Orthoptera as ecological indicators for succession in steppe grassland

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ARTICLE INFO

ABSTRACT

Understanding the effects of land-use on threatened ecosystems is of special relevance for nature conservation. The aim of our study was to use Orthoptera as ecological indicators for succession in Central European steppe grasslands.

Orthoptera showed a clear response to succession. Each successional stage harboured a unique assemblage. Species richness of habitat specialists was highest in the earliest seral stages. In contrast, density of all species peaked at the intermediate successional stage. Early successional stages are mostly likely to be preferred by specialized Orthoptera because they provide warm suitable oviposition sites (bare ground) and microclimatic conditions. The density peak in the mid-successional stage probably reflects a trade-off between favourable ambient temperatures for optimal development, sufficient food and shelter against predators.

Although all successional stages of steppe grassland are relevant for conservation, early and mid-successional stages are the most important. Consequently, conservation management should aim at re-introduction of a traditional, low-intensive land use for abandoned steppe grasslands. As an optimal land use, we recommend traditional rough grazing with sheep and goats, which creates a heterogeneous habitat structure with bare ground, and avoids the accumulation of litter, favouring Orthoptera.

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1. Introduction

Grasslands are among the dominant habitat types throughout Europe, accounting for almost a quarter of the total EU-25 land surface (EEA, 2005). Semi-natural grasslands in particular harbour high numbers of plant and animal species and are therefore of high nature conservation value (Veen et al., 2009). However, area and biodiversity of these grasslands have considerably decreased across Europe during recent decades (Stoate et al., 2009; Watt et al., 2007). Land-use changes are assumed to be the major driver of this development (Chapin et al., 2000; Sala et al., 2000). Agricultural intensification and abandonment have especially been identified as the main reasons for the strong decline of species-rich grasslands since the 1950s (Stoate et al., 2009; Van Dijk, 1991).

Among semi-natural grasslands, steppes belong to the most species-rich habitat types (Cremene et al., 2005). At their north-western range limit in Central Europe, steppes are restricted to extraordinarily dry areas (<500 mm annual precipitation) with warm summers (Hensen, 1995; Fig. 1). Due to their role as biodiversity hotspots, and the great threats they face, they are priority habitats of the EU Habitats Directive (Ssymank et al., 1998).

Orthoptera appear to be suitable model organisms to monitor the effects of global-change on steppe ecosystems (cf. Poniatowski and Fartmann, 2008): (i) they are highly sensitive to environmental changes such as grazing and abandonment (Kruess and Tscharntke, 2002a; Marini et al., 2009, 2010; Schirmel et al., 2010b); and (ii) orthopterans are key organisms in grassland ecosystems, as they are the main arthropod consumers (Curry, 1994) and food source for vertebrates (e.g. birds or lizards) (Belovsky and Slade, 1993).

Habitat selection in Orthoptera depends on a complex combination of different and often interrelated environmental factors (see review in Ingrisch and Köhler, 1998). The main determinants are vegetation structure (Gardiner et al., 2002; Poniatowski and Fartmann, 2008) and microclimate (Gardiner and Dover, 2008; Willott and Hassall, 1998). Predation and food availability are partly interrelated with the aforementioned parameters, and may also be important, particularly in sparsely vegetated habitat types (Belovsky and Slade, 1993; Wünsch et al., 2012).

