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Effects of landscape and habitat quality on Orthoptera assemblages of pre-alpine calcareous grasslands

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ABSTRACT

Due to the transition from traditional land use to modern agriculture throughout Europe, semi-natural grasslands are subject to severe environmental changes. Both agricultural intensification and abandonment have caused degradation, loss and fragmentation of semi-natural grasslands with adverse effects on biodiversity.

We analysed the effects of landscape and habitat quality on Orthoptera in pre-alpine calcareous grasslands of the Northern Limestone Alps. At the landscape level, we focused on the effects of functional connectivity, patch size and habitat heterogeneity on Orthoptera species richness of 13 randomly selected grassland patches. At the habitat level, we studied the effects of land use on vegetation structure and microclimate as well as on Orthoptera species richness and abundance on 50 randomly chosen plots within these patches.

At the landscape level, the number of Orthoptera species in well-connected pre-alpine calcareous grasslands increased with habitat heterogeneity, which was inter-related with patch size. Functional connectivity, however, had no effect on species richness. At the habitat level, species richness and abundance of Orthoptera were driven by land use together with vegetation structure and microclimate. In general, the explanatory power of our abundance models was at least twice as high as those of the species richness models. Based on the results of our study, conservation management of grassland Orthoptera should primarily focus on improving habitat heterogeneity and habitat quality within patches.

1. Introduction

For many centuries, traditional land-use practices contributed to the development of semi-natural ecosystems harbouring an outstanding species richness (Plieninger et al., 2006; Uchida et al., 2016). However, with the massive increase in man-made habitat alterations since the industrial era, a substantial loss in wild biota has occurred. The global rate of species extinction has now reached an unprecedented extent, exceeding the limits of our planet (Rockström et al., 2009). Consequently, many scientists argue that we are heading for the sixth global extinction crisis (Chapin et al., 2000; De Vos et al., 2014). In terrestrial ecosystems, land-use change has been identified as the most important driver of this alarming development (Sala et al., 2000).

In Europe, grasslands are among the dominant ecosystems and represent almost 25% of the land surface (EEA, 2005). The vast majority of these grasslands are the result of human cultivation from the arrival of the first Neolithic farmers onwards (Veen et al., 2009). To date, many of these semi-natural habitats have been important refuges for threatened and specialized species (Poschlod and WallisDeVries, 2002; Veen et al., 2009). Especially nutrient-poor grasslands, such as calcareous grasslands, rank among the most species-rich habitats throughout Europe (Poschlod and WallisDeVries, 2002; van Swaay, 2002). Therefore, they are protected under the European Habitats Directive (EC, 2007).

However, due to the ongoing transition from traditional land use to modern agriculture, these grasslands are still subject to severe environmental changes (Poschlod and WallisDeVries, 2002). This development mainly entails two contrasting processes: (i) intensification on productive sites and (ii) abandonment of marginal land (Henle et al., 2008; Kleijn et al., 2009). Both agricultural intensification and abandonment have caused degradation, loss and fragmentation of semi-natural grasslands and usually have adverse effects on biodiversity (Uchida and Ushimaru, 2014). Whereas the intensive exploitation of agricultural land is mainly restricted to lowlands, mountain areas are more frequently influenced by the abandonment of semi-natural grasslands (Caraveli, 2000; MacDonald et al., 2000). Severe losses of habitat and species diversity due to abandonment of traditional land use have been reported for most European mountain ranges (e.g.

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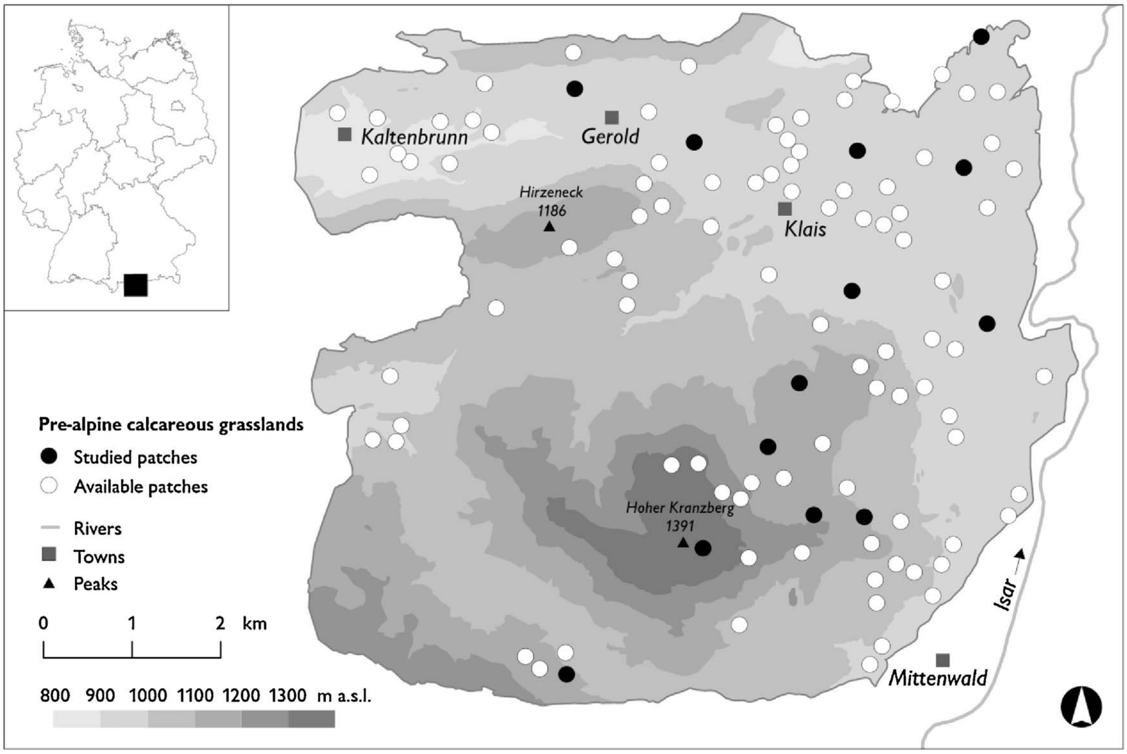

Fig. 1. Location of the study area in Germany (inlay), and the sampling design of the studied patches ($n = 13$) and all available patches in the study area.

MacDonald et al., 2000 Lasanta Martinez et al., 2005). However, in many mountain regions, large, semi-natural grasslands with a high biodiversity remain. This also applies to our study area in the Northern Limestone Alps, which is one of the few German biodiversity hotspots (Ackermann and Sachteleben, 2012).

Orthoptera are excellent model organisms to study the effects of environmental change in grasslands (Bazelet and Samways, 2011; Fartmann et al., 2012; Poniatowski et al., 2016). Connectivity, patch size and habitat quality are usually considered as the main drivers of biodiversity in fragmented landscapes (Fahrig, 2003; Krauss et al., 2010; Krämer et al., 2012). However, in Orthoptera, the latter is of prime importance (Marini et al., 2009; Poniatowski and Fartmann, 2010). Habitat quality in Orthoptera is determined by a complex and often interrelated combination of vegetation structure (Poniatowski and Fartmann, 2008; Fartmann et al., 2012) and microclimate (Gardiner and Dover, 2008). Both vegetation structure and microclimate strongly depend on land use (O'Neill et al., 2003; Fartmann et al., 2012). Whereas the negative impacts of grassland intensification on Orthoptera have been repeatedly verified (Kruess and Tscharntke, 2002; Marini et al., 2008; Uchida and Ushimaru, 2014), less attention has been paid to the effects of grassland abandonment (but see Marini et al., 2009; Fartmann et al., 2012).

