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The effects of grassland management and aspect on Orthoptera diversity and abundance: site conditions are as important as management

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Abstract Calcareous grasslands represent local hotspots of biodiversity in large parts of Central and Northern Europe. They support a great number of rare species which are adapted to these xerothermic habitats. Due to massive changes in land use, calcareous grasslands have become a rare habitat type and their conservation has been given a high priority in the habitats directive of the European Union. It is well known that grassland management may affect biodiversity substantially. However, the quality of calcareous grasslands is also influenced by abiotic conditions, such as aspect (i.e. sun exposure), which affects the local mesoclimate. We studied the combined effects of aspect and grassland management on Orthoptera diversity on 16 sites in Central Germany, in an unbalanced crossed design with three factors: aspect, management type and management intensity. For both response variables (diversity and abundance) we obtained a similar pattern. South-facing pastures maintained a greater diversity than north-facing pastures, but both had a greater diversity than extensively used meadows. Intensively used meadows maintained the lowest diversity and abundances. A multivariate analysis revealed that the abundance of rare Orthoptera species correlated with bare ground cover and forb cover, both of which were greatest at south-facing pastures. Our results suggest that grazing is a more suitable management for maintaining a high biodiversity in calcareous grasslands than mowing. Moreover, the mesoclimate (in this studied measured by its surrogate: aspect) is a crucial factor determining species richness and needs to be considered in reserve planning.

Keywords Grassland management · Grazing · Insect conservation · Mesofilter · Mowing · Open land management

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Introduction

Since the end of the nineteenth century, xeric grasslands have been destroyed, degraded and fragmented in Central Europe as a result of changes in land use (Muller et al. 1998; Bakker and Berendse 1999). Species-rich grasslands have become rare habitat types due to agricultural intensification, abandonment, eutrophication or plantation of coniferous forests. Nowadays, oligotrophic grasslands represent local hotspots of biodiversity in Central and Northern Europe (Muller et al. 1998; Pywell et al. 2002; Steffan-Dewenter and Tscharntke 2002). They support a rich flora and invertebrate fauna, including a high number of threatened species. This is particularly true for calcareous grasslands which used to be a characteristic element of the Central German Uplands until the early twentieth century (Poschlod and WallisDeVries 2002). As a consequence, calcareous grasslands are earmarked for conservation and listed on annex 1 of the European habitats directive (Council directive 92/43/EEC).

Conservation planning aims to maintain a maximum number of threatened species by appropriate reserve selection. The quality of a site can be influenced by a variety of factors, including for example age, size, shape, soil type, management, macro- and mesoclimate or the colonization history (e.g. Wellstein et al. 2007; Bazelet and Samways 2011b). As most endangered invertebrate species on calcareous grassland prefer a xerothermic microclimate (Ingrisch and Köhler 1998a), it is reasonable to suggest that sun exposure is one of the most important determinants of biodiversity. Another central question concerning the conservation of calcareous grasslands is the appropriate type of management, which needs to be optimized in order to promote a maximum of biodiversity, and particularly a high number of characteristic grassland species. Traditionally, calcareous grasslands have been grazed by sheep (Willerding and Poschlod 2002), but this type of management is usually not profitable any more in Central Europe. Therefore, mowing and cattle grazing have often replaced traditional agricultural practices. It is well known that the type of management has vast effects on biodiversity (van Teeffelen et al. 2008; Batary et al. 2007; Bazelet and Samways 2011b). In order to focus conservation action on the most important sites, we need a better understanding of the combined effects of aspect and management on biodiversity.