The impact of land use on Orthoptera species richness in Central European grasslands is widely known (e.g. Gardiner, 2009; Kruess and Tscharntke, 2002a; Marini et al., 2008). However, there is a gap in our knowledge about the community level. By considering communities or species groups for certain successional stages, we expect to provide distinctly deeper insights into the response of orthopterans to land-use change.
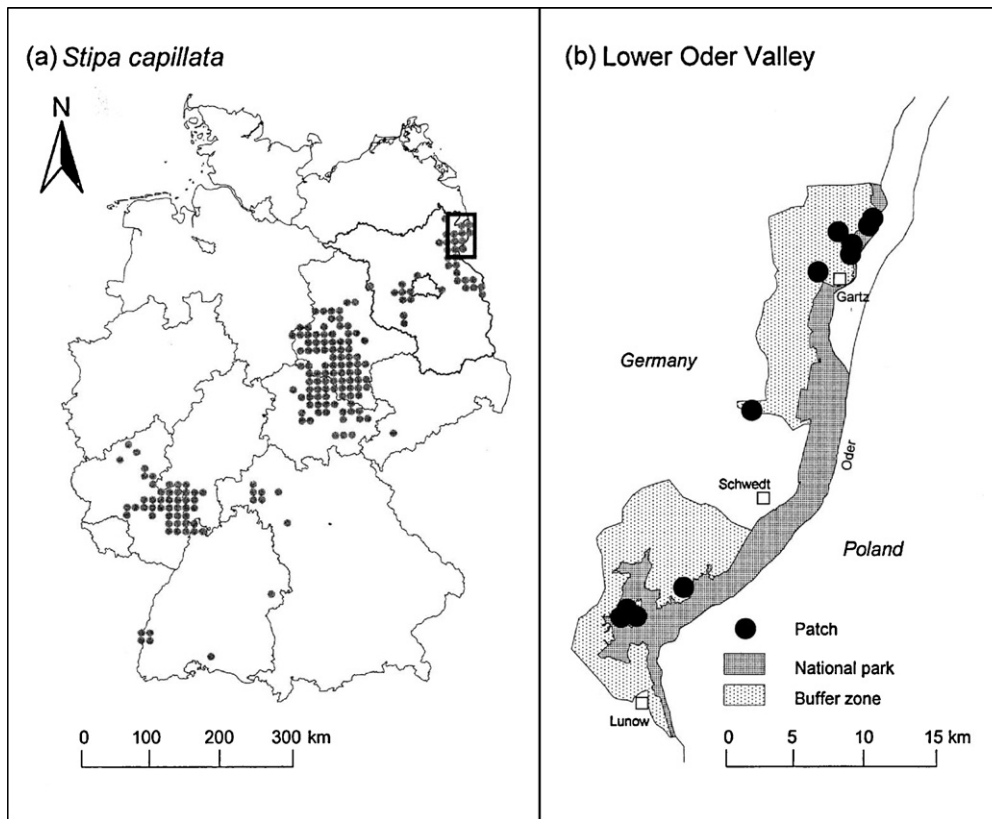
Fig. 1. Range of *Stipa capillata* as a proxy for the distribution of steppe grassland (a) and the study area Lower Oder Valley (b) in Germany. Distribution data of *Stipa capillata*: R. May, pers. comm. (Federal Agency for Nature Conservation).

The aim of this study was to use Orthoptera as ecological indicators for succession in Central European steppe grasslands. In particular we addressed the following research questions:

(i) Does Orthoptera species richness or density differ among successional stages?
(ii) Do all species, habitat generalists or habitat specialists show different diversity patterns?
(iii) How should steppe grasslands be management to promote Orthoptera?

2. Material and methods

2.1. Study area

The study area (hereafter called Lower Oder Valley) of about 285 km^2 is located at the north-eastern edge of the German federal state of Brandenburg (NE Germany) near the border with Poland (51°22′N/8°38′E and 51°38′N/9°25′E) (Fig. 1). The study area is consistent with the Lower Oder Valley National Park and its buffer zone. The Lower Oder Valley is one of the most continental and driest regions in Germany, having a mean annual precipitation of 532 mm. The mean temperature for January is −1.2 °C and for August, 17.5 °C (weather station Angermünde, 1961–1990) (DWD, 1998). Within the study area, steppe grasslands are restricted to the hilly region (10–60 m a.s.l.) west of the Oder floodplain. The area is formed by Pleistocene moraines consisting of marly till and sometimes sand (Scherf and Viehrig, 1995).

Due to the subcontinental climatic conditions, together with the occurrence of calcareous soils, the region is one of the hotspots of steppe grasslands in Germany (Fartmann et al., 2001, Fig. 1). Since soil type and aspect can greatly vary within steppe grasslands, diversity of vegetation types is high. Characteristic vegetation types within steppe grasslands are acidic grasslands (*Corynephorion*, *Plantagini-Festucion*), calcareous grasslands (*Cirsio-Brachypodion*, *Festucion valesiacae*, *Koelerion glaucae*) and fringe communities (*Trifolio-Geranietea*, different dominance stands) (Fartmann et al., 2001).