Several studies showed the importance of habitat heterogeneity for Orthoptera in grassland ecosystems (Kruess and Tscharntke, 2003; Joern, 2005; Schouten et al., 2007). However, there have been only few studies that focused on the effects of habitat connectivity on Orthoptera (Poniatowski and Fartmann, 2010; Torma et al., 2014; Uchida and Ushimaru, 2014). More recent concepts dealing with the effect of functional connectivity have only been applied for single species (Keller et al., 2013; Poniatowski et al., 2016). However, this approach might yield a better understanding of the metapopulation ecology of Orthoptera, as it considers the composition of the landscape matrix (cf. Adriaensen et al., 2003; Poniatowski et al., 2016). In agreement with this assumption, evidence for the importance of landscape quality was found for specialized species, as the matrix may act as a corridor or movement barrier (Keller et al., 2013; Poniatowski et al., 2016). Thus, there is an urgent need to apply this approach for Orthoptera communities, in order to gain new insights for Orthoptera conservation in fragmented landscapes.

In this study, we analysed the effects of landscape and habitat quality on Orthoptera in pre-alpine calcareous grasslands of the Northern Limestone Alps. At the landscape level, we focused on the effects of functional connectivity, patch size and habitat heterogeneity on Orthoptera species richness of 13 randomly selected grassland patches. At the habitat level, we studied the effects of land use on vegetation structure and microclimate as well as on Orthoptera species richness and abundance on 50 randomly chosen plots within these patches. Non-threatened and threatened species were analysed separately in order to give recommendations for a sustainable habitat management of the grasslands.

The hypotheses of our study are the following:

(i) Habitat heterogeneity is an important driver of Orthoptera species richness at the landscape level, whereas functional connectivity plays a minor role.
(ii) Species richness and abundance of Orthoptera are strongly determined by habitat quality.
(iii) Habitat quality in Orthoptera is particularly driven by land use.
(iv) The maintenance of grassland Orthoptera assemblages with high species richness and abundance depends on low-intensity land use.

2. Material and methods

2.1. Study area

The study area is located in the Northern Limestone Alps, approximately 100 km south of Munich (47°26′N, 11°10′E and 47°30′N,11°17′E) at an elevation of 800–1350 m a.s.l. (Fig. 1). The climate in the study area is generally cool and wet with an annual mean temperature of 6.7 °C and an annual precipitation of 1437 mm (DWD, 2016). The study was carried out on pre-alpine calcareous grasslands – the so-called 'hummocky meadows' (in German, known as

"Buckelwiesen") around Mittenwald. This unique calcareous grassland type is characterized by a pit and mound microrelief of glacial origin: a geomorphological peculiarity, also known for its great species richness (Gutser and Kuhn, 1998a). However, the area size of this vegetation type in the Alps has declined by more than 95% over the last century (Gutser and Kuhn, 1998a). This dramatic loss was mainly caused by land-use intensification (flattening and fertilization), abandonment and afforestation. Despite this decline, the 'hummocky meadows' cover currently more than a quarter of the open landscape in the study area. These remnants have a patchy distribution and are isolated from each other by matrix biotopes such as forests or improved grassland (Krämer et al., 2012). However, the patches are well-connected, as the average distance from a habitat patch to the next three available patches usually does not exceed 500 m. The study area contains the most important remnants of 'hummocky meadows' in Central Europe (Gutser and Kuhn, 1998a) and belongs to one of the German biodiversity hotspots (Ackermann and Sachteleben, 2012). Consequently, large parts are now protected as EU Natura 2000 sites (EEA, 2017).

2.2. *Experimental design*

In August 2011, we studied 13 randomly selected calcareous grassland patches. Patches were regarded as discrete when they were isolated from the nearest neighbouring calcareous grassland patch by more than 50 m of non-habitat matrix (Poniatowski et al., 2016). Patch size ranged from 1.2 to 47.8 ha.

According to Fartmann et al. (2012), each patch was divided into sections with homogenous vegetation structure (cf. Krebs, 1999). Within these homogenous sections, 50 plots were randomly selected (stratified random sampling). To avoid edge effects (Schirmel et al., 2010), the size of each plot was at least 500 m^2 and Orthoptera species richness and abundance (cf. Section 2.2.1) were recorded in the centre of the plot. The plots belonged to the following three land-use types: abandoned ($n = 17$), mowing ($n = 20$) and grazing ($n = 13$). Abandoned plots were young fallow grasslands that had been established on former meadows. This land-use type included young fallows (< 10 years of abandonment) and irregularly managed grasslands that are mown every 3–5 years. In contrast, old fallows (> 10 years) or afforested grasslands were excluded. Mown plots were grasslands, which are traditionally mown by scythe once per year. Traditional mowing of these meadows dates back to 1406 and has been practiced for centuries without any fertilization (Gutser and Kuhn, 1998a). Due to the long continuity of land use and only low atmospheric nitrogen deposition in the study area (~ 12 kg ha^{-1} a^{-1}; UBA, 2016), nutrient-poor grasslands with an extremely short sward developed (Gutser and Kuhn, 1998a). Mowing usually takes place in August and is practiced in a mosaic-like pattern on a small spatial scale. Orthoptera sampling (see below) in these meadows took place before the mowing event. Grazed plots were formerly abandoned grasslands in which grazing by goats and sheep had been introduced at least 5 years before the study in order to prevent succession. However, land-use intensity was compared with mown grasslands, as grazed plots were generally used as paddocks, which were grazed up to three times a year. Furthermore, grazing usually started early in the season (from May/June) and was carried out for several weeks with stock densities of > 10 goats or sheep per ha (Gutser and Kuhn, 1998a; Kraus pers. comm.).

2.2.1. *Orthoptera sampling*

Each of the 13 patches and all habitat structures (=sections with homogenous vegetation structure, cf. Section 2.2) within each patch were surveyed for Orthoptera under favourable weather conditions (temperature > 15 °C, cloud cover $< 50\%$) during 1 h between 10 am and 5 pm using acoustic and visual search as well as sweep-netting. Arbusticolous and arboricolous species that occasionally occur in grasslands and *Gryllus campestris* that lives in burrows in the ground were excluded from further analyses as our sampling techniques do not produce reliable data for these species. Species identification was performed in the field, mainly by sound according to Bellmann (2004) and by morphological characteristics using Bellmann (2006). Following determination, all individuals were released. The occurrence of quiet or high-frequency stridulating species, such as *Metrioptera brachyptera*, was assessed using a bat detector (Fischer et al., 2016).

