	Value	Description
No land use	0	Abandoned semi-natural grassland
Very low	0.5	Semi-natural grassland: sporadically grazed, at most two to four weeks per year
Low	1	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 and a rotation cycle of two to four weeks
High	4	Improved grassland with liquid-manure fertilization: meadows mown thrice or highly intensive strip grazing with a rotation cycle of two to five days
Very high	5	Improved grassland with liquid-manure fertilization: meadows mown four times

We ascertained land-use intensity on an ordinal scale. 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 1). 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 coverage within the respective plot.

2.2.2.2. Orthoptera assemblages. Orthoptera species were sampled at three times between June and August 2018 with at least three weeks between each visit. In each plot, all available habitat structures were surveyed for the occurrence of Orthoptera species under favorable weather conditions (temperature > 15 °C, cloud cover < 50%) using acoustic and visual detection as well as sweep netting (Fischer et al., 2016; Samways, 2019). Arbusticolous and arboricolous species that rarely occur in grasslands were excluded from all analyses, as our sampling techniques do not produce reliable data for these species. Species identification was performed in the field using song and morphological characteristics in line with Fischer et al. (2016). 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 3.6.3 statistical environment (R Core Team, 2020). Differences in environmental parameters between the three studied grassland types were tested using Kruskal–Wallis’ *H* test and Dunn’s test as a post-hoc test using the ‘dunn.test’ package (Dinno, 2017). We chose this nonparametric approach because mixed-effects models could not be applied due to overdispersion. Differences in numbers of (i) all and (ii) threatened species between the three studied grassland types were tested using Generalized Linear Mixed-effects Models (GLMM) with Poisson error structure, *grassland type* as a categorical predictor and *sub-area* as a random factor. ‘Threatened species’ considered all species identified as nearly threatened or threatened in the current red list of Orthoptera species for the federal state of Baden-Württemberg (Detzel, 2020; see also Table A1). Pairwise comparisons between the grassland types were made using the ‘glht’ function in the ‘multcomp’ package by Hothorn et al. (2008), using Tukey’s test as a post hoc test (homogeneity of variance and equal group sizes were given).

To assess the effects of the environmental parameters on species richness of (i) all and (ii) threatened species, we conducted GLMMs with Poisson error structure for each grassland type separately.