Orthoptera have become one of the most important invertebrate group for environmental monitoring and assessment (Henle et al. 1999; Maas et al. 2002). In Germany, approximately 50 % of Orthoptera species are red-listed (Ingrisch and Köhler 1998b) and many of them are associated with open, xeric habitats (Ingrisch and Köhler 1998a). Orthoptera are pivotal elements in trophic food webs as they represent first order consumers and often comprise a considerable fraction of the arthropod biomass in grassland ecosystems (Jamison et al. 2002; Odum et al. 1962). Furthermore, they are important food for many endangered bird taxa, particularly for birds, reptiles and mammals (e.g. Kok and Louw 2000). The most important variables determining Orthoptera occurrence are vegetation structure and climate (Hochkirch et al. 2007a; Hochkirch et al. 2008; Weyer et al. 2012). Therefore, they are ideal organisms to study effects of climate and agricultural land use on biodiversity.

In order to analyze the effects of mesoclimate and management on biodiversity of calcareous grasslands, we studied Orthoptera responses to the combined effects of three types of management (intensive mowing, extensive mowing and grazing) and two aspects (north-facing vs. south-facing) on 16 calcareous grassland sites in Central Germany. We hypothesized (1) that greater sun exposure will positively affect Orthoptera biodiversity, and therefore south-facing slopes maintain a greater Orthoptera species richness and

abundance than north-facing slopes and (2) that pastures promote more species and greater abundances than meadows. As differences between meadows and pastures can potentially be explained by different vegetation structure, we also analyzed the correlation of Orthoptera occurrence with vegetation structure.

Methods

Study area and sites

The study area "Huhnsberg" is located near Göttingen close to the village Scheden (Lower Saxony, Germany, 51°27′50″N 9°45′10″E; Fig. 1). The region is part of the natural region "Weser-Leine-Bergland", a mountainous landscape with forests and agricultural areas. The study area is situated 270–320 m above sea level on shell limestone. It is part of the Natura 2000 site "Buchenwälder und Kalk-Magerrasen zwischen Dransfeld und Hedemünden". The mean annual temperature in Göttingen is 8.7 °C with an average annual precipitation of 645 mm and 90–120 frost days per year. During the study period, both temperature and precipitation were higher than the long-term mean (1961–1990). The study area is mainly composed of grasslands, either used as pastures (i.e. grazed) or meadows (i.e. mown). Based on compensation contracts between the local conservation administration and farmers, most of the sites are used extensively. Grasslands that are part of the contract have either to be mown once a year (extensive meadows) or grazed with low livestock densities (extensive pastures). Both grazing and mowing are not allowed before 15 June and not later than 31 October. Fertilization, supplementary feeding and ploughing are also not permitted. After mowing, the hay has to be removed from the sites and soil damage due to high livestock densities has to be avoided. Grazing took place between mid
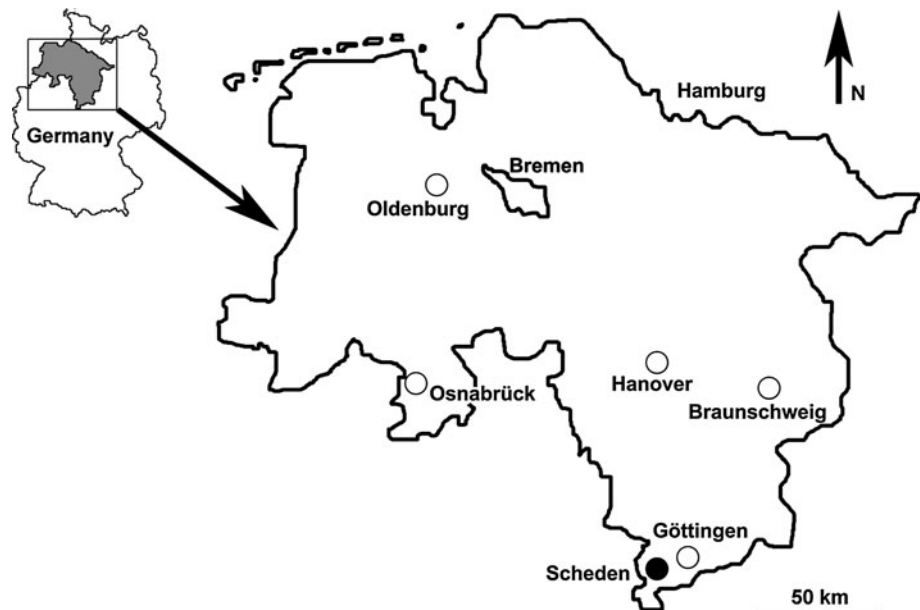