On the plot level, Orthoptera species richness and abundance were recorded using a box quadrat ($0.71\ m \times 0.71\ m \triangleq 0.5\ m^2$), which ranks among the best sampling methods to ascertain Orthoptera diversity and abundance (Gardiner and Hill, 2006). The box quadrat was randomly dropped at 40 different points per plot covering an area of 20 m^2 per plot. The scientific nomenclature of the species follows Fischer et al. (2016).

2.2.2. *Landscape parameters*

We recorded landscape parameters based on aerial photographs and land-use data from the real estate cadastre system (ALKIS). All biotopes within the study area were classified in three categories as habitat (calcareous grasslands), low-growing non-habitats (e.g. mesic grassland) and high-growing non-habitats (e.g. forest) at a scale of 1:5000 (cf. Krämer et al., 2012; Poniatowski et al., 2016). Patch size, habitat heterogeneity and functional connectivity were calculated for each focal patch. Patch size was calculated using the calculate-area tool in ArcGIS 10.0. For each studied patch, we calculated a habitat-heterogeneity score. Therefore, we detected the number of land-use types (abandoned, mowing, grazing) and aspect categories (N, E, S, W) as well as the elevational variation within a patch. The final score was built by adding up the scores for the number of different land-use types (score: 1–3), aspect categories (score: 1–4) and elevational variation (one score per 50-m step).

Functional connectivity was defined using Hanski's index (Hanski, 1999) modified according to Moilanen and Nieminen (2002):

$$I_i = \sum_{i \neq j} \exp(-\alpha \cdot d_{ij}) \cdot A_j^b,$$

where A_j is the size (in m^2) of the neighbouring habitat patch and d_{ij} is the functional distance between the neighbouring patch j and the studied patch i. For each studied patch, the functional distances to all neighbouring patches within a radius of 2 km were calculated. The functional distances were based on least-cost modelling using the cost-distance tool in ArcGIS 10.0 (Adriaensen et al., 2003; Krämer et al., 2012). They were calculated by defining the influence of the biotope types of the matrix elements on Orthoptera movement. We therefore allocated lower resistance values (RV) to matrix biotope types that favour movement than to those that limit movement of Orthoptera. As a simple classification of biotopes provided the best results for Orthoptera (Poniatowski et al., 2016), we also used this approach, which distinguished between three matrix categories: (i) habitat (RV: 1); (ii) low-growing non-habitats (RV: 4); (iii) high-growing non-habitats (RV: 8). For the scaling parameter b, we chose $b = 0.5$, as the ratio of patch edge to patch size decreases with $A^{0.5}$ when the patch size increases (Moilanen and Nieminen, 2002). The parameter α is scaling the effect of distance to Orthoptera migration ($1/\alpha$ is the average migration distance of Orthoptera). According to Poniatowski et al. (2016), the average migration distance for Orthoptera was set to $1/\alpha = 0.5$ km. Larger values of the connectivity index I indicate better connectivity of a patch than smaller values.

2.2.3. *Habitat-quality parameters*

We recorded vegetation-structure and microclimate parameters. In the field, we noted land-use type of the plots. On each study plot, we ascertained environmental parameters in a randomly selected undisturbed part of the plot with a size of 3 m × 3 m (Table 1). We recorded the following parameters of horizontal vegetation structure (in 5% steps): cover of total vegetation, shrub layer, field layer, litter layer, moss layer, bare ground, herbs and grasses. In cases where cover was

Table 1
Overview of all sampled parameters and their statistical analysis. GLM = generalized linear model, GLMM = generalized linear mixed-effects model, ISA = indicator species analysis, NMDS = non-metrical multidimensional scaling, RM ANOVA = repeated measures ANOVA.

Sampled parameter	**Correlation**			**Scale levels**	**Statistics**
	r_s	**Summarized variable**			
Response					
No. species[1]				metric	GLM, GLMM
Abundance[1]				metric	GLM, GLMM, NMDS, ISA
Predictor variables					
(a) Landscape level					
Patch size (m²)[2]	0.74	▶	Habitat heterogeneity	metric	GLM
Habitat heterogeneity[2]	1.00			metric	GLM
Functional connectivity[3]				metric	GLM
(b) Habitat level					
Microclimate					
Temperature (°C)				metric	RM ANOVA
Humidity (%)				metric	RM ANOVA
Aspect (°)[4]		▶	Heat load	metric	GLMM, NMDS
Slope (°)[4]					
Land use					
Land-use type[5]				categorial	GLMM, ISA
Vegetation structure					
Cover (%)					
Total vegetation[6]	0.66	▶	Horizontal vegetation	metric	GLMM, NMDS
Bare-ground layer[6]	–0.54			metric	GLMM, NMDS
Field layer[6]	0.58			metric	GLMM, NMDS
Grasses[7]	0.59	▶	Grass-herb ratio	metric	GLMM, NMDS
Herbs[7]	–0.72			metric	GLMM, NMDS
Mosses				metric	GLMM
Shrub layer				metric	GLMM
Litter layer[8]	0.81	▶	Vertical vegetation	metric	GLMM, NMDS
Vegetation density (%)[8]	0.95			metric	GLMM, NMDS
Vegetation height (cm)[8]	0.90			metric	GLMM, NMDS

[1] Three response variables: all species, threatened species (BayLfU, 2016) and non-threatened species (BayLfU, 2016).
[2] Due to inter-correlations (r_s = 0.74, $P < 0.01$) between patch size and habitat heterogeneity we used habitat heterogeneity for further analyses.
[3] Simple approach according to Poniatowski et al. (2016).
[4] Slope and aspect were used to calculate the heat load (cf. McCune and Keon, 2002).
[5] Three categories: abandoned (ABA), mowing (MOW) and grazing (GRA).
[6] Variables were summarized to a new variable 'horizontal vegetation' (explained variance: 68.3).
[7] Variables were summarized to a new variable 'grass-herb ratio' (explained variance: 88.8).
[8] Variables were summarized to a new variable 'vertical vegetation' (explained variance: 80.6).

above 95% or below 5%, 2.5% steps were used. Furthermore, vertical vegetation structure was ascertained by measuring vegetation height and vegetation density. The average vegetation height was measured at an accuracy of 2.5 cm. We used a wire-framed box (50 cm × 30 cm × 30 cm), which was open on all sides except the front, to estimate vegetation density. The front of the box was horizontally divided into six height layers of 5 cm each to estimate the vegetation density between 0 and 30 cm above ground. The cover of each layer was viewed horizontally against the bright back of the box, using the same classes as for the horizontal structure (Poniatowski and Fartmann, 2008; Fartmann et al., 2012). For further analyses, the cover of the six layers was averaged. Microclimate measurements took place