2.2. Study design

In the Lower Oder Valley, 18 steppe grassland patches are known (I. Kämpf, pers. comm.). Of these, the eleven largest and most representative patches were selected for the study. The size of the patches ranged from 1.2 to 50.3 ha (mean ± SE = 16.8 ± 5.0 ha). Four (36%) of them were grazed, especially by sheep. The remaining seven patches (64%) did not have any specific land use. However, at three of these patches, grazing has been neglected during the last ten years (own observation). Each patch was divided into sections with homogenous vegetation structure according to Sänger (1977). Structural heterogeneity within the patches was the result of management activities and natural site conditions (soil type, aspect, slope; see 'Study area' [Section 2.1]). Within each homogenous section, a plot was randomly chosen (stratified random sampling). Hence, the number of plots corresponded to the structural heterogeneity of the patch (Poniatowski and Fartmann, 2010) and ranged from two to 22 per patch. In total, 96 plots were studied. To avoid edge effects (Schirmel et al., 2010a) the size of each plot was at least 500 m^2 and the Orthoptera densities were recorded in the centre of the plot.

Measurement of environmental parameters took place after quantitative sampling of Orthoptera in an undisturbed part of the plot. We recorded the following parameters of the horizontal structure (in 5% steps): total vegetation cover, cover of grass/herb,

litter, moss, lichen and bare ground. Grasses, as the dominant plant growth form of steppe grassland, were further divided into tall-growing and low-growing grasses (mean height >50 cm and <50 cm, respectively); moreover, low-growing grasses were grouped into tussock and rhizomatous grasses (Fartmann, 1997). In cases where cover was above 95% or below 5%, 2.5% steps were used, according to Behrens and Fartmann (2004). The average turf height was ascertained to an accuracy of 2.5 cm. Vegetation density was estimated using a 50 cm wide and 30 cm deep wire-framed box, which was open on all sides except the back. Horizontal wires on the front side of the box divided it into six layers (0–5, 5–10, etc. up to 25–30 cm). The cover of each layer was horizontally viewed against the bright back of the box, using the same classes as for the horizontal structure (Poniatowski and Fartmann, 2008).

Orthoptera sampling took place once per plot at the beginning of September 2009. Densities were recorded with a box quadrat, which is among the best sampling methods to ascertain Orthoptera abundance (Gardiner and Hill, 2006). The box quadrat had an area of $2\,m^2$ ($1.41 \times 1.41\,m$), with white gauze-covered sides of 0.8 m height. It was randomly dropped over the vegetation at 10 different points per plot; i.e., in total an area of $20\,m^2$ was studied on each plot (Fartmann et al., 2008; Poniatowski and Fartmann, 2008, 2010). Orthoptera species were identified in the field using Bellmann (2006) and then released. To distinguish between the related species *Chorthippus biguttulus*, *Chorthippus brunneus* and *Chorthippus mollis*, wing length and width were measured with a calliper gauge (accuracy 0.5 mm). Scientific nomenclature follows Coray and Lehmann (1998).

2.3. Statistical analysis

Plots with similar vegetation structure were classified using Ward's method of agglomerative clustering based on Euclidean distance to successional stages (e.g. Poniatowski and Fartmann, 2008). Five variables were imported to the statistical package SPSS 17.0: total vegetation cover, cover of herbs/grasses, cover of bare ground, vegetation height and vegetation density. Prior to the analysis, values were z-transformed.

All species that are, according to Fartmann (1997) and Haupt (1997), restricted to dry grasslands in east Brandenburg were classified as habitat specialists (Appendix 1). All others were referred to as habitat generalists. To evaluate if environmental variables as well as the number of Orthoptera species (all, habitat generalists, habitat specialists) and Orthoptera density differ between successional stages, generalized linear mixed-effects models (GLMMs) (*lmer*, Bates et al., 2008) using R-2.9.2 (R Development Core Team, 2009) were conducted. For all GLMMs, the variable patch was setup as a random factor. Non-significant predictors were excluded from the final model by stepwise backward-selection. The level of significance was set to 0.05 (cf. Crawley, 2002), and the significance of the predictor variables were assessed with likelihood ratio tests (Type III test). In the case of normal distribution and variance homogeneity, a Tukey test was used as a post hoc test; in all other cases Dunn's test was applied.