Fig. 1 Map illustrating the location of the study area (*filled circle*): Scheden, Lower Saxony, Germany

June and end of September, usually for not longer than 4–6 weeks. Some grasslands in the area are not part of the contract and are managed conventionally as intensive meadows (i.e. mown 3 times a year and fertilized).

For our analyses, we chose 16 sites. In order to analyze the effect of aspect, we studied four extensively used pastures at south-facing and four extensively used pastures at north-facing slopes (*ca*. 280 m a.s.l.). Most pastures were grazed by horses, but two (one north-facing, one south-facing) were grazed by cattle. Meadows were only present at the upper southern slope (300–320 m a.s.l.). We chose four intensive and four extensive meadows for data sampling. The extensive meadows were mown once a year (between 16 July and 22 August), whereas the intensive meadows were mown three times (3 May, 9 July, 18 August) and fertilized with urea.

Orthoptera sampling

Orthoptera abundance was sampled by visual and acoustic counts on 25 m transects in the period from 07 June to 14 August 2007 between 10:00 and 18:00. As songs of Orthoptera are species-specific and nearly all Central European species produces songs, they represent an ideal tool to map these insects (Hochkirch and Adorf 2007; Hochkirch et al. 2007b). All individuals, which were heard or seen along the transects were noted. The transect count method represents an efficient way to achieve quantitative data on Orthoptera abundance as it is less influenced by the vegetation type than sweep netting (Hochkirch and Adorf 2007). However, the method strongly depends on the insects' activity, which is affected by weather conditions. All counts were, therefore, performed during sunny and windless weather. To investigate secondary effects of the vegetation structure on Orthoptera abundance, we measured the vegetation cover for each 5 m section of the transects during the period of maximum Orthoptera abundance (15–18 August). The cover of grasses, forbs, litter, moss and bare ground were measured across the central line of the transect, which allows rather accurate measures (25 cm = 1 %) compared to traditional cover estimation (Hochkirch and Adorf 2007). Moreover, the maximum vegetation height was measured every metre as well as the average sward height. To account for the slightly differing phenologies of Orthoptera, the counts were repeated three times on each transect (first census: 07 and 08 June; second census: 15 and 16 July; third census: 14 and 18 August). For the single-species analyses, only the second and third census were considered as adult individuals were very rare during the first census.

Statistical analysis

Differences in Orthoptera abundance between the four grassland types (north-facing pastures, south-facing pastures, intensive meadows, extensive meadows) and between census dates ('census') were analyzed by a repeated measures analysis of variance (ANOVA, nested design) to avoid temporal pseudoreplication. If necessary, the data were transformed using Box-Cox-transformation, which uses a maximum likelihood approach to find the optimal power transformation (λ) to fit the data to the model assumptions (Venables and Ripley 2002). Pairwise *t* tests with Bonferroni correction were performed afterwards to compare each pair of grassland types. To test for differences in the vegetation structure, we performed an ANOVA with 'grassland type' as the explanatory variable and vegetation height, grass cover, forb cover, litter cover, bare ground cover as response variables. All tests were carried out in *R* 2.15.1 (R Development Core Team 2012).

To analyze the correlation of Orthoptera abundances to the vegetation structure, we performed a detrended correspondence analysis (DCA) based upon the Orthoptera data using the community ecology package vegan 2.0–4 for R (Oksanen et al. 2007). We tested for correlations of environmental factors (i.e. vegetation structure) with the DCA using the function 'envfit' in the vegan package. This procedure also generates an R^2 measure and significance values based on the probability that random permutations of the environmental variables would yield a higher degree of fit than the true environmental variables (Oksanen et al. 2007).

