

Impacts of succession and grass encroachment on heathland Orthoptera

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Abstract For the conservation of biodiversity, heathlands present important ecosystems throughout Europe. The formerly widespread habitats are nowadays restricted to small and isolated remnants. Without land use heathland vegetation undergoes succession and, in addition, the increasing amount of atmospheric nitrogen deposition has resulted in an encroachment of grasses. In the present study we analysed the effects of succession and grass encroachment on Orthoptera in a coastal heathland on the Baltic island of Hiddensee, Germany. Vegetation, microclimate, soil humidity and Orthoptera were sampled in the five main stages of heathland succession, namely grey dunes, dwarf-shrub heath, grassy heath, heath with shrubs, and birch forest. Vegetation and environmental parameters showed strong differences among the successional stages. Orthoptera species richness was highest in transitional stages. The high proportion of grasses offer favourable habitat conditions for graminivorous, chorto- and thamnobiont species. Orthoptera

density was highest in grey dunes. Threatened and specialised species were restricted to the young stages grey dunes and dwarf-shrub heath. Hence, in order to maintain a high diversity of Orthoptera in heathlands, maintaining different successional stages is of critical importance and this should be integrated into heathland management practices.

Keywords Biodiversity · *Calluna* heath · Eutrophication · Global change · Microclimate · Vegetation structure

Introduction

European heathlands are important ecosystems for the conservation of biodiversity (Webb 1998) and thus protected by the EU Habitats Directive (Ssymank et al. 1998). Due to intensification of land use and afforestation these formerly widespread habitats are today restricted to small and isolated remnants (Rose et al. 2000; Webb 1998). As a man-made habitat the presence and quality of heathlands strongly depend on traditional land uses like sheep grazing, sod cutting and burning. Without land use or management, the depletion of nutrients is inhibited and heathland vegetation undergoes succession towards shrub or tree dominated vegetation (Britton et al. 2001; Gimingham 1972; Webb 1998). In addition, the increasing amount of atmospheric nitrogen deposition during the last decades resulted in an eutrophication of nutrient-poor heathland ecosystems (Heil and Diemont 1983; Remke et al. 2009a), causing encroachment of grasses like *Deschampsia flexuosa* and *Molinia caerulea* (Britton et al. 2001; Marrs 1993; Roem et al. 2002). As shown for heathlands and dune ecosystems in the Baltic Sea region, even low nitrogen inputs can lead to such grass encroachment, especially of *Carex arenaria* (Remke 2003; Remke et al. 2009a, b).

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The responses of open terrestrial ecosystems to successional processes have been studied for several invertebrate groups indicating both positive (butterflies: Balmer and Erhardt 2000) and negative effects on diversity (Orthoptera: Köhler and Kopetz 1993; Marini et al. 2009). While most studies concentrate on grassland ecosystems (e.g. Balmer and Erhardt 2000; Baur et al. 2006; Kruess and Tschardt 2002a, b; Marini et al. 2009; Öckinger et al. 2006; Skórka et al. 2007), the knowledge of successional effects on insects in heathlands is rare. Moreover, effects of eutrophication on arthropods have poorly been analyzed in general (Cuesta et al. 2008; Sjørnsen et al. 2005) and particularly the impact of grass encroachment in heathland ecosystems is hardly known.

Orthoptera are highly sensitive to environmental changes like grazing, mowing and abandonment (Báldi and Kisbenedek 1997; Fartmann and Mattes 1997; Samways 1997). They have an important position in food webs of open ecosystems where they often are both the main invertebrate consumers (Curry 1994) and food source (Samways 1997).

The present study investigates the effects of succession and grass encroachment, as the main recent threats to heathland ecosystems, on Orthoptera in a coastal heath at the Baltic Sea island of Hiddensee, Germany. The study aims to assess changes in Orthoptera species richness and assemblage structure along a successional gradient. In addition, we try to determine the impact of the potential drivers (microclimate, vegetation, soil humidity) of these changes. Based on our results, we give recommendations for the management of heathland ecosystems. The following questions are addressed: (1) How do the successional stages differ in their abiotic conditions and vegetation composition? (2) Do Orthoptera species richness and density differ along the successional gradient, and

how does the Orthoptera composition change? (3) Which are the most important drivers for the shifts in Orthoptera composition?