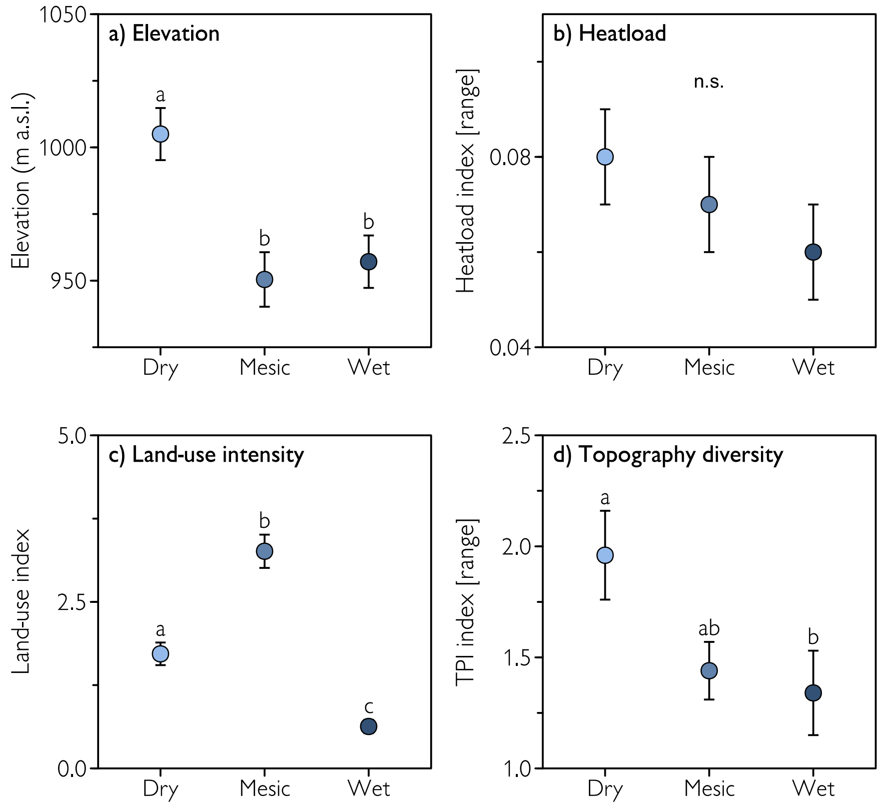

Fig. 2. Mean (±SE) elevation (a), heatload (b, range), land-use intensity (c) and topography (d, range) in the three studied grassland types (*N* for each type = 29). Differences were tested using Kruskal–Wallis' *H* test and Dunn's post-hoc test. Different letters indicate significant differences between grassland types. $Chi^2_{Elevation} = 14.47$; $Chi^2_{Heatload} = 2.5$; $Chi^2_{Land\text{-}use\ intensity} = 50.08$; $Chi^2_{Topography\ diversity} = 7.89$.

Multicollinearity was low for all predictors in all models ($|r_s| < 0.5$, VIF < 2) (see Graham, 2003; Zuur et al., 2010). Possible spatial autocorrelation was taken into account by adding *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 $\Delta AIC_C < 3$ (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.

We conducted an indicator species analysis for the three studied grassland types using the 'multipatt' function in the R package 'indicspecies' by de Cáceres and Legendre (2009). We considered indicator relationships of single species with single and combined grassland 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 de Cáceres and Legendre, 2009).

3. Results

3.1. Environmental conditions

Land-use intensity was the only environmental parameter that differed between all three grassland types; it varied from high intensity

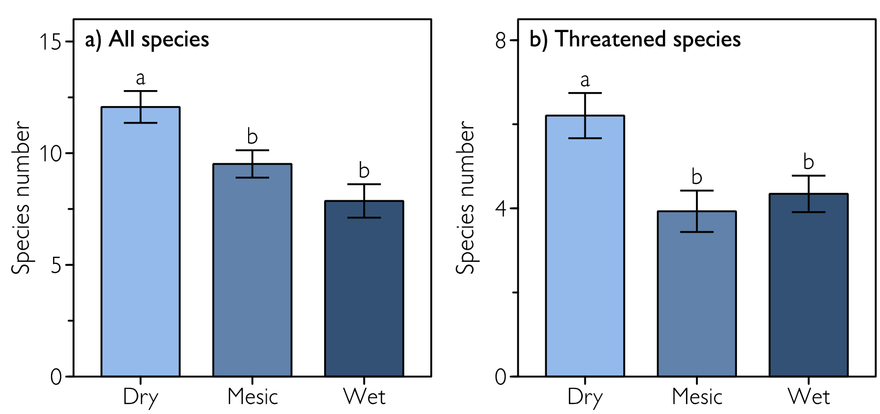

Fig. 3. Mean species richness (±SE) of all (a) and threatened (b) Orthoptera species in the three studied grassland types (*N* for each type = 29). Differences between the grassland types were tested using mixed-effects models (GLMM) with *sub-area* (*N* = 4) as a random factor. Different letters indicate significant differences between grassland types (P < 0.05).

Table 2
Indicator species for the three studied grassland types. Threatened species (cf. Table A1) are indicated in bold type. Specificity indicates the degree of grassland-type restriction of the species (0 = species occurred exclusively in other grassland types; 1 = species occurred in no other grassland type). Sensitivity indicates the fidelity of the species to the considered grassland type (0 = species did not occur in any study plot of the focal grassland type; 1 = species occurred in all study plots of the focal grassland type). The indicator value (IV) indicates the association of the species with the respective grassland type, considering both, Specificity and sensitivity (0 = species not associated with the focal grassland type; 1 = species perfectly associated with the focal grassland type). Significances are indicated as follows: *P > 0.05, *P < 0.05, **P < 0.01, ***P < 0.001.*