Prior to non-metric multidimensional scaling (NMDS) ordination (see below) intercorrelations of all predictor variables were examined by applying a Pearson's correlation matrix that included all metric predictor variables. In cases of high intercorrelation (Pearson correlation coefficient [r] of >|0.6|) among variables, one of them was excluded from the analyses (Fielding and Haworth, 1995). Moreover, a summarizing factor, hereafter called vegetation density and cover, was created by a principal component analysis (PCA) (cf. Poniatowski and Fartmann, 2011). The new variable represents an independent principal component with an eigenvalue of 3.69. It explained 74% of total variance in the data set, and was positively correlated with total vegetation cover

Table 1
Overview of metric variables used in non-metric multidimensional scaling (NMDS).

Climate
Aspect (°) ('eastness', 'northness')[a]
Inclination (°)[*]
Heat load[b]
Potential daily sunshine duration (h)[c]
Vegetation structure
Vegetation height (cm)
Cover (%)
Total vegetation[**]
Herbs/grasses[**]
Tall-growing grasses[**]
Low-growing grasses[**]
Tussock grasses
Rhizomatous grasses[***]
Mosses
Lichens
Bare ground[**]
Litter
Vegetation density (%)[**]

[a] Conversion of aspect by sine and cosine into 'eastness' and 'northness' (eastness = 0 and northness = 1 meaning 360°, eastness = 1 and northness = 0 meaning 90°).

[b] Conversion of aspect, inclination and latitude by heat load index according to McCune and Keon (2002).

[c] Measured using a horizontoscope (Tonne, 1954), mean April to September, accuracy: ½ h.

[*] Inclination was not used for NMDS, because it was highly intercorrelated with heat load (Pearson correlation).

[**] As they were highly intercorrelated (Pearson correlation), total vegetation cover, herb/grass cover, tall grass cover, vegetation density and bare ground were summarized in a new variable 'vegetation density and cover' using principal component analysis.

[***] Cover of rhizomatous grasses was not used for NMDS, because it was highly intercorrelated with cover of low-growing grasses (Pearson correlation).

(Pearson $r = 0.90$, $P < 0.01$), herb/grass cover ($r = 0.92$, $P < 0.01$), tall grass cover ($r = 0.73$, $P < 0.01$) and vegetation density ($r = 0.82$, $P < 0.01$), but negatively with bare ground ($r = 0.90$, $P < 0.01$); i.e., the summarizing factor represents a clear gradient from dense and closely covering vegetation (positive values) to bare ground-rich vegetation (negative values). For variables finally included in the models, see Table 1.

For ordination of vegetation and Orthoptera data, a NMDS was used (VEGAN, Oksanen et al., 2008; MASS, Venables and Ripley, 2008; software package R 2.9.2). For vegetation we used the Euclidean and for Orthoptera the Bray-Curtis distance as distance measures, with a maximum number of 20 random starts in the search for stable solutions. Only Orthoptera species that occurred in at least 5% of all plots were included in the analysis.

All analyses were performed using R-2.9.2 (R Development Core Team, 2009), SigmaPlot 11.0 and SPSS 17 statistical packages.

3. Results

3.1. Environmental conditions

Based on the results of the cluster analysis, the 96 plots were grouped into five successional stages following a gradient from early (EARLY) to late stages (LATE) (Table 2). Except for the cover of mosses and rhizomatous grasses, all vegetation-structure parameters differed substantially among the stages. In contrast, none of the climatic variables showed significant differences. Vegetation height, vegetation density and the cover of total vegetation, herbs/grasses, tall-growing grasses and litter increased from EARLY to LATE, while cover of tussock grasses, lichens and bare ground decreased. Cover of low-growing grasses was highest in the intermediate stage (INTER).

Table 2
Mean values (±SE) of climate and vegetation-structure parameters in five successional stages of steppe grassland. Differences between the successional stages were tested for all predictor variables using a GLMM (climate variables: Poisson; vegetation-structure variables: proportional binomial) with *patch* as a random factor. Different letters indicate significant differences between stages (Tukey test for herbs/grasses, otherwise Dunn's test; $P < 0.05$).