Materials and methods

Study site

The study was conducted in a coastal heathland on the Baltic island of Hiddensee (54°32'N, 13°5'E) in north-eastern Germany in spring/summer 2008. Mean annual temperature in this region is 7.5°C and mean annual precipitation is 547 mm (Reinhard 1962).

We chose an area of approx. 2.5 km² in the centre of the island where the five main stages of heathland succession could be found. The number of replicates per stage corresponded approximately to their respective area fraction in the study area. In total, 31 plots were established with a size of 500 m² each and a homogeneous vegetation structure (for the representing stage type). The following successional stages were studied: (1) open and sparsely vegetated grey dunes (GD) dominated by *Corynephorus canescens*, *Carex arenaria* and cryptogams ($N = 6$). (2) the main (dominant) vegetation type, dwarf-shrub heath (DH) with dominance of *Calluna vulgaris*, *Empetrum nigrum*, *Salix repens* and *Erica tetralix* as less frequent species ($N = 10$). (3) Grassy heath (HG; $N = 7$), where heather species are regularly displaced by tall graminoids, especially by *C. arenaria*. This species, usually a pioneer plant of acidic coastal dunes at the Baltic Sea (Remke et al. 2009b), can build up very dense and high (>1 m) stands within heathland vegetation (Fig. 1; Remke 2003; own observations). In the following, we therefore distinguish between “tall *C. arenaria*” as the eutrophic form occurring

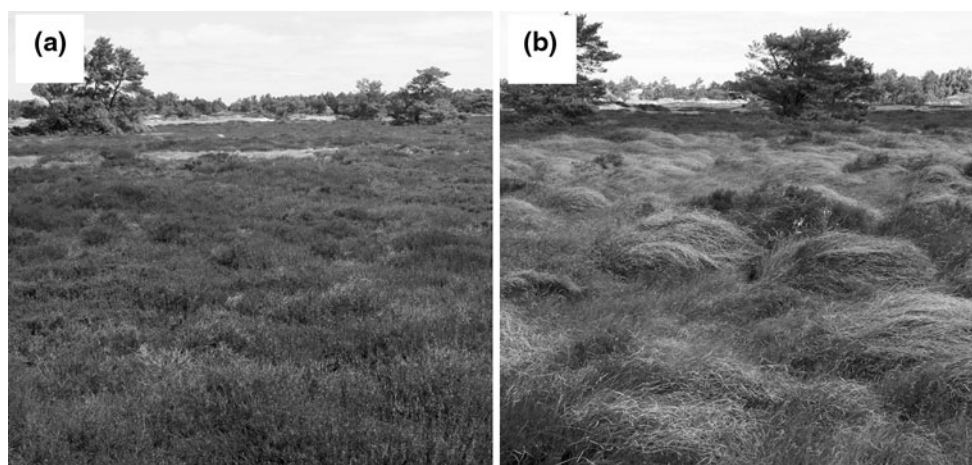


Fig. 1 Typical stands of **a** dwarf-shrub heath and **b** heath encroached by tall *Carex arenaria* within the study area of the coastal heath on the Baltic isle of Hiddensee, Germany

in grassy heath (HG) and “small *C. arenaria*” as the typical pioneer form occurring in grey dunes (GD). (4) Unmanaged heath encroached by shrubs like *Betula pendula*, *B. pubescens* or *Prunus serotina* (HS; $N = 4$). (5) Young birch forest (BF), which had developed due to the lack of land use during the last 30–40 years ($N = 4$).

Vegetation

Vegetation was sampled three times during May and August 2008 in all plots. In each plot, two sub-plots were established with a specific size depending on the vegetation type: 25 m² in grey dunes (GD) and dwarf-shrub heath (DH), 50 m² in grassy heath (HG) and heath with shrubs (HS) and 100 m² in birch forest (BF). In each sub-plot, we recorded cover of total vegetation (CTV), trees (CTR), shrubs (CSH), grasses (CGR), tall *C. arenaria* (CTC), small *C. arenaria* (CSC), cryptogams (CCR) and bare soil (CBS). Species cover was estimated according to the scale of Londo (1976, 1984). Density of field layer was estimated in % for the vegetation heights 0–10, 10–20, 20–30, 30–40, and 40–50 cm (Sundermeier 1998) and summed up for further analyses (DFL). Height of field layer (HFL) was measured in cm.