Indicator species	Grassland type			Specificity	Sensitivity	IV	*P*
	Dry	Mesic	Wet				
Decticus verrucivorus	✓	.	.	0.65	0.76	0.70	***
Stenobothrus stigmaticus	✓	.	.	0.68	0.72	0.70	***
Bicolorana bicolor	✓	.	.	1.00	0.28	0.53	***
Myrmeleotettix maculatus	✓	.	.	0.82	0.31	0.50	**
Psophus stridulus	✓	.	.	1.00	0.14	0.37	*
Pseudochorthippus parallelus	✓	✓	.	0.90	0.95	0.93	***
Chorthippus biguttulus	✓	✓	.	0.82	1.00	0.90	***
Stenobothrus lineatus	✓	✓	.	0.88	0.78	0.83	***
Gomphocerippus rufus	✓	✓	.	0.89	0.72	0.80	***
Gryllus campestris	✓	✓	.	0.97	0.64	0.79	***
Chrysochraon dispar	.	✓	✓	0.82	0.71	0.76	***
Conocephalus fuscus	.	✓	✓	1.00	0.22	0.47	*
Pseudochorthippus montanus	.	.	✓	0.71	0.86	0.79	***
Metrioptera brachyptera	.	.	✓	0.66	0.86	0.75	***
Stethophyma grossum	.	.	✓	0.77	0.34	0.52	**

Table 3
Results of multivariable GLMM (Poisson error structure): relationship of Orthoptera species richness of all (a) and threatened (b) species with environmental parameters in the three studied grassland types (*N* for each type = 29). Sub-area (N = 4) was set up as a random factor. Presented are the averaged models (full average) from the top-ranked models (ΔAICc < 3). Both conditional and marginal R^2 are given. R^2_c = variance explained byboth fixed and random effects, R^2_m = variance explained by fixed effects only (Nakagawa et al., 2017). Significances are indicated as follows: n.s. (not significant), *P > 0.05, *P < 0.05, **P < 0.01, ***P < 0.001.*

Parameter	All species			Threatened species		
	Estimate ± SE	z	*P*	Estimate ± SE	z	*P*
(i) Dry	R^2_c 0.21–0.32; R^2_m 0.21–0.31			R^2_c 0.36–0.41; R^2_m 0.35–0.41		
Intercept	2.19 ± 1.05	2.06	*	1.32 ± 1.75	0.74	n.s.
Land-use intensity	–0.14 ± 0.08	1.67	n.s.	–0.28 ± 0.13	2.09	*
TPI [range][a]	0.07 ± 0.06	1.05	n.s.	0.08 ± 0.09	0.97	n.s.
Heatload [range]	0.10 ± 0.49	0.20	n.s.	0.2 ± 0.78	0.32	n.s.
Elevation	0 ± 0	0.38	n.s.	0 ± 0	0.46	n.s.
(ii) Mesic	R^2_c 0.39–0.4; R^2_m 0.39–0.39			R^2_c 0.53–0.53; R^2_m 0.53–0.53		
Intercept	2.86 ± 0.73	3.75	***	2.5 ± 1.12	2.13	*
Land-use intensity	–0.19 ± 0.04	4.12	***	–0.38 ± 0.07	5.31	***
TPI [range][a]	0 ± 0.03	0.02	n.s.	–0 ± 0.05	0.01	n.s.
Heatload [range]	0.09 ± 0.5	0.16	n.s.	0.11 ± 0.8	0.13	n.s.
Elevation	0 ± 0	0.03	n.s.	–0 ± 0	0.02	n.s.
(iii) Wet	R^2_c 0.41–0.47; R^2_m 0.4–0.46			R^2_c 0.28–0.29; R^2_m 0.28–0.29		
Intercept	1.45 ± 0.9	1.55	n.s.	0.83 ± 1.24	0.64	n.s.
Land-use intensity	0.54 ± 0.17	3.13	**	0.58 ± 0.17	3.12	**
TPI [range][a]	0.02 ± 0.05	0.42	n.s.	0.01 ± 0.04	0.19	n.s.
Heatload [range]	–0.41 ± 1.38	0.29	n.s.	–0.1 ± 1	0.1	n.s.
Elevation	0 ± 0	0.12	n.s.	0 ± 0	0.17	n.s.