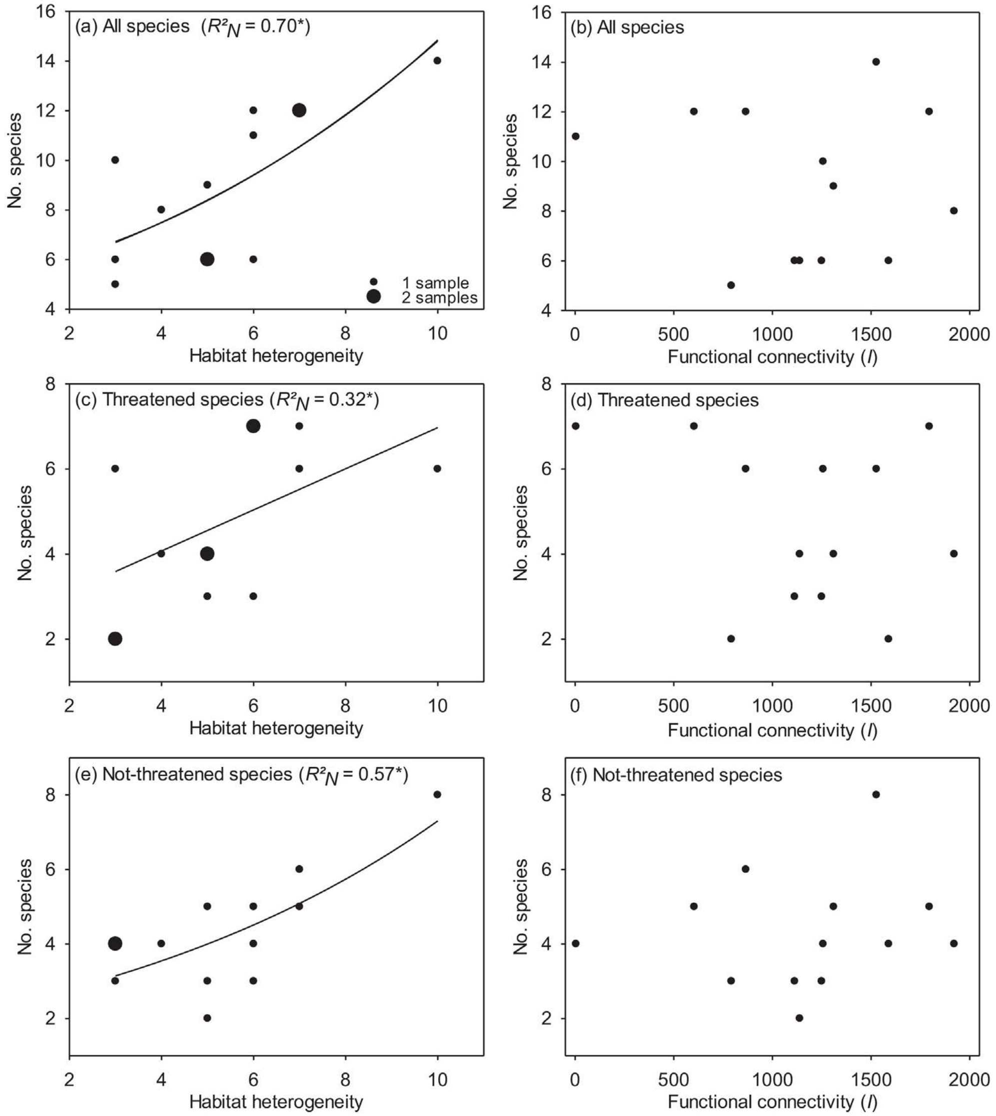

Fig. 2. Relationship between the number of all (a, b), threatened (c, d) and non-threatened species (e, f) and predictor variables assessed in multivariate landscape GLM (Table 1). The significances and model accuracy presented in the figures were tested using univariate GLM with Poisson error structure (n = 13). Significance levels are indicated as follows: * $P < 0.05$. (a) $y = f(x) = \exp(0.11 \times 1.56)$; (c) $y = f(x) = 0.54 \times 1.77$; (e) $y = f(x) = \exp(0.12 \times 0.78)$, (b) $P = 0.76$, (d) $P = 0.38$, (f) $P = 0.70$.

at 15 randomly selected plots representing all three land-use types with equal sample sizes (n = 5). Data loggers for temperature and humidity (Fourier Systems Microlog PRO®) were placed 10 cm above ground and protected by a radiation shield. Data were recorded hourly from 30 July to 05 August 2011. Furthermore, we recorded aspect (°) and slope (°) using a compass with an inclinometer. Together with the latitude of the study area (47.3° N), slope and aspect served to calculate the heat load (McCune and Keon, 2002).

2.3. Statistical analysis

To assess the factors that explain the diversity and abundance of Orthoptera, we conducted analyses at the landscape (patches) and habitat levels (plots). Landscape-level analyses were performed using generalized linear models (GLM) with a Poisson error structure and patch size, habitat heterogeneity and functional connectivity as predictors for species numbers. The number of all, threatened and non-threatened species were analysed separately. The threat status of Orthoptera species was gathered from BayLfU (2016). To account for possible spatial autocorrelations, we calculated Moran's I statistic for each of the response variables using ArcGIS 10.0 (Getis and Ord, 1992). As we did not detect significant spatial autocorrelations for any of the response variables, the patches were considered as independent samples in the landscape-level analyses.

In order to detect habitat-quality parameters that explain species numbers and abundance of Orthoptera (all species, threatened species, non-threatened species) at the plot level, generalized linear mixed-effects models (GLMM) with several environmental parameters (Table 1) as predictors were calculated (Crawley, 2007). The variable *patch* was set as a random factor in each GLMM. Stepwise-backward selection was used to remove non-significant predictor variables using the *step-function* in GLM and *drop1-function* in GLMM. The best models were assessed using Akaike's Information Criterion (AIC) (Zuur et al., 2009). Furthermore, we conducted univariate GLMM with a Gaussian error structure and *patch* as a random factor in order to detect significant differences in species number and abundance of Orthoptera, as well as for the abundance of each single species between the land-use types. The comparison of environmental parameters was done in the same way. Repeated-measures ANOVA with Tukey's post hoc test was used to detect land-use specific differences in temperature and relative humidity. Prior to the analysis, we calculated the hourly mean of the measured values for all plots within the respective land-use type. Afterwards, the hourly averaged values were treated as chronologically paired samples.

In order to define indicator species for the land-use types, we carried out an indicator species analysis (ISA) using *indicspecies* (De Cáceres et al., 2012). The assemblage structure of Orthoptera was analysed using non-metric multidimensional scaling (NMDS; Oksanen et al., 2016). NMDS ordination was based on three dimensions using Manhattan distance and 100 random starts in the search for stable solutions. Rare species with a frequency of < 5% were excluded from the NMDS.

To avoid multi-collinearity, some variables were summarized prior to GLM, GLMM and NMDS analyses using Principal Component Analysis (PCA) (Table 1, cf. Dormann et al., 2012; Helbing et al., 2014). Statistical analyses were performed using R 3.2.5, SigmaPlot 12.5 and SPSS statistical packages.

3. Results

In total, we recorded 19 Orthoptera species, 13 Caelifera and 6 Ensifera, at the 13 calcareous grassland patches (Table A1). Ten of these species are considered threatened in Bavaria. The most widespread one at the patch level was the non-threatened species, *Pseudochorthippus parallelus*, occurring on all patches. The two non-threatened species, *Chorthippus biguttulus* and *Euthystira brachyptera,* together with the two threatened species, *Decticus verrucivorous* and *Metrioptera brachyptera,* were found on 85% of the patches.