	EARLY	EARLY-INTER	INTER	INTER-LATE	LATE	P
Climate						
Heat load	0.83 ± 0.02	0.80 ± 0.02	0.84 ± 0.01	0.76 ± 0.02	0.80 ± 0.02	n.s.
Daily sunshine duration [h]	11.6 ± 0.6	11.3 ± 0.6	12.1 ± 0.4	10.7 ± 0.6	9.7 ± 0.8	n.s.
Vegetation structure						
Vegetation height [cm]	15.2 ± 2.7[a]	25.0 ± 2.8[ab]	40.8 ± 4.8[b]	40.4 ± 3.7[b]	53.3 ± 5.2[c]	***
Cover [%]						
Total vegetation	47.7 ± 7.2[a]	64.5 ± 6.7[ab]	83.9 ± 3.3[bc]	86.0 ± 2.5[bc]	94.8 ± 2.0[c]	***
Herbs/grasses	25.4 ± 3.9[a]	48.5 ± 4.4[b]	71.5 ± 3.3[c]	75.3 ± 3.0[c]	88.3 ± 2.3[d]	***
Tall-growing grasses	1.6 ± 1.2[a]	3.6 ± 1.7[ab]	25.6 ± 5.3[bc]	35.9 ± 4.5[cd]	62.5 ± 5.5[d]	***
Low-growing grasses	18.1 ± 2.9[ab]	31.5 ± 4.3[a]	29.7 ± 4.8[a]	16.7 ± 3.1[ab]	13.0 ± 3.9[b]	***
Tussock grasses	20.4 ± 4.0[a]	23.0 ± 3.8[a]	13.6 ± 3.3 [a]	10.9 ± 3.6[ab]	0.3 ± 0.3[b]	***
Rhizomatous grasses	1.9 ± 1.3	9.0 ± 4.6	16.0 ± 5.0	8.5 ± 2.5	12.8 ± 3.9	n.s.
Mosses	12.2 ± 3.7	13.6 ± 2.1	17.4 ± 3.9	27.5 ± 5.3	33.9 ± 8.1	n.s.
Lichens	13.1 ± 6.5[a]	11.8 ± 7.0[ab]	2.9 ± 1.2[ab]	0.8 ± 0.4[ab]	0.2 ± 0.1[b]	***
Bare ground	51.4 ± 7.3[a]	32.6 ± 6.4[ab]	13.7 ± 3.2[b]	12.6 ± 2.3[b]	4.0 ± 1.7[c]	***
Litter	3.9 ± 1.2[a]	3.6 ± 0.5[a]	9.2 ± 1.7[a]	13.1 ± 3.3[a]	33.1 ± 5.9[b]	***
Vegetation density [%]	8.4 ± 1.3[a]	16.7 ± 2.3[ab]	27.2 ± 3.2[b]	31.1 ± 3.3[b]	55.2 ± 3.5[b]	***
N plots	13	10	23	30	20	

n.s. not significant.
*** $P < 0.001$.

3.2. Orthoptera

In total, we recorded 20 Orthoptera species (8 Ensifera, 12 Caelifera) (Appendix 1), comprising a total of 1838 individuals on the 96 plots. The clearly dominating species was *C. mollis* with 1343 individuals (73% of all individuals) occurring in 92% of all plots (Appendix 1). The species with the next highest numbers were *C. biguttulus*, *C. brunneus*, *Metrioptera bicolor*, *Myrmeleotettix maculatus*, *Omocestus haemorrhoidalis* and *Tetrix tenuicornis*, with 42–88 caught individuals, all together accounting for 352 individuals (19% of all individuals).

3.3. Species richness and densities

Overall species number and the number of habitat generalists did not differ among the five successional stages (Fig. 2). In contrast, the number of habitat specialists decreased from EARLY to LATE, with the first three successional stages having significantly higher species numbers than the latest successional stage. Orthoptera densities also differed among the stages. However, the pattern was different. Numbers were highest in the intermediate stages (INTER), significantly differing from EARLY and LATE.

3.4. Species response to environmental variables

NMDS ordination (stress: 14.37, four dimensions) showed a clear separation of Orthoptera species, and nine of the eleven

Table 3
Summary of NMDS: Pearson's correlation coefficients with NMDS-axes scores. P values based on 1000 permutations. Abb. = abbreviation.