[a] The topographic position index (TPI) range reflects the difference between the least and the most prominent elevation grid cell within the respective plot. It thus indicates the topographic diversity of the plots.

in mesic grasslands to low intensity in dry grasslands to near-zero intensity in wet grasslands. Dry grasslands were situated at the highest elevations, differing from both mesic and wet grasslands. The topographic diversity was highest in dry grasslands, differing from wet grasslands; mesic grasslands had an intermediate position. Contrastingly, the HLI range did not differ between the three grassland types (Fig. 2).

3.2. Orthoptera assemblages and their response to environmental conditions

In total, we recorded 32 Orthoptera species in the 87 plots (Table A1). Species richness per plot ranged from 1 to 21 species, with a mean (±SE) of 9.1 ± 0.4 species. The number of threatened species varied from 0 to 13 with a mean of 4.8 ± 0.3 species. The most widespread species were *Roeseliana roeselii*, *Chorthippus biguttulus* and *Pseudochorthippus parallelus*, which were present in 80%, 76% and 65% of the plots, respectively (Table A1). The mean numbers of (i) all species and (ii) threatened species were highest in the dry grasslands, differing from mesic and wet grasslands (Fig. 3).

The dry grasslands had the highest number of indicator species: ten species, among them six threatened species (Table 2). Mesic grasslands followed with seven characteristic species (one threatened species) and wet grasslands with five species (two threatened species). Additionally, dry grasslands had the highest number of exclusive indicator species with five species mainly occurring in this grassland type. Wet grasslands followed with three exclusive indicator species. In contrast, none of the indicator species of mesic grasslands were solely restricted to this grassland type.

Land-use intensity was the only predictor of species richness of (i) all and (ii) threatened Orthoptera species in the multivariable GLMMs (Table 3, Fig. 4). With increasing land-use intensity, the number of all and threatened species increased in the wet grasslands and decreased in the mesic grasslands. In the dry grasslands, only threatened species decreased with an increase in land-use intensity.

4. Discussion

In our study, we detected considerable variation in land-use intensity across three grassland types in a German biodiversity hotspot. Average land-use intensity dropped from high in mesic to low in dry and again to near-zero in wet grasslands. The mean number of both all and