At the habitat level, the two non-threatened species, *Euthystira brachyptera* and *Pseudochorthippus parallelus,* were the most common ones, with a frequency of 96% and 94%, respectively. The species with the next highest frequency were the threatened species, *Decticus verrucivorus*, *Metrioptera brachyptera* and *Stenobothrus lineatus,* being found on 64%–82% of the plots.

3.1. Landscape effects

Orthoptera species richness of all, threatened and non-threatened species significantly increased with habitat heterogeneity, which was inter-related to patch size (Fig. 2, Table 1). Functional connectivity, however, had no effect on species richness (Fig. 2).

3.2. Habitat-quality effects

3.2.1. Land-use and environmental conditions

Land-use significantly affected most vegetation characteristics and the microclimate of pre-alpine calcareous grasslands (Table 2, Fig. 3). Except for the cover of the moss layer, all sampled vegetation parameters differed significantly between land-use types (Table 2). Abandoned plots were characterized by a higher grass cover and vegetation density than plots of the two other land-use types. Abandoned and mown plots had a higher total-vegetation and field-layer cover than grazed plots. The cover of shrubs and litter together with vegetation height, decreased in the order: abandoned > grazed > mown plots. In contrast, the cover of herbs peaked in mown plots and the cover of bare ground in grazed plots differing from those of the other land-use types.

Table 2

Differences (mean ± SE) of environmental parameters between the land-use types: ABA = abandoned (n = 17); MOW = mowing (n = 20); GRA = grazing (n = 13). Significant differences were calculated using GLMM with a Gaussian error structure and *patch* as a random factor (n = 50). Different letters indicate significant differences between the treatments. Significances are indicated as follows: n.s. not significant, ** $P < 0.01$, *** $P < 0.001$.

Parameter	ABA	MOW	GRA	P
Heat load	0.80 ± 0.0	0.81 ± 0.0	0.82 ± 0.0	n.s.
Cover of total vegetation (%)	96.9 ± 0.9^a	97.0 ± 0.5^a	92.3 ± 1.8^b	**
Cover of shrubs (%)	6.2 ± 1.2^a	0.6 ± 0.3^b	1.9 ± 0.8^c	***
Cover of field layer (%)	95.0 ± 0.8^a	96.1 ± 0.7^a	84.2 ± 4.4^b	***
Cover of grasses (%)	77.1 ± 3.8^a	51.0 ± 2.8^b	56.9 ± 5.8^b	***
Cover of herbs (%)	22.1 ± 3.5^a	49.3 ± 3.3^b	28.8 ± 4.2^a	***
Cover of moss layer (%)	17.1 ± 3.4	12.4 ± 2.8	22.5 ± 4.9	n.s.
Cover of litter layer (%)	70.1 ± 5.1^a	3.5 ± 0.9^b	18.3 ± 3.4^c	***
Cover of bare ground (%)	1.4 ± 0.4^a	2.5 ± 0.4^b	6.0 ± 1.5^c	***
Vegetation density 0–30 cm (%)	63.2 ± 3.0^a	41.1 ± 3.7^b	35.4 ± 2.4^b	***
Vegetation height (cm)	37.1 ± 2.6^a	20.5 ± 1.5^b	24.2 ± 1.8^c	***

Although the heat load did not differ among land-use types (Table 2), both temperature and humidity differed significantly (Fig. 3). During the day, temperature decreased in the order: mown > grazed > abandoned plots. At night, temperatures were higher on mown and grazed plots compared with abandoned plots. In contrast, humidity only differed during the day and decreased in the following order: abandoned > mown > grazed plots.

3.2.2. Orthoptera assemblages and environmental conditions

The number and abundance of all, threatened and non-threatened Orthoptera species were significantly affected by land use (Fig. 4). Species richness was highest on abandoned plots, differing from that on grazed plots. Mown plots had an intermediate position, however, species richness did not differ from those of the two other land-use types. The pattern for Orthoptera abundance was similar. Abundance decreased in all three groups (all, threatened and non-threatened Orthoptera species) in the following order: abandoned > mown > grazed plots. For all and non-threatened species, abundance differed between abandoned plots and the two other land-use types, and for threatened species, among all three land-use types.

Species richness was best explained by horizontal and vertical vegetation (Table 3). The number of all species significantly increased with increasing vertical vegetation and decreasing horizontal vegetation. Horizontal vegetation also had a significantly negative effect on species richness of threatened species, and vertical vegetation also had a significantly positive effect on species richness of non-threatened species.

For Orthoptera abundance, besides horizontal and vertical vegetation, further predictors contributed to the models (Table 4). The predictors of abundance of all and non-threatened species were identical. Vertical vegetation and shrub cover had a significantly positive, horizontal vegetation, and the grass-herb ratio a significantly negative effect on abundance. In contrast, the abundance of threatened species decreased significantly with horizontal vegetation and the grass-herb ratio. In general, the explanatory power of the abundance models (Nagelkerke'sR^2 [R_N^2] = 0.18–0.36) was always at least twice as high as those of the species-richness models (R_N^2 = 0.10–0.18) (Tables 3 and 4).

NMDS ordination (stress: 16.1, three dimensions) showed a clear separation of Orthoptera species and land-use types along the first axis (Fig. 5). Two of the nine environmental variables contributed significantly to the ordination model. The variation in species composition was mainly determined by one environmental gradient, representing a vertical vegetation and grass-herb ratio gradient. Vegetation height, vegetation density, the cover of litter summarized in the variable vertical vegetation and the grass-herb ratio were highly positively correlated with the first axis. Mown plots were negatively and abandoned plots positively associated with this axis. Grazed plots had an intermediate position.

The ISA supports the findings of the NMDS and identified seven Orthoptera as indicator species for a certain land-use type (Table 5). Especially abandoned grasslands were rich in indicator species. *Chorthippus dorsatus*, *Euthystira brachyptera*, *Metrioptera brachyptera*, *Omocestus viridulus* and *Pholidoptera aptera* were characteristic forthis land-use type. The two indicator species of mown grasslands were *Chorthippus biguttulus* and *Stenobothrus lineatus*. In contrast, grazed plots had no indicator species.