	Abb.	Axis 1	Axis 2	R²	P
Sunshine duration	SUN	−0.57	−0.82	0.09	**
Lichen cover	LIC	−0.98	−0.19	0.09	*
Litter cover	LIT	0.77	0.23	0.11	***
Low-growing grasses	LG	−0.52	−0.85	0.08	*
Moss cover	MO	0.93	0.37	0.09	*
Northness	N	0.43	0.90	0.12	**
Tussock grasses	TG	−0.90	−0.44	0.17	***
Vegetation density and cover	VD	0.96	0.27	0.47	***
Vegetation height	VH	0.99	0.11	0.16	***

*$P < 0.05$, ** $P < 0.01$, ***$P < 0.001$.

environmental variables contributed significantly to the ordination model (Fig. 3, Table 3). The variation in species composition was mainly determined by two environmental gradients. The first axis represents a vegetation density, cover and height gradient (hereafter referred to as vegetation gradient). Moss and litter cover were also highly positively correlated with this axis. In contrast, the cover of lichens and tussock grasses was negatively correlated with the first axis. *M. maculatus* and *Oedipoda caerulescens* were characteristic for EARLY and negatively associated with the vegetation gradient. *Chorthippus dorsatus* and *Metrioptera roeselii*, characteristic for LATE, and *Chorthippus apricarius*, *C. biguttulus*, *C. mollis*, *Decticus verrucivorus*, *M. bicolor*, *Phaneroptera falcata*, typical for INTER-LATE, were positively correlated with this gradient.

The second axis represents a microclimate gradient. Northness was positively correlated with this axis, while sunshine duration showed a negative relationship. Moreover, cover of low-growing grasses was negatively correlated with the second axis. The two species (*C. dorsatus* and *M. roeselii*) associated with LATE were positively related with this gradient, while *O. haemorrhoidalis*, *Platycleis albopunctata* and *Stenobothrus lineatus*, characteristic for INTER, showed a negative relationship.

4. Discussion

Orthoptera of steppe grasslands showed a clear response to succession. Each successional stage harboured a unique assemblage. Species richness of habitat specialists was highest in the earliest seral stages (EARLY to INTER). In contrast, density of all species peaked at the intermediate successional stage (INTER).