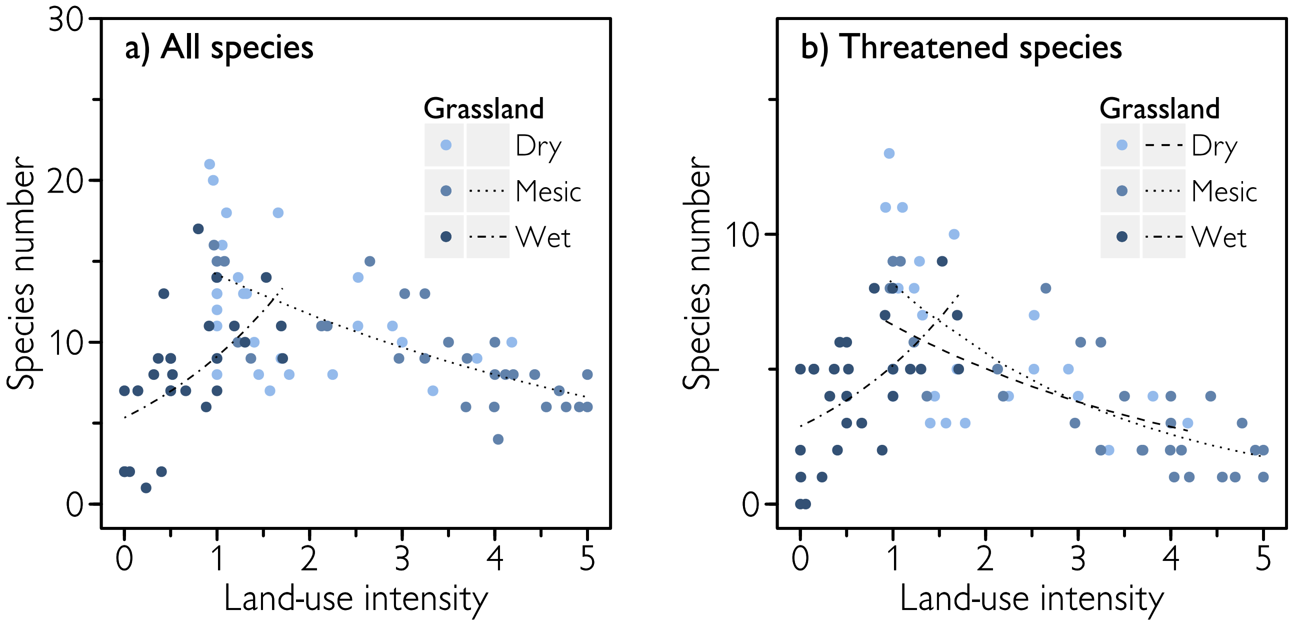

Fig. 4. Relationship of Orthoptera species richness of all (a) and threatened (b) species with land-use intensity in the three studied grassland types (*N* for each type = 29). The curves (dashed: dry grasslands, dotted: mesic grasslands; dot-dashed: wet grasslands) depict the averaged models with significant coefficients from Table 3 (see there for details on the models).

threatened species was highest in the grassland type with low land-use intensity, the dry grasslands, differing from those in mesic (high land-use intensity) and wet (mostly abandoned) grasslands. Additionally, the dry grasslands had the highest numbers of all and threatened as well as overall and exclusive indicator species. For all grassland types, land-use intensity was the only predictor of Orthoptera species richness in the multivariable GLMMs.

Generally, the main parameters determining habitat quality for Orthoptera are (i) a favorable (warm) microclimate, (ii) sufficient food, (iii) adequate oviposition sites and (iv) shelter against predators or extreme weather (Gardiner and Dover, 2008; Willott and Hassall, 1998; Wünsch et al., 2012). Such complex requirements are often best fulfilled in heterogeneous habitats (Fartmann et al., 2012; Helbing et al., 2014; Kruess and Tscharntke, 2002; Löffler and Fartmann, 2017; Schirmel et al., 2010). Habitat heterogeneity is associated with high availability of microsites and, hence, is generally known to foster species richness (Steinmann et al., 2011; Tews et al., 2004). Due to a mostly low land-use intensity, the dry grasslands had the most heterogeneous swards (own observation) and were the hotspots of Orthoptera diversity in our study. Most dry grasslands were used as cattle pastures with low to at most intermediate stocking rates (own observation, Bogenrieder, 2012). Such pastures are known for their spatial heterogeneity, consisting of patches with bare ground, latrines, short grazing laws and spots with taller vegetation (Bogenrieder, 2012; Ellenberg and Leuschner, 2010; Gardiner, 2018; Török et al., 2014).

Mesic and wet grasslands represented the two extremes across the land-use-intensity gradient. Mesic grasslands had the highest land-use intensity with adverse effects on Orthoptera species richness. Intensive grassland management results in homogeneous and dense swards (Ellenberg and Leuschner, 2010) which lack in key microhabitats for Orthoptera. For instance, such swards lack in suitable oviposition sites, such as bare ground or patches of taller vegetation which remain during winter (see above) (Gardiner, 2018). Additionally, each mowing event and each period of intensive grazing cause direct mortality of Orthoptera and increase the risk of predation through insectivorous vertebrates (e.g. birds) (Buri et al., 2013; Humbert et al., 2012; Wünsch et al., 2012).