Results

Orthoptera species richness and abundance

A total of 2,039 counts of 13 Orthoptera species was obtained, including four regionally red-listed species (Grein 2005): *Tetrix tenuicornis*, *Tetrix bipunctata*, *Stenobothrus lineatus* and *Metrioptera brachyptera*. Three habitat generalists were found on >90 % of the sites (*Chorthippus biguttulus* & *Chorthippus parallelus*: 100 %, *Metrioptera roeselii*: 94 %). Mean species richness differed significantly among grassland types (Table 1, Fig. 2a). It was highest on south-facing pastures, followed by north-facing pastures, extensive meadows and intensive meadows. The total abundance was also significantly higher on south-facing pastures than on other grassland types (Fig. 2b, Table 1). The percentage of nymphs decreased significantly during the season, but there was also a near-significant interaction between census date and grassland type ($P = 0.057$). During the second census, the number of nymphs was still high on the north-facing pastures and intensive meadows, but significantly lower on the south-facing pastures and extensive meadows.

Significant main effects of grassland type were found for the abundance of three grasshopper species: *Stenobothrus lineatus*, *Chorthippus biguttulus* and *Omocestus*

Table 1 Results of repeated measures ANOVAs with grasshopper abundance as the response variable and 'grassland type' and 'census' as the explanatory variables

Response	λ	Grassland type	Census	Grassland type: census
Species richness	–	$F_{3,19} = 7.50**$	–	–
Nymph ratio	–	$F_{3,34} = 3.17*$	$F_{1,34} = 196.1***$	$F_{3,34} = 2.76$
Total Orthoptera abundance	0.15	$F_{3,30} = 4.75**$	$F_{2,30} = 10.81***$	$F_{6,30} = 1.45$
C. biguttulus	0.44	$F_{3,17} = 9.35***$	$F_{1,17} = 7.58*$	$F_{3,17} = 4.69*$
C. parallelus	0.34	$F_{3,17} = 2.67$	$F_{1,17} = 11.60**$	$F_{3,17} = 3.20*$
C. brunneus	−0.005	$F_{3,17} = 1.26$	$F_{1,17} = 0.14$	$F_{3,17} = 0.55$
S. lineatus	0.02	$F_{3,17} = 7.22**$	$F_{1,17} = 3.96$	$F_{3,17} = 0.72$
O. viridulus	−0.18	$F_{3,17} = 6.67**$	$F_{1,17} = 2.41$	$F_{3,17} = 2.22$
T. viridissima	−0.14	$F_{3,17} = 1.21$	$F_{1,17} = 0.63$	$F_{6,30} = 0.60$
M. roeselii	0.04	$F_{3,17} = 0.68$	$F_{1,17} = 9.48**$	$F_{3,17} = 0.33$
M. brachyptera	−0.18	$F_{3,17} = 3.07$	$F_{1,17} = 1.73$	$F_{3,17} = 1.23$
P. falcata	−0.72	$F_{3,17} = 2.65$	$F_{1,17} = 0.35$	$F_{3,17} = 0.32$