There are some studies that have already shown negative effects of succession on Orthoptera of open habitats. However, the results are only partly consistent among the studies and with our study. Marini et al. (2009) observed the highest overall species number in mown and young abandoned meadows, followed by old abandoned meadows and then by forests. Along a gradient from open grey dunes over different heath stages to birch forests, Schirmel et al. (2010b) found the highest species richness in the intermediate stage, the grassy heath. Surprisingly, in our study, species richness of all species and habitat generalists were not affected by succession. Only for habitat specialists were effects visible. A possible explanation for the lack of impact might be the short ecological
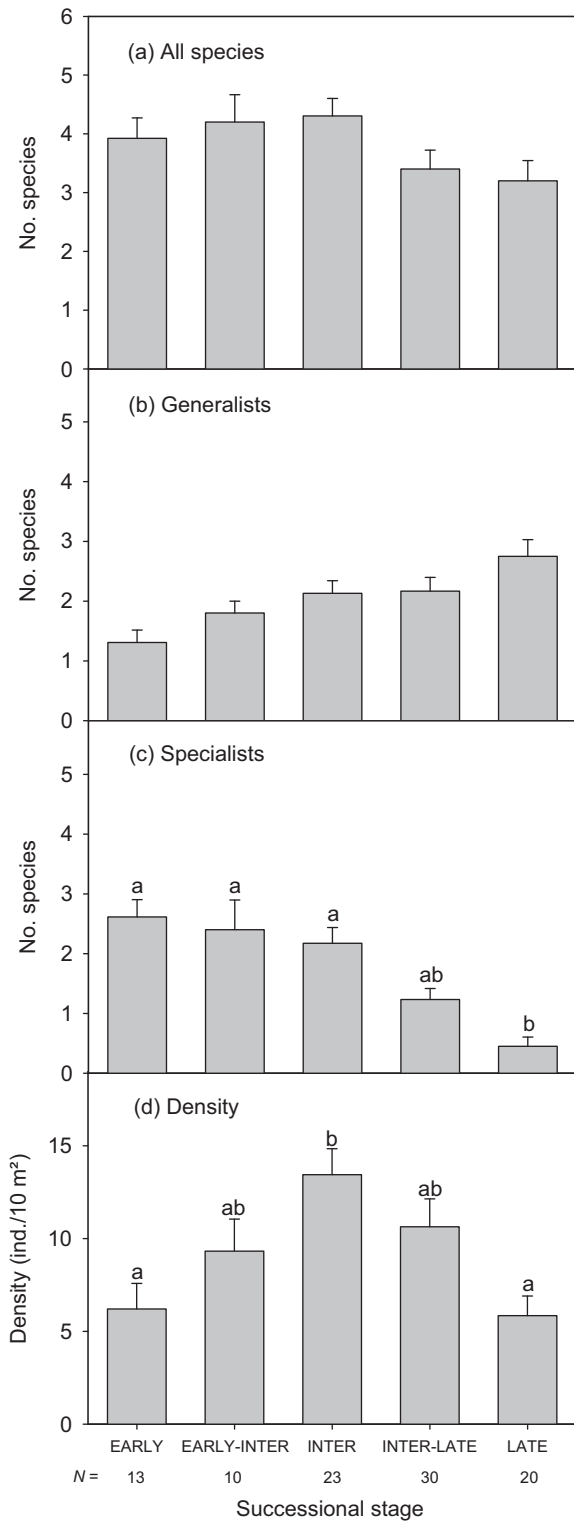
Fig. 2. Mean values (±SE) of (a) all Orthoptera species, (b) habitat generalists, (c) habitat specialists and (d) Orthoptera density in five successional stages of steppe grassland. Differences between the successional stages were tested for all four response variables using a Poisson GLMM with *patch* as a random factor. Statistics of GLMM: all species: $\chi^2 = 5.120$, df = 4, $P = 0.28$; habitat generalists: $\chi^2 = 8.653$, df = 4, $P = 0.07$; habitat specialists: $\chi^2 = 37.916$, df = 4, $P < 0.001$, density: $\chi^2 = 1536.8$, df = 4, $P < 0.001$. Different letters indicate significant differences between stages (Dunn's test; $P < 0.05$).
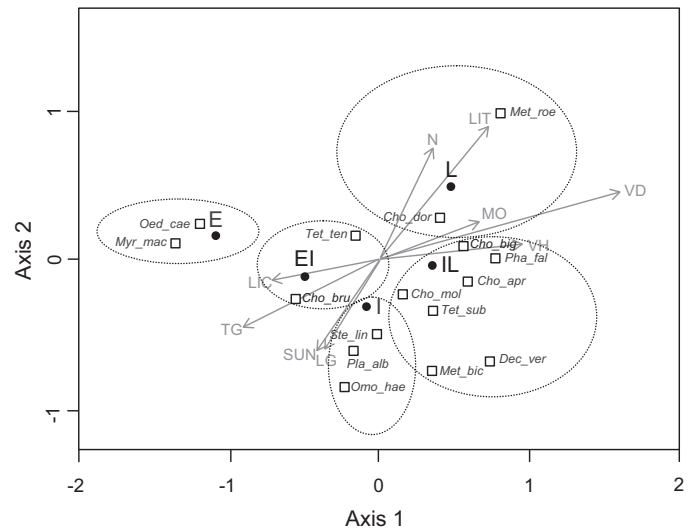

Fig. 3. NMDS (stress: 14.37, four dimensions) based on the most frequent orthopteran species and environmental parameters of steppe grassland. Only significant environmental parameters (arrows) are shown (at $P < 0.05$, based on 1000 permutations). Quadrats indicate Orthoptera species and black dots successional stages. Full names of Orthoptera species are given in Appendix 1. For abbreviations of environmental parameters see Table 3.

gradient in our study, without consideration of a forest stage. In line with this, Kruess and Tscharntke (2002a) studied the effects of grazing on Orthoptera species across an also relatively short gradient, from intensively grazed to ungrazed grasslands, and were also unable to detect an effect on overall species richness. However, species richness of habitat specialists was also affected.

The vast majority of the habitat specialists in our study are thermophilous (Detzel, 1998), oviposit into or near the ground (Fartmann and Mattes, 1997; Wünsch et al., 2012) and were, hence, associated with bare ground-rich and low-growing vegetation (Fig. 3, Table 3) of the first three successional stages. Schirmel et al. (2010b) and Wünsch et al. (2012) also mentioned the high relevance of early successional stages for specialized Orthoptera.

Intermediate successional stages favoured overall species density. As cold-blooded organisms, most Orthoptera require high ambient temperatures for optimal growth and development (Chappell and Whitman, 1990; Willott and Hassall, 1998). Accordingly, a warm, but not too hot microclimate (cf. Gardiner and Hassall, 2009), favours high population densities (Gardiner and Dover, 2008). Besides favourable microclimatic conditions, sufficient food and shelter against predators also promote high abundances (Schuhmacher and Fartmann, 2003; Wünsch et al., 2012). These different requirements are best fulfilled in the intermediate successional stage, probably explaining the Orthoptera density peak.