In contrast, in wet grasslands Orthoptera species had suffered from abandonment or irregular land use. Abandonment of management in the wet, formerly species-rich grasslands had mostly resulted in homogeneous and high-growing stands, rich in litter and dominated by tall forbs (e.g. *Filipendula ulmaria*) or grasses (e.g. *Molinia caerulea*) (cf. Section 2.1). In such stands, patches of bare ground for soil-breeding species are largely missing (own observation) and the microclimate is rather cool (Stoutjesdijk and Barkman, 1992), hampering the establishment of species-rich Orthoptera assemblages (Bieringer, 2003; Helbing et al., 2014; Marini et al., 2009).

The only group of Orthoptera species that was not affected by land use was that of all species in dry grasslands. We explain the lack of relationship by (i) the generally low land-use intensity in dry grasslands and (ii) the lower sensitivity of non-threatened species compared to that of threatened species to more intensive land use. It is well-known that at least some non-threatened, generalist Orthoptera species are able to cope with much higher land-use intensity compared to most threatened, specialist species (Detzel, 1998; Schlumprecht and Waeber, 2003).

All three grassland types were characterized by certain indicator species. However, only the two grassland types with low land-use intensity, dry and wet grasslands, had exclusive indicator species. Concerning the soil moisture, mesic grasslands mediate between dry and wet grasslands. Hence, some similarities in indicator species of mesic grasslands and one of the other grassland types are plausible. Additionally, we explain the absence of unique indicator species in the mesic grasslands by a homogenization of the Orthoptera assemblages due to the high land-use intensity. The high numbers of indicator species, especially of exclusive indicator species, indicate that the studied grassland types feature rather specific and definable Orthoptera assemblages. Hence, Orthoptera diversity on the landscape level relies on all three grassland types, especially the dry and wet grasslands.

In summary, land-use intensity was the key driver of Orthoptera species richness in the studied grasslands. Both (i) intensive land use—mostly in the mesic grasslands—and (ii) abandonment—mostly in the wet grasslands—led to a homogenization of the habitat structures and the species assemblages. By contrast, grasslands with low land-use intensity and high habitat heterogeneity, which applied to most of the dry, but also to some of the mesic and wet grasslands, were hotspots of Orthoptera species richness.

5. Implications for conservation

Throughout Europe, grasslands with low land-use intensity and high biodiversity have endured especially at higher elevations of mountain areas, as these are generally characterized by an adverse climate or soil conditions that hamper more intensive land use (MacDonald et al., 2000). This was also true for the study area in a German biodiversity hotspot: the species-rich, mostly dry grasslands were generally located at the highest elevations and had the highest topographic diversity. By contrast, at lower elevated sites with lower topographic diversity, land use has been strongly intensified in the productive mesic grasslands and completely abandoned in the unproductive wet grasslands (cf. Section 2.1).

Our study has shown that grasslands with low land-use intensity are of prime importance for the conservation of species-rich Orthoptera assemblages. Besides their outstanding conservation value, which has also been acknowledged for other taxa (e.g. birds; Fumy and Fartmann, 2021), these heterogeneous habitats are more resilient against the negative effects of climate warming (Fumy et al., 2020).

Due to their topographic diversity, land-use intensification is unlikely for most of the dry grasslands. However, in the future, abandonment may become a threat. Accordingly, we recommend a conservation policy that secures the maintenance of low-intensity land use, in particular grazing in the dry grasslands. In mesic grasslands, management should aim at a reduction of land-use intensity and creation of more heterogeneous swards. Suitable measures are: omitting the application of liquid manure and chemical fertilizers, reducing pasture stocking rates, not exceeding more than two cuts per year on meadows and leaving annually about 10% of the meadow area uncut in a rotational manner (Buri et al., 2013; Humbert et al., 2012). For wet grasslands and their specific Orthoptera assemblages, we recommend the reintroduction of at least irregular low-intensity management. Both grazing and mowing are possible management alternatives. Additionally, special attention has to be payed to an intact hydrology in the wet grasslands.

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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.