Microclimate and soil moisture

Microclimate (air temperature and air humidity) was recorded from June to October 2008 with micro-weather stations consisting of an air temperature and a capacitive air humidity sensor (DS 1923, Maxim/Dallas, USA) equipped with a self-constructed radiation shield (Leuschner and Lenzion 2009). One micro-weather station was installed in the centre of each plot at middle height of the field layer. Air temperature (ATE) and air humidity (AHU) were measured and recorded hourly. For statistical analysis, mean values of only the daylight period (8:00–18:00 h) were used excluding incompletely measured days (24–25 June, 05–06 August, 25–26 September 2008).

Soil moisture (SHU) was determined gravimetrically at different intervals between July and September 2008. On each occasion and plot, three soil samples were taken at depths of 5 cm and combined to one sample.

Orthoptera survey

Orthoptera assemblages and relative abundances were estimated by using a transect method. Transect counts belong to the most commonly used sampling methods for Orthoptera (Gardiner et al. 2005), and the adopted method was more feasible in the stiff dwarf-shrub vegetation in comparison to sweep-netting or the use of a box quadrat. All study plots were paced off in loops, and within a band

of 1 m all optically and acoustically observed Orthoptera were counted (total observed area per plot: 70 m²). Individuals which could not be determined by observation were caught (by sweep net or hand) and released after determination in the field. The loops had a distance of about 5 m to each other to minimize double counting. Surveys were conducted at three dates during main activity period of adult Orthoptera between the end of July and the end of August under favorable weather conditions (warm, sunny and calm days) between 10:00 and 17:00 h (CET + 1). Prior to starting transect counts all plots were visited at least two times (beginning of July and mid-July) for a qualitative survey in order to detect the species spectrum of each plot. Species were determined according to Bellmann (2006), and the scientific nomenclature followed Coray and Lehmann (1998).

Data analyses

Orthoptera species were classified into the life-forms geobionts (*Oedipoda caerulescens*, *Myrmeleotettix maculatus*, *Tetrix undulata*), geo-chortobionts (*Chorthippus biguttulus*, *Platycleis albopunctata*, *Decticus verrucivorus*), chortobionts (*Omocestus viridulus*, *Chrysochraon dispar*, *Conocephalus dorsalis*, *Metrioptera roeselii*, *Chorthippus albomarginatus*) and thamnobionts (*Pholidoptera griseoaptera*, *Tettigonia viridissima*) according to Racz (1998), Nagy et al. (2007) and Schirmel et al. (2010a). Geobiont species live in open and sparsely vegetated habitats, chortobiont species mainly occur in grassy vegetation (“grass-dwelling”) and thamnobiont species prefer dense stands of grasses or live in the canopy. Geo-chortobionts are a transitional type between geo- and chortobionts (Racz 1998). Classification of threatend species follows Wranik et al. (2008).

Differences in vegetation parameters, abiotic parameters, Orthoptera species richness and density (individuals per 10 m²) among successional stages were tested using one-way ANOVA followed by Scheffé post-hoc tests with the software package SPSS 11.5.

For ordination of vegetation data a nonmetric multidimensional scaling (NMDS) was used (VEGAN, Oksanen et al. 2008; MASS, Venables and Ripley 2008; software package R 2.9.2). We used the Euclidean distance as distance measure with a maximum number of 100 random starts in search for stable solutions.

In order to analyse the relationship between Orthoptera species abundance and environmental variables a Canonical Correspondence Analysis (CCA) was conducted, as a prior conducted Detrended Correspondence Analysis (DCA) revealed a gradient length of >4 SD (Leyer and Wesche 2007). Environmental and species data were log transformed [$y' = \log(y + 1)$] and rare Orthoptera species

downweighted. Only significant variables (Monte Carlo permutation test with 499 unrestricted permutations at $P < 0.05$) were stepwise included in the model. In addition to the CCA we also conduct the unconstrained Correspondence Analysis (CA) in order to compare the explained variation in our species data, disregarding the environmental variables, with that from the constrained ordination (related to the environmental factors; Lepš and Šmilauer 2003). CCA and CA ordination were done using Canoco 4.5.