5. Implications for conservation

The protection of steppe grasslands by the EU Habitats Directive implies the prohibition of regression and the duty to monitor potential changes in habitat quality (Ssymank et al., 1998). As shown by our study, Orthoptera are sensitive indicators for succession in steppe grasslands.

All successional stages are relevant for the conservation of steppe grasslands (cf. Cremene et al., 2005). Each seral stage has a unique Orthoptera community. Moreover, many Orthoptera species depend on mosaics of different stages, since they fulfil microhabitat shifts during their nymphal development (Wünsch et al., 2012), or adults regularly shift between different stages

(Schirmel et al., 2010a). However, the early and mid-successional stages are the most important. They are characterized by the highest species richness and overall density.

Consequently, conservation management should aim at re-introduction of a traditional low-intensive land use for the abandoned grasslands (Kruess and Tscharntke, 2002b; Wettstein and Schmid, 1999). This is especially true for larger patches. The bigger the patch, the higher should be the habitat heterogeneity and the number of different stages. As an optimal land use, we recommend traditional rough grazing with sheep and goats, which creates a heterogeneous habitat structure with bare ground and avoids the accumulation of litter, favouring Orthoptera (Poniatowski and Fartmann, 2010). The creation of bare surfaces and prevention of litter accumulation in steppe grasslands through grazing is not only beneficial for Orthoptera, but also for plant species diversity (Enyedi et al., 2008; Ruprecht et al., 2010).

Besides abandonment, steppe grasslands in Central Europe are threatened by atmospheric nitrogen deposition and leaching of nitrogen from arable fields (Gunnemann and Fartmann, 2001; Süß et al., 2004). Eutrophication favours tall and competitive plant species such as *Arrhenatherum elatius*, *Calamagrostis epigejos* and *Rubus caesius*. Recent studies (Dostalek and Frantik, 2008) show that sheep grazing is a useful tool to suppress these competitors in favour of bare ground and low-competitive plant species.

Until the mid of the last century, steppe grasslands in Brandenburg were regularly burnt in autumn and spring (Krausch, 1961). The positive influence of burning on Orthoptera of Central European steppe grasslands has been shown by Bieringer and Sauberer (2010). Hence, prescribed burning, if applied in a mosaic-like pattern (Fartmann, 2010; Marini et al., 2010; Möllenbeck et al., 2009), might be a suitable accompanying measure.

Appendix 1.

Frequency (%) of Orthoptera species in each of the five successional stages of steppe grassland and habitat specifity of each species. S = habitat specialist, G = habitat generalist. For further information see 'Statistical Analysis' (Section 2.3).

Species	Habitat specifity	EARLY	EARLY-INTER	INTER	INTER-LATE	LATE	Frequency
Calliptamus italicus	S	8	–	–	–	–	1
Chorthippus apricarius	G	–	–	4	27	30	16
Chorthippus biguttulus	G	–	10	26	23	15	18
Chorthippus brunneus	G	62	60	52	7	–	29
Chorthippus dorsatus	G	8	10	17	43	45	29
Chorthippus mollis	G	69	100	100	93	90	92
Decticus verrucivorus	S	–	–	9	23	–	10
Gryllus campestris[a]	S	15	–	4	–	–	3
Leptophyes albovittata	G	–	–	4	–	–	1
Metrioptera bicolor	S	8	10	48	60	35	40
Metrioptera roeselii	G	–	–	–	3	60	14
Myrmeleotettix maculatus	S	77	20	–	–	–	13
Oedipoda caerulescens	S	92	80	–	–	–	23
Omocestus haemorrhoidalis	S	23	30	43	–	–	20
Phaneroptera falcata	G	–	–	–	13	25	10
Platycleis albopunctata	S	23	50	35	–	–	17
Stenobothrus lineatus	S	–	40	43	20	–	22
Tetrix subulata	G	–	–	4	7	10	5
Tetrix tenuicornis	S	8	10	22	10	0	10
Tettigonia viridissima	G	–	–	4	–	–	1
N plots	–	13	10	23	30	20	–

[a] Excluded from all statistical analyses because of its partially hidden life in the ground.

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