All data were Box-Cox-transformed (λ) to comply with the models assumptions ($P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$)
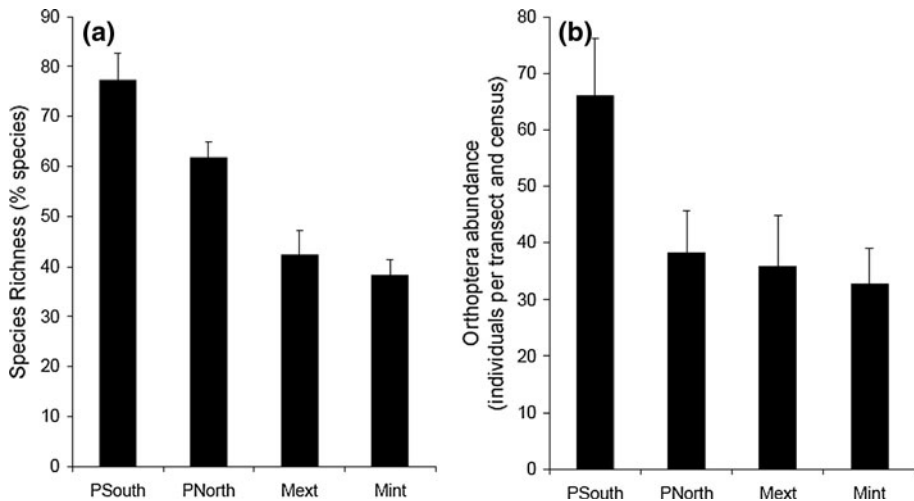
Fig. 2 **a** Mean species richness (% of total recorded Orthoptera species) and **b** mean total Orthoptera abundance (number of individuals per 25 m transect) on the four grassland types (PSouth: south-facing pastures; PNorth: north-facing pastures; Mext: extensive meadows; Mint: intensive meadows). *Error bars* indicate standard errors

viridulus (Table 1; Fig. 3). *C. biguttulus* had significant lower abundances on the extensive north-facing pastures than in other grassland types in both censuses (Fig. 3a). The abundance of *S. lineatus* followed the pattern of the total Orthoptera abundance, i.e. the species had the highest abundance on the south-facing pastures, followed by north-facing pastures, extensive meadows and intensive meadows although absent from meadows in census 3 (Fig. 3b). *O. viridulus* was only recorded on pastures, where it was more common on south-facing than on north-facing slopes (Fig. 3d). Three species showed a weak near-significant trend for differences between grassland types ($P < 0.1$): *Metrioptera brachyptera* and *Chorthippus parallelus* had slightly higher abundances on pastures than on meadows (Fig. 3c). *Phaneroptera falcata* was exclusively found on the south-facing pastures (Table 1).

For two species we found a significant interaction between grassland type and census date (Table 1), which means that phenology varied among grassland types. In *C. biguttulus* the abundance increased on the north-facing pastures and intensive meadows from the second to the third census, while it remained constant on the extensive meadows and south-facing pastures (Fig. 3a). A similar interaction was found for *Chorthippus parallelus*, but this species strongly decreased in abundance from the second to the third census on the south-facing pastures and the extensive meadows, whereas abundance remained more or less constant on the other sites (Fig. 3c).