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Appendix A

Table A1
Frequency (mean ± SE) of Orthoptera species in the three studied grassland types and their threat status. Differences were tested using Kruskal–Wallis' *H test and Dunn's post-hoc test. Significantly differing groups are indicated with the individual letters a, b and c. n.s. not significant, *P < 0.05.*

Species	Threat status	Grassland type		
		Dry	Mesic	Wet
Bicolorana bicolor	✓	27.6 ± 8.4	0.0 ± 0.0	0.0 ± 0.0
Calliptamus italicus	✓	0.0 ± 0.0	0.0 ± 0.0	3.4 ± 3.4
Chorthippus biguttulus	·	100 ± 0.0	100 ± 0.0	44.8 ± 9.4
Chorthippus brunneus	·	51.7 ± 9.4	24.1 ± 8.1	27.6 ± 8.4
Chrysochraon dispar	·	31 ± 8.7	62.1 ± 9.2	79.3 ± 7.7
Conocephalus fuscus	·	0.0 ± 0.0	17.2 ± 7.1	27.6 ± 8.4
Decticus verrucivorus	✓	75.9 ± 8.1	24.1 ± 8.1	17.2 ± 7.1
Euthystira brachyptera	✓	79.3 ± 7.7	65.5 ± 9.0	55.2 ± 9.4
Gomphocerippus rufus	·	75.9 ± 8.1	69 ± 8.7	17.2 ± 7.1
Gryllus campestris	·	82.8 ± 7.1	44.8 ± 9.4	3.4 ± 3.4
Mecostethus parapleurus	·	13.8 ± 6.5	13.8 ± 6.5	13.8 ± 6.5
Metrioptera brachyptera	✓	27.6 ± 8.4	17.2 ± 7.1	86.2 ± 6.5
Miramella alpina	✓	0.0 ± 0.0	10.3 ± 5.8	20.7 ± 7.7
Myrmeleotettix maculatus	✓	31.0 ± 8.7	3.4 ± 3.4	3.4 ± 3.4
Nemobius sylvestris	·	13.8 ± 6.5	10.3 ± 5.8	0.0 ± 0.0
Omocestus rufipes	✓	10.3 ± 5.8	0.0 ± 0.0	0.0 ± 0.0
Omocestus viridulus	✓	44.8 ± 9.4	48.3 ± 9.4	48.3 ± 9.4
Pholidoptera griseoaptera	·	13.8 ± 6.5	20.7 ± 7.7	3.4 ± 3.4
Platycleis albopunctata	✓	10.3 ± 5.8	0.0 ± 0.0	0.0 ± 0.0
Pseudochorthippus montanus	✓	3.4 ± 3.4	31.0 ± 8.7	86.2 ± 6.5
Pseudochorthippus parallelus	·	96.6 ± 3.4	93.1 ± 4.8	20.7 ± 7.7
Psophus stridulus	✓	13.8 ± 6.5	0.0 ± 0.0	0.0 ± 0.0
Roeseliana roeselii	·	89.7 ± 5.8	86.2 ± 6.5	79.3 ± 7.7
Stauroderus scalaris	✓	55.2 ± 9.4	24.1 ± 8.1	17.2 ± 7.1
Stenobothrus lineatus	✓	93.1 ± 4.8	62.1 ± 9.2	20.7 ± 7.7
Stenobothrus stigmaticus	✓	72.4 ± 8.4	27.6 ± 8.4	6.9 ± 4.8
Stethophyma grossum	·	0.0 ± 0.0	10.3 ± 5.8	34.5 ± 9
Tetrix bipunctata	✓	24.1 ± 8.1	13.8 ± 6.5	3.4 ± 3.4
Tetrix subulata	✓	0.0 ± 0.0	3.4 ± 3.4	3.4 ± 3.4
Tetrix tenuicornis	✓	6.9 ± 4.8	3.4 ± 3.4	0.0 ± 0.0
Tetrix undulata	·	17.2 ± 7.1	6.9 ± 4.8	0.0 ± 0.0
Tettigonia cantans	✓	44.8 ± 9.4	58.6 ± 9.3	62.1 ± 9.2

Source threat status: Detzel (2020).

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