4. Discussion

This study showed, at the landscape level, that the number of Orthoptera species in well-connected pre-alpine calcareous grasslands increased with habitat heterogeneity, which was inter-related to patch size. Functional connectivity, however, had no effect on species richness. At the habitat level, species richness and abundance of Orthoptera

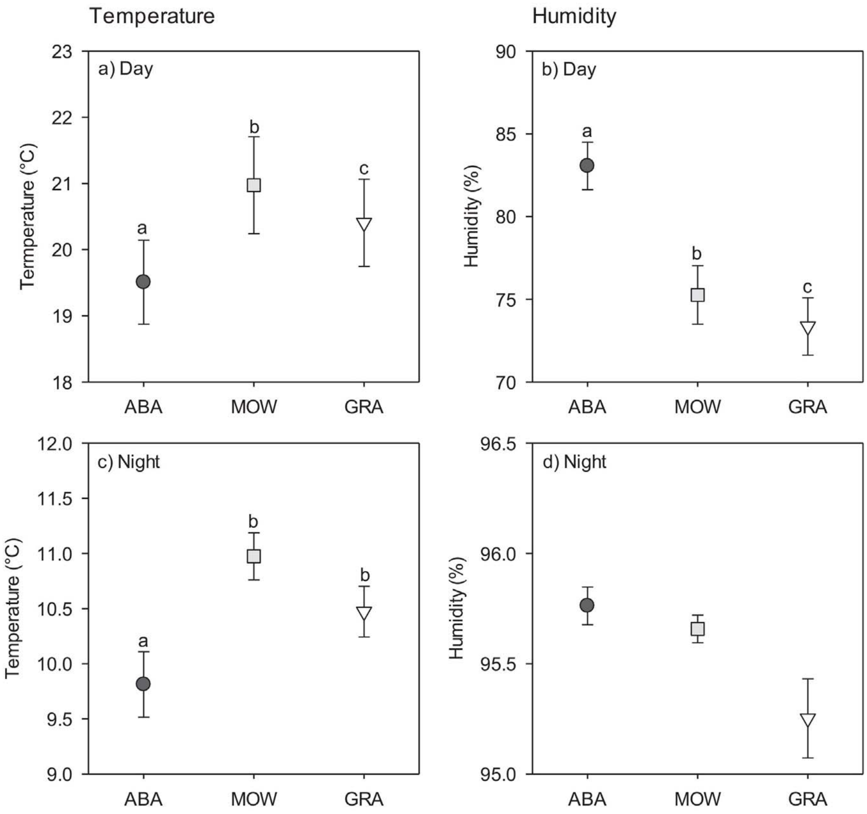

Fig. 3. Differences in hourly mean (± SE) (a, c) temperature and (b, d) humidity during the day and night between land-use types. ABA = abandoned ($n = 5$), MOW = mowing ($n = 5$), GRA = grazing ($n = 5$); day = 8 a.m.–10 p.m., night = 10 pm–8 am. Comparisons were carried out using repeated-measures ANOVA. Statistics: temperature day: $Chi^2 = 67.4$, $P < 0.001$; night: $Chi^2 = 76.1$, $P < 0.001$; humidity day: $Chi^2 = 107.2$, $P < 0.001$; night: $Chi^2 = 1.8$, $P = 0.41$. Different letters indicate significant differences between the groups (Tukey's post hoc test, $P < 0.05$).

were driven by land use and its influence on vegetation structure and microclimate. In general, the explanatory power of our abundance models was at least twice as high as those of the species richness models.

A strong relationship between Orthoptera species richness and patch size has already been reported in some studies (Wettstein and Schmid, 1999; Poniatowski and Fartmann, 2010). Usually, this positive species-area relationship is mainly due to increased habitat heterogeneity in larger patches, favouring the coexistence of species with contrasting habitat requirements (Joern, 2005; Schouten et al., 2007; Eckert et al., 2017). However, in some Orthoptera species, the existence of different microhabitats in close proximity within a habitat patch is even a prerequisite for its occurrence as each life-cycle stage requires different environmental conditions (Schirmel et al., 2010; Wünsch et al., 2012). A famous example of such microhabitat shifts during ontogenesis is the large-sized Ensifera, *Decticus verrucivorus*, which was a common species in the studied grassland patches. *Decticus verrucivorus* depends on bare ground for oviposition, sparsely vegetated microhabitats for its thermophilous nymphs and taller vegetation as shelter or song posts for the adults (Schirmel et al., 2010; Wünsch et al., 2012). Additionally, Schouten et al. (2007) showed that many Orthoptera species can persist even in small patches, if habitat heterogeneity is high enough. Consequently, we conclude that habitat heterogeneity plays a more important role than the mere patch size for Orthoptera diversity within habitat patches.

In contrast, functional connectivity did not affect Orthoptera diversity in our study. The few studies that revealed positive effects of connectivity on patch occupancy of Orthoptera were mostly conducted in highly fragmented landscapes (e.g. Keller et al., 2013; Poniatowski et al., 2016; Eckert et al., 2017). Our study area, however, was characterized by an outstandingly high density and proportion of calcareous grasslands (cf. Section 2.1; Krämer et al., 2012). Thus, we assume that in well-connected landscapes, habitat heterogeneity of the patches is generally the more important driver of species richness. This applies even more as most Orthoptera species are assumed to be less sensitive to habitat fragmentation than more mobile insect groups, such as butterflies (e.g. Krauss et al., 2010; Krämer et al., 2012), and can therefore persist for a long time in isolated habitats (Poniatowski et al., 2016).

To the best of our knowledge, our study is the first to use a connectivity measure based on functional distances (least-cost modelling, cf. Adriaensen et al., 2003) as a predictor of species richness of Orthoptera assemblages. Although our study failed to detect an effect of functional connectivity, we recommend testing this approach on Orthoptera assemblages of more fragmented landscapes. Indeed, Poniatowski et al. (2016) were already able to show an influence of functional connectivity on patch occupancy of single Orthoptera species in fragmented calcareous grasslands.

Habitat quality in Orthoptera is usually determined by land use (Marini et al., 2009; Fabriciusova et al., 2011), vegetation structure (Poniatowski and Fartmann, 2008; Fartmann et al., 2012) and the interrelated microclimate (Gardiner and Dover, 2008). In our study, land-use affected most vegetation characteristics and the microclimate of pre-alpine calcareous grasslands. Species richness and abundance of Orthoptera assemblages also differed among land-use types. Both Orthoptera diversity and abundance were highest in young fallows, followed by grasslands traditionally mown once a year. Several studies highlight the positive effect of traditional land-use practices on grassland Orthoptera (Joubert et al., 2016; Uchida et al., 2016). However, there are also some studies that show that young grassland fallows can also foster Orthoptera. Marini et al. (2009) detected a similar Orthoptera diversity in young abandoned compared to regularly managed grasslands and Smettan (1991) even found a slightly higher diversity in fallows.

The environmental conditions of the studied calcareous grasslands are unique. Intensive nutrient leaching due to a high precipitation and, additionally, centuries of nutrient removal by haymaking have resulted in extremely nutrient-poor grasslands with very short swards (mean height in our study: 21 cm) and a low succession speed (Gutser and Kuhn, 1998a; see also Section 2.2). Due to delayed succession, it takes longer periods for the negative effects of abandonment (litter