Vegetation structure and orthoptera assemblages

Vegetation height, grass cover, forb cover and litter cover did not differ significantly among grassland types. The only parameter which showed a significant difference was the percentage of bare ground (ANOVA, $F_{3,12}$: 3.53, $P = 0.048$) which was greater on south-facing pastures (5.76 % ± 1.48) than on north-facing pastures (3.07 % ± 1.03), extensive meadows (2.00 % ± 0.88) and intensive meadows (1.14 % ± 0.73).
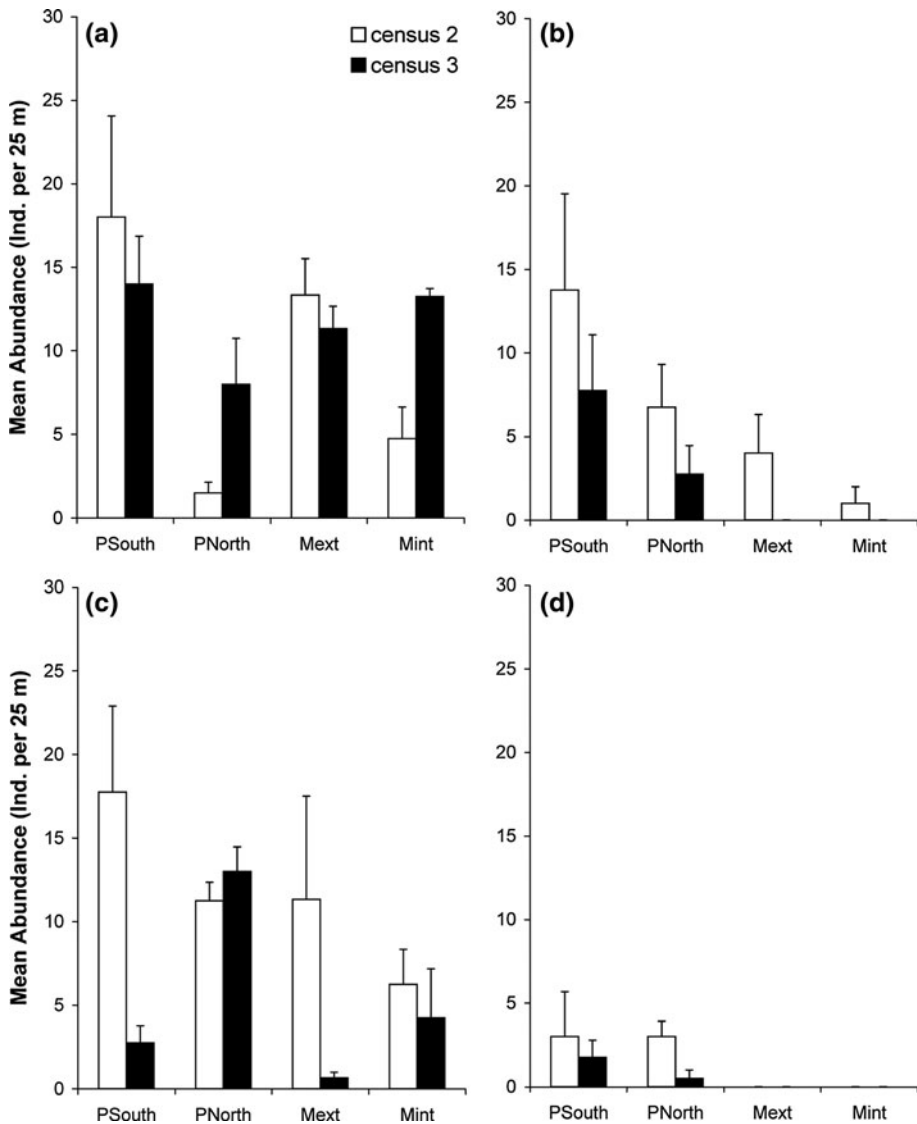
Fig. 3 Mean abundance (number of individuals per 25 m transect) of four Orthoptera species that showed significant or near-significant differences between the four grassland types: **a** *Chorthippus biguttulus*, **b** *Stenobothrus lineatus*, **c** *Chorthippus parallelus*, **d** *Omocestus viridulus* (PSouth: south-facing pastures; PNorth: north-facing pastures; Mext: extensive meadows; Mint: intensive meadows). *Error bars* indicate standard errors