Poisson generalized linear models (GLM) were used for testing relations between species or life-form abundance data, respectively, and environmental data. As overdispersion was detected, we corrected standard errors using quasi-GLM models (Zuur et al. 2009). F-statistics were assessed using an Analysis of Deviance (Zuur et al. 2009). For measuring the goodness of fit for each model the residual deviance by calculating the pseudo R^2 was used (Dobson 2002). To eliminate multicollinearity, prior to CCA and CA ordination and GLM analyses bivariate correlation analyses of environmental variables using Spearman's rank correlation coefficient were performed. In case of high intercorrelation ($\rho > 0.7$) among variables, one of them was excluded from analysis (Fielding and Haworth 1995). Variables finally included in the models were CTV, CGR, CTC, CBS, DFL, ATE, and SHU (for abbreviations see Table 1 and text above).

Results

Vegetation

NMDS ordination (stress: 6.37, two dimensions) showed a clear separation among the five successional types (Fig. 2). Vegetation parameters differed substantially among

successional stages (Table 1). Cover of total vegetation as well as height and density of field layer strongly increased from grey dunes to birch forests. Cover of grasses was highest in grassy heath and in birch forest plots reaching values around 80% followed by heath with shrubs and grey dunes were values between 44 and 39% were recorded. By far poorest in grasses was the dwarf-shrub heath with only about 1% cover. Tall *Carex arenaria* reached the highest densities in grassy heath with around 74% followed by heath with shrubs (27%). In contrast, small *C. arenaria* exclusively occurred in grey dunes with cover values around 20%. Cryptogams had highest cover in dwarf-shrub heath (66%) and grey dunes (60%) and lowest (19%) in grassy heath. Cover of bare soil reached high values only in grey dunes (14%), while shrubs exclusively occurred in heath with shrubs (51%) and birch forests (26%). Trees only occurred in the birch forest (cover of 70%).

Microclimate and soil moisture

The five successional stages showed significant differences in microclimate and soil moisture (for all parameters one-way ANOVA: $P < 0.001$; Fig. 3). Mean daytime air temperature in the middle of the field layer was highest (23.1°C) in grey dunes. High mean temperatures also occurred in grassy heath and dwarf-shrub heath (both 22.4°C). Significantly lower temperature values were recorded in heath with shrubs (20.3°C) and birch forest (19.2°C). Mean daytime air humidity was lowest in grey dunes with values around 62% and highest in heath with shrubs (78%) and birch forest (77%). The lowest soil humidity (water content in % of the upper 5 cm) was recorded in grey dunes with values of 2.3%. The highest soil moisture was found in grassy heath (39%) and heath with shrubs (37%).

Table 1 Mean values (\pm SE) of vegetation parameters in the five succession stages

	Abbr	GD	DH	HG	HS	BF	F	P
Cover [%]								
Total vegetation	CTV	59.8 \pm 1.3 ^a	88.9 \pm 1.4 ^b	95.3 \pm 1.3 ^c	94.3 \pm 1.7 ^{b, c}	96.3 \pm 1.0 ^c	102.3	< 0.001
Trees	CTR	0 ^a	0 ^a	0 ^a	0 ^a	70.0 \pm 2.1 ^b	2,133.8	< 0.001
Shrubs	CSH	0 ^a	0 ^a	0 ^a	51.0 \pm 2.2 ^b	26.0 \pm 3.0 ^c	145.5	< 0.001
Grasses	CGR	39.3 \pm 1.9 ^a	1.3 \pm 0.2 ^b	80.3 \pm 2.6 ^c	43.8 \pm 2.4 ^a	80.0 \pm 2.0 ^c	410.1	< 0.001
Tall <i>C. arenaria</i>	CTC	0 ^a	2.4 \pm 0.7 ^a	73.6 \pm 3.6 ^b	26.8 \pm 7.1 ^a	7.0 \pm 2.4 ^a	403.2	< 0.001
Small <i>C. arenaria</i>	CSC	19.8 \pm 1.3 ^a	0 ^b	0 ^b	0 ^b	0 ^b	17.1	< 0.001
Cryptogams	CCR	59.3 \pm 3.0 ^a	66.3 \pm 1.3 ^a	19.3 \pm 1.2 ^b	21.0 \pm 1.5 ^b	37.0 \pm 2.5 ^c	95.6	< 0.001
Bare soil	CBS	13.5 \pm 3.0 ^a	1.0 \pm 0.6 ^b	0 ^b	0 ^b	0.8 \pm 0.8 ^b	94.4	< 0.001
Height of field layer [cm]	HFL	26.5 \pm 1.1 ^a	57.3 \pm 1.7 ^b	70.0 \pm 2.2 ^c	94.3 \pm 8.6 ^{b, c, d}	112.5 \pm 3.2 ^d	136.3	< 0.001
Density ¹ of field layer	DFL	91.8 \pm 5.2 ^a	297.3 \pm 10.4 ^b	349.4 \pm 14.9 ^{b, c}	330.8 \pm 8.2 ^b	395.5 \pm 8.3 ^c	264.2	< 0.001