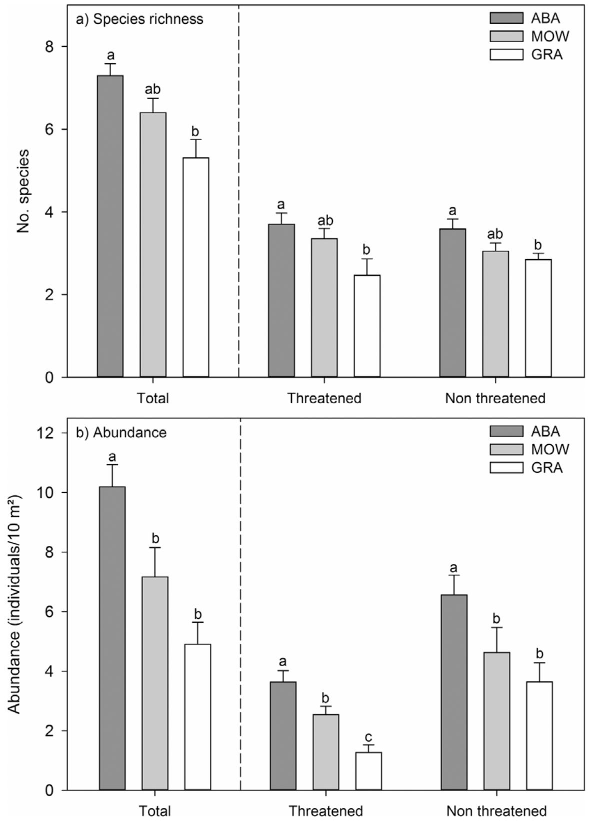

Fig. 4. Differences (mean ± SE) in (a) species richness and (b) abundance of all, threatened and non-threatened Orthoptera species between land-use types: ABA = abandoned ($n = 17$), MOW = mowing ($n = 20$), GRA = grazing ($n = 13$). Significant differences between the land-use types were calculated using GLMM with a Gaussian error structure (predictor land use) and *patch* as a random factor. Different letters indicate significant differences. Statistics: (a) all species: ABA vs. MOW: $t = 1.97$, $P = 0.06$; ABA vs. GRA: $t = 4.01$, $P < 0.001$; MOW vs. GRA: $t = 2.00$, $P = 0.06$; threatened species: ABA vs. MOW: $t = 0.99$, $P = 0.33$; ABA vs. GRA: $t = 2.77$, $P < 0.01$; MOW vs. GRA: $t = 2.03$, $P = 0.06$; non-threatened species: ABA vs. MOW: $t = 1.78$, $P = 0.09$; ABA vs. GRA: $t = 2.48$, $P < 0.05$; MOW vs. GRA: $t = 0.75$, $P = 0.46$; (b) all species: ABA vs. MOW: $t = 2.83$, $P < 0.01$; ABA vs. GRA: $t = 5.12$, $P < 0.001$; MOW vs. GRA: $t = 1.63$, P = 0.11; threatened species: ABA vs. MOW: t = 2.40, P < 0.05; ABA vs. GRA: t = 4.93, $P < 0.001$; MOW vs. GRA: $t = 3.20$, $P < 0.001$; non-threatened species: ABA vs. MOW: $t = 2.46$, $P < 0.05$; ABA vs. GRA: $t = 3.18$, $P < 0.01$; MOW vs. GRA: $t = 0.74$, $P = 0.46$.

Table 3
Relationship between the number of (a) all, (b) threatened and (c) non-threatened species and habitat-quality parameters. The significances and model accuracy were tested using multivariate GLMM with a Gaussian error structure and *patch* as a random factor ($n = 50$). Non-significant parameters were excluded by stepwise-backward selection. Significance levels are indicated as follows: n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Estimate	SE	*t*	*P*
a) All species ($R^2_N = 0.18$)				
(Intercept)	7.09	0.24	29.80	**
Vertical vegetation	0.50	0.20	2.46	*
Horizontal vegetation	−1.19	0.42	−2.85	**
b) Threatened species ($R^2_N = 0.10$)				
(Intercept)	3.71	0.19	19.19	***
Horizontal vegetation	−0.70	0.32	−2.20	*
c) Non-threatened species ($R^2_N = 0.10$)				
(Intercept)	3.27	0.15	21.92	***
Vertical vegetation	0.29	0.14	2.15	*

Table 4
Relationship between the abundance (individuals/10 m^2) of (a) all, (b) threatened and (c) non-threatened species and habitat-quality parameters. The significances and model accuracy were tested using multivariate GLMM with a Gaussian error structure and *patch* as random factor ($n = 50$). Non-significant parameters were excluded by stepwise-backward selection. Significance levels are indicated as follows: n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Parameter	Estimate	SE	*t*	*P*
a) All species ($R^2_N = 0.36$)				
(Intercept)	3.70	7.53	0.49	n.s.
Vertical vegetation	9.48	2.45	2.87	***
Horizontal vegetation	−5.20	2.14	−2.44	*
Grass-herb ratio	−9.27	3.45	−2.69	*
Cover of shrubs (%)	1.37	0.50	2.76	*
b) Threatened species ($R^2_N = 0.18$)				
(Intercept)	6.49	0.48	13.53	***
Horizontal vegetation	−1.98	0.82	−2.42	*
Grass-herb ratio	−1.19	0.40	−2.96	**
c) Non-threatened species ($R^2_N = 0.34$)				
(Intercept)	7.86	1.43	5.51	***
Vertical vegetation	9.09	2.11	4.30	***
Horizontal vegetation	−3.97	1.79	−2.22	*
Grass-herb ratio	−10.22	2.98	−3.43	**
Cover of shrubs (%)	1.41	0.43	3.27	**

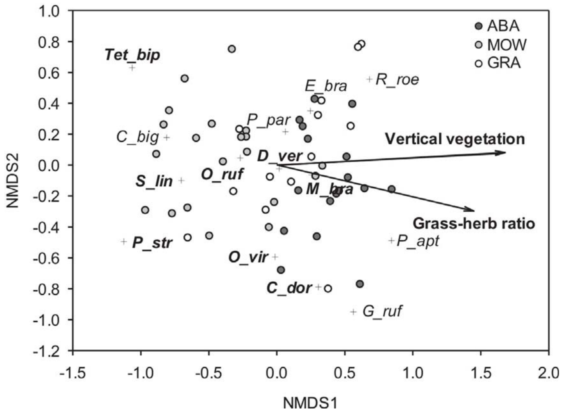

Fig. 5. NMDS plot (stress = 16.1, three dimensions, Manhattan distance, 1000 permutations, for details see Oksanen et al., 2016) based on the abundance of the most frequent Orthoptera species (frequency > 5%) and environmental parameters. Only significant parameters are shown: vertical vegetation ($P < 0.001$); grass-herb ratio ($P < 0.001$). ABA = abandoned ($n = 17$), MOW = mowing ($n = 20$), GRA = grazing ($n = 13$). For abbreviations of species see Appendix A, for abbreviations of environmental parameters see Table 1. Threatened species according to BayLfU (2016) are highlighted in bold type.

accumulation, adverse microclimate) (Fartmann and Mattes, 1997) to influence Orthoptera. Additionally, a taller and more dense vegetation due to abandonment of the originally very short swards provides more shelter against predators (Fartmann et al., 2012; Helbing et al., 2014) and offers further niches for species requiring such vegetation as the five indicator species of abandoned grasslands (*C. dorsatus*, *E. brachyptera*, *M. brachyptera*, *O. viridulus* and *P. aptera*) (Schlumprecht and Waeber, 2003). In line with this, an increase in vegetation height, vegetation density and litter cover summarized in the synthetic variable vertical vegetation promoted species richness and abundance of all and non-threatened species in our study. Additionally, the occurrence of some shrubs also favoured species richness and abundance of both Orthoptera groups.