The first two axes of the DCA explained 69 % of the variance (first axis: 41 %, second axis: 28 %; Fig. 4). Nearly all vegetation parameters correlated significantly with the DCA plot, except for litter (Table 2). On the first axis habitat specialists found on pastures had positive loadings (e.g. *M. brachyptera*, *S. lineatus*, *P. falcata*), whereas habitat generalists found mainly on meadows had negative loadings (e.g. *M. roeselii*, *C. parallelus*). The first axis also had a strong positive correlation with bare ground ($R^2 = 0.27$, $P < 0.001$), while
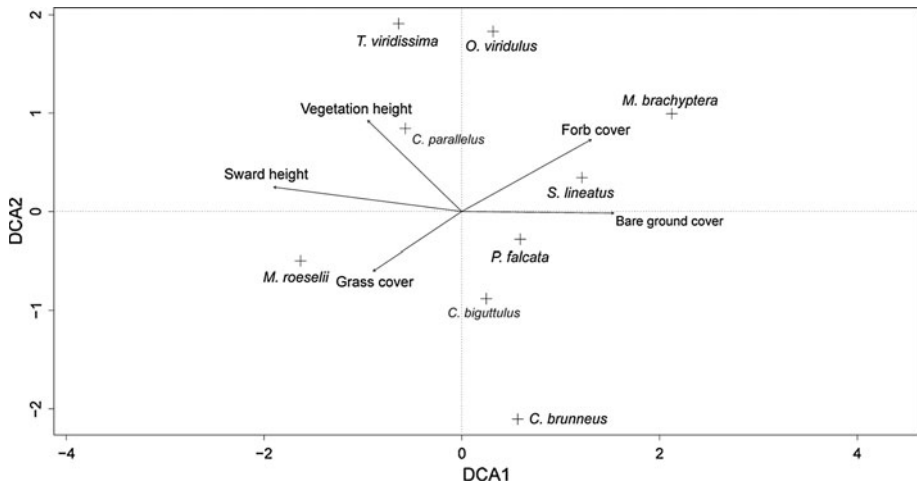
Fig. 4 Plot of the two first axes of the DCA (the *first axis* explains 41 %, the *second axis* explains 28 % of the variance)

Parameter	R^2	P
Vegetation height	0.1994	0.001***
Sward height	0.4157	0.001***
Forb cover	0.2544	0.002***
Grass cover	0.1316	0.012*
Litter cover	0.0216	0.460
Bare ground cover	0.2674	0.001***

Table 2 Squared correlation coefficients (R^2) and significance (based on 10.000 random permutations of the data) of vegetation descriptors with the Orthoptera assemblages revealed by a detrended correspondence analysis (DCA)

the second axis correlated positively with vegetation height ($R^2 = 0.20$, $P < 0.001$). On this second axis, *Tettigonia viridissima* had a positive and *Chorthippus brunneus* a negative loading.

Discussion

The results of our study suggest that Orthoptera species richness and abundance on calcareous grasslands is strongly influenced by both habitat management and aspect. Generally, extensive grazing seems to be beneficial for Orthoptera as both abundance and species richness was higher on pastures than on meadows, independent of their aspect. Only in some generalist species (e.g. *C. parallelus*, *C. biguttulus*, *C. brunneus*, *M. roeselii*), the abundance on south-facing extensive meadows was higher than or as high as on north-facing pastures. These results corroborate findings of other studies on management effects on Orthoptera (Welch et al. 1991; Branson and Sword 2010; Fabriciusova et al. 2011), but similar to meadows the positive effects of grazing seem to depend on intensity (O'Neill et al. 2003; DeBano 2006). As pastures with intensive management did not exist in the study area, we were not able to test this effect here. However, aspect also had a significant influence on Orthoptera as for nearly all species the abundance was higher on

south-facing than on north-facing pastures and species richness also peaked on the south-facing pastures. Studies on the effect of aspect on Orthoptera are surprisingly scarce (but see Vadkerti and Szozvenyi 2005; Oschmann 1973; Froehlich 1994). This might possibly be due to the rather obvious relationships between Orthoptera life histories and micro-climate (Ingrisch and Köhler 1998a). Our results indicate that optimal management alone is not sufficient to maintain a diverse Orthoptera fauna. Additionally, the best topographic position has to be chosen in terms of mesoclimate.