For abbreviation of successional stages, see Fig. 2. Different letters indicate significant differences (Scheffé post-hoc test at $P < 0.05$)

¹ Sum of mean densities (%) in five different heights of the field layer (0–10, 10–20, 20–30, 30–40, 40–50 cm; maximum = 500%)

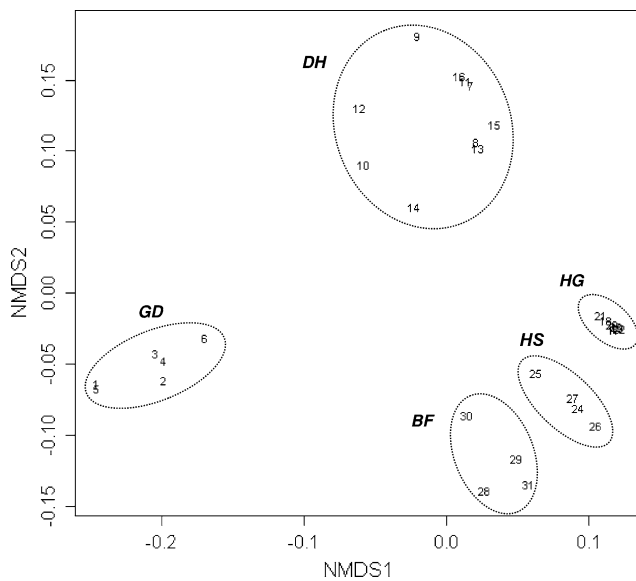


Fig. 2 Nonmetric multidimensional scaling (NMDS) ordination (stress = 6.37, two dimensions) of the 31 plots based on the Euclidean dissimilarity matrix of ten vegetation parameters (Cover of total vegetation, trees, shrubs, grasses, tall *Carex arenaria*, small *C. arenaria*, cryptogams and bare soil; Height of field layer and density of field layer). Plots 1–6: Grey dunes (GD); 7–16: Dwarf-shrub heath (DH); 17–23: Heath encroached by grasses (HG); 24–27: Heath encroached by shrubs (HS); 28–31: Birch forest (BF)

Orthoptera

Capture statistics

In the 31 plots we caught a total of 1,639 Orthoptera individuals belonging to 13 species, seven Caelifera and six Ensifera. Most abundant were the Acrididae *Myrmeleotettix maculatus* (n = 659), *Chorthippus biguttulus* (n = 350) and *Omocestus viridulus* (n = 313), which together comprised 81% of all Orthoptera catches. Three species were rare (*Tettigonia viridissima*, *Tetrix undulata* and *Oedipoda caerulescens*) and made up less than 1.3%. Most widespread were *C. biguttulus* occurring in 24

(fidelity 77%), *M. maculatus* in 20 (65%) and *Decticus verrucivorus* in 19 (61%) of the plots. Species numbers per plot ranged from zero (one plot in birch forest) to eight (two plots in grassy heath).