Orthoptera are ectothermic organisms whose egg and nymphal development, egg production and life span are decisively correlated with temperature (Chappell and Whitman, 1990). Taller and more dense vegetation with less bare ground result in lower temperatures near the ground (this study; cf. also Stoutjesdijk and Barkman, 1992). Additionally, bare ground is an important oviposition substrate for many species (Fartmann and Mattes, 1997; Wünsch et al., 2012). Especially, many threatened Orthoptera species depend on bare-ground rich and warm early successional stages (Fartmann et al., 2012; Borchard et al.,

Table 5
Results of indicator species analysis (De Cáceres et al., 2012) for the different land-use types: ABA = abandoned (n = 17); MOW = mowing (n = 20); GRA = grazing (n = 13). Species are sorted by indicator value (IV) for the considered land-use type. Only significant species are shown. ab = relative abundance comparing all land-use types, fr = percentage frequency. Grey shaded values show significant indicator species according to the land-use type. Significances are indicated as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species	**ABA**			**MOW**			**GRA**			***P***
	IV	ab	fr	IV	ab	fr	IV	ab	fr	
Metrioptera brachyptera	57.9	62	94	–	16	55	–	23	69	***
Euthystira brachyptera	52.0	52	100	–	21	95	–	27	92	*
Omocestus viridulus	41.8	55	76	–	18	30	–	27	54	*
Pholidoptera aptera	41.2	100	41	–	0	0	–	0	0	**
Chorthippus dorsatus	34.5	84	41	–	9	15	–	7	15	*
Stenobothrus lineatus	–	11	47	67.5	75	90	–	14	46	***
Chorthippus biguttulus	–	0	0	55.5	74	75	–	26	31	***

2013; Helbing et al., 2014). Consequently, we observed in all models, except for species richness of non-threatened species, a negative effect of the synthetic variable horizontal vegetation on species richness and abundance. This means that the total-vegetation and field-layer cover had negative, whereas bare ground had positive effects on Orthoptera diversity and density.

We interpret the negative effect of the grass-herb ratio on Orthoptera abundance in a similar way. Those pre-alpine calcareous grasslands in the study area with a wide ratio and high cover of grasses usually form dense, species-poor and uniform stands where bare ground rarely occurs (Gutser and Kuhn, 1998a). Consequently, the microclimate is cooler with adverse effects on Orthoptera abundance (see below). Additionally, grasslands with a narrow grass-herb ratio probably offer a better food supply. The amount of grasses was high in all three land-use types (> 50%). Hence, food shortage for graminivorous Orthoptera is very unlikely. However, in grazed and especially in abandoned plots, the cover of herbs was low (< 30%) and the grass-herb ratio wide. Herbs are an important food source for herbivorous Orthoptera (Schlumprecht and Waeber, 2003). Additionally, herb-species richness promotes overall insect diversity (Krämer et al., 2012; Lin et al., 2015) with possible positive effects on food availability of insectivorous Orthoptera.

In contrast to the majority of calcareous grasslands in Central Europe (Ellenberg and Leuschner, 2010), the grasslands of the study area are traditionally used as meadows, and paddock grazing has only been introduced more recently in order to prevent succession in abandoned grasslands (Gutser and Kuhn, 1998b). In our study, grazing negatively affected Orthoptera diversity and abundance. Gutser and Kuhn (1998b) showed for vascular plants and Krämer et al. (2012) for butterflies that the current grazing regime in the pre-alpine calcareous grasslands has negative effects on both groups due to excessive intensity. We assume that the same is true for Orthoptera. Grazing mostly started early in the season and was performed up to three times a year (see Section 2.2). Our assumptions agree with other studies (Kruess and Tscharntke, 2002; Jauregui et al., 2008), which also found negative impacts of an increased grazing intensity on Orthoptera assemblages.

The explanatory power of our abundance models was much higher than those of the species-richness models. This indicates that Orthoptera abundance is more sensitive than Orthoptera diversity to land use and its influence on vegetation structure and microclimate. Our results are in line with some other studies, which showed that changes in land use and vegetation structure usually lead to rapid changes in Orthoptera abundance (Fartmann et al., 2012; Adu-Acheampong et al., 2016). In contrast, species extinction and new colonization mostly occur in a time-delayed manner (Krauss et al., 2010; Piqueray et al., 2011). Consequently, in studies on land-use change and, in particular, on changes in land-use intensity, we recommend that Orthoptera abundance especially be used as an indicator.

4.1. Implications for conservation

Based on the results of our study, conservation management of grassland Orthoptera should focus primarily on improving habitat heterogeneity and habitat quality within patches. An important tool for increasing habitat heterogeneity in the study area is the enlargement of the habitat patches at the expense of spruce forests. Such habitat restoration measures adjacent to the existing patches should, in particular, aim at increasing aspectual variety and extending elevational gradients within a patch. Both different aspects and a long elevational gradient are not only important for increasing Orthoptera diversity in general: they can also buffer populations against extreme weather events due to climate change (Malinowska et al., 2014; Streitberger et al., 2016).

Land use had strong effects on Orthoptera assemblages. Traditional low-intensity land use favours, as shown by our study, a high Orthoptera diversity and abundance. For the calcareous grasslands of the study area we recommend the maintenance of traditional mowing by scythe once per year. Where this is not possible, mowing every few years can also be a cost-effective alternative with beneficial effects on Orthoptera, due to the low succession speed of the very nutrient-poor grasslands. Although grazing had negative effects on Orthoptera assemblages, we recommend that alternative, less intensive grazing practices be tested as further alternatives.

5. Conclusion

In conclusion, habitat heterogeneity is the main driver of Orthoptera diversity within habitat patches. Its effect on species richness was much stronger than the mere patch size and, at least in well-connected landscapes, than functional connectivity of habitat patches. As already shown by several other studies, traditional land-use (here, mowing once a year) is beneficial for grassland Orthoptera. However, in extremely nutrient-poor grasslands with very short swards and hence, a low succession speed, such as the pre-alpine calcareous grasslands of our study area, young fallows are even characterized by a higher diversity and abundance. In general, Orthoptera abundance is the more sensitive indicator of land use and its influence on vegetation structure and microclimate than Orthoptera diversity.

Acknowledgments

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Appendix A

Table A1
Species frequency (%) and threat status. ● = threatened according to BayLfU (2016).

Species	Threat status	Patch frequency (%)	Plot frequency (%)
Chorthippus biguttulus	.	85	38
Chorthippus brunneus	.	15	4
Chorthippus dorsatus	●	31	24
Decticus verrucivorus	●	85	82
Euthystira brachyptera	.	85	96
Gomphocerippu srufus	.	23	12
Metrioptera brachyptera	●	85	72
Omocestus rufipes	●	31	12
Omocestus viridulus	●	62	52
Pholidoptera aptera	.	15	14
Pholidoptera griseoaptera	.	15	2
Pseudochorthippus montanus	●	8	2
Pseudochorthippus parallelus	.	100	94
Psophus stridulus	●	15	6
Roeseliana roeselii	.	62	36
Stenobothrus lineatus	●	66	64
Tetrix bipunctata	●	15	6
Tetrix tenuicornis	●	15	4
Tettigonia cantans	.	31	.

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