The main reason for the higher suitability of pastures compared to meadows is probably due to the greater environmental heterogeneity (vegetation structure) caused by grazing (Joern 2004; Stoner and Joern 2004; Adler et al. 2001; Parsons and Dumont 2003). For example, the cover of bare ground was greater on pastures than on meadows in our study area. It is well known that bare ground is a key resource for Orthoptera, which is used mainly for basking, but plays also a role as oviposition substrate or courtship ground for many species (Gröning et al. 2007; Fartmann et al. 2012; Bazelet and Samways 2011a; DeBano 2006). Even though cover of bare ground only reaches very low values (<10 %), these small patches seem to be vital for many insects (Swengel 2001). Another important difference between meadows and pastures is the uneven vegetation height and density on the latter (Atkinson et al. 2005). Due to the movements of grazing animals, some parts of a pasture are more heavily grazed or trampled than others. Thus, higher vegetation can be found in close proximity to short sward, creating habitat for terricolous species (*Tetrix* species, *Chorthippus brunneus*) as well as phytophilous species (*Tettigonia viridissima*, *Phaneroptera falcata*). For species ovipositing in plants (e.g. *Phaneroptera falcata*, *Metrioptera brachyptera*) the occurrence of perennial plants is also crucial. In addition to the secondary effects on the vegetation structure, the cutting event itself is probably also of high significance (Morris 2000). In contrast to the continuous effect of grazing, large parts of the biomass are removed during a very short time. This is particularly problematic on the intensively used meadows, which are mown three times during the Orthoptera season for silage production: once during nymphal development (May) and twice during the main adult season (July, August). During each cut a large part of the Orthoptera population is lost. It is likely that Orthoptera mortality is higher on silage meadows than on hay meadows as the drying of hay allows the insects to move into adjacent vegetation. Alto-gether, grazing seems to favour a higher number of Orthoptera species mainly due to the existence of several microhabitats on pastures (Guido and Gianelle 2001). Even north-facing pastures had a higher species richness and higher abundances than south-facing meadows.

It is not surprising that in Northern Hemisphere temperate regions south-facing slopes maintain a higher insect diversity and higher abundances than north-facing slopes (Greatorexdavies et al. 1994; Hjermann and Ims 1996). The temperature is one of the most fundamental parameters affecting insects during all environmental stages (Uvarov 1931). An interesting result in this context is the delayed phenology, which we found for some species on north-facing slopes compared to south-facing slopes. This delay is probably caused by the lower temperature sums, which are likely to hamper metabolic processes and reduce the speed of development of eggs and nymphs (Uvarov 1977). It can thus be hypothesized that the absence or low abundance of some species on the north-facing sites is due to the fact that a higher proportion are not able to finish their life cycles in time. In fact, it has been suggested that this process may be the major factor determining the northern range margin of European Orthoptera (Ingrisch and Köhler 1998a).

Most studies that try to evaluate optimal grassland management for nature conservation aim at preserving a maximum biodiversity in terms of species richness (e.g. Cousins and

Eriksson 2002; Olff and Ritchie 1998; Proulx and Mazumder 1998). However, it can be argued that conservation should focus on preserving those sites that maintain the most threatened taxa, which do not necessarily have to overlap with sites promoting the maximum number of species. Nevertheless, in our study area there was a strong overlap between the occurrence of red-listed species and species richness. All four regionally red-listed species were found on the south-facing pastures, two of them were even exclusively found there (*T. bipunctata*, *T. tenuicornis*). This underlines the high importance of preserving these sites. One major reason for the extensive land use on the south-facing pastures in our study area might be found in their steepness. Intensive land use practices are often not possible on steep slopes (Luoto 2000). Thus, the high quality caused by aspect is reinforced by steepness, which increases the climatic suitability and promotes extensive land use systems. On the other hand, the difficulty to intensify grassland management on steep slopes can also trigger abandonment, which would then lead to a loss of the most important sites for nature conservation (Cocca et al. 2012).

These findings may offer opportunities to develop unsophisticated tools to locate high quality sites for conservation of xero-thermophilous invertebrates, even without studying their biodiversity. The approach to use 'mesofilters', i.e. habitat elements that show a close affiliation with the conservation targets (species or assemblages), has recently been proposed by Hunter (2005). Geographic information systems can be used to integrate information on aspect, steepness and land use in a mesofilter to locate candidate sites for nature conservation. However, it also needs to be warned not to completely rely on mesofilter systems. An in situ evaluation of the quality of the site is always necessary after applying mesofilters.

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