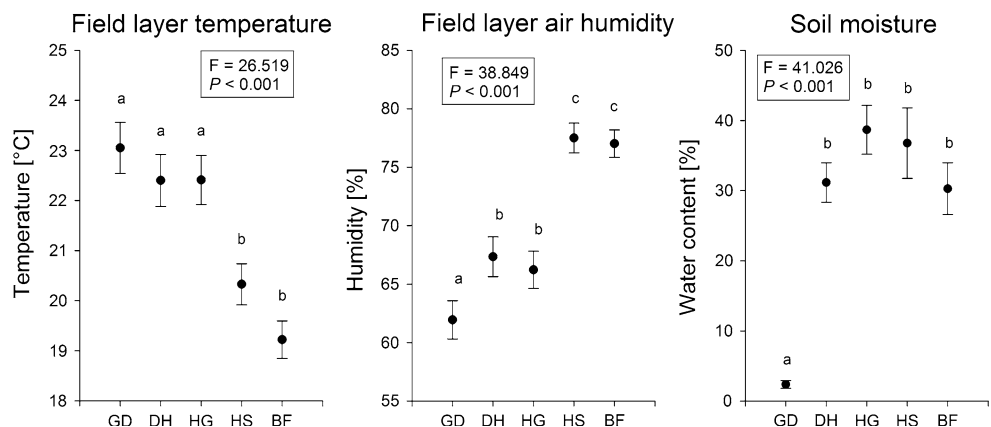
Species richness and densities

Orthoptera species richness differed significantly among successional stages (F = 22.126, P < 0.001). Grassy heath had the highest number of species followed by heath with shrubs, while birch forests had the lowest number (Fig. 4a). Cover of tall *C. arenaria* (CTC) was the only significant predictor of species richness and was positively related with Orthoptera species richness (P < 0.001, goodness of fit of the model 60.72%; GLM). Orthoptera densities also showed significant differences among habitat types (F = 16.673, P < 0.001). Grey dunes had the highest densities followed by grassy heath and heath with shrubs (Fig. 4b). Again, CTC was the only (and positively) related variable (P < 0.001, 68.84%; GLM).

Orthoptera species composition

CCA ordination showed a clear separation of species, and three of the seven environmental variables contributed significantly to the ordination model (Fig. 5, Table 2). The variation in species composition was mainly determined by two environmental gradients: grass cover and air temperature. Occurrences of *O. caerulescens*, *P. albopunctata* and *M. maculatus* were negatively correlated with the cover of tall *C. arenaria* and grasses (GD, DH). In contrast, *C. dorsalis*, *C. albomarginatus* and *O. viridulus* were positively associated with a high cover of grasses and tall *C. arenaria* (HG). *P. griseoptera*, *T. viridissima* and *M. roeselii* were negatively correlated with air temperature and associated with heath with shrubs (HS). While the first two axes of the CCA explained 95% of the variance of the species-environment relations (Table 2), the first two axis

Fig. 3 Comparison of mean values (standard error bars) of **a** field layer temperature, **b** field layer air humidity and **c** soil moisture in five different successional stage of a coastal heath. For abbreviation of successional stages, see Fig. 2. Differences between successional stages were significant for all parameters (one-way ANOVA). Different letters indicate significant differences (Scheffé post-hoc test, P < 0.05)



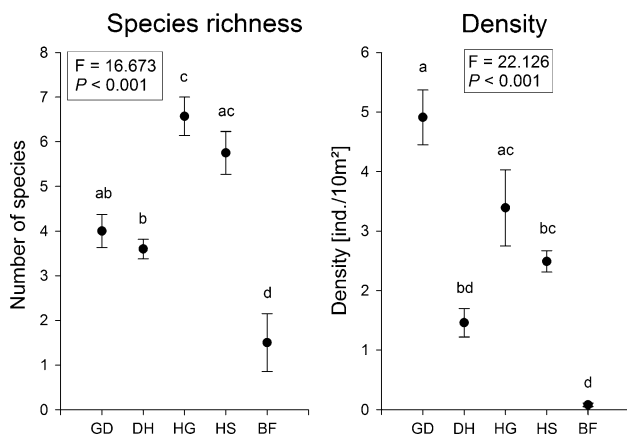


Fig. 4 Orthoptera species richness (*left*) and density (*right*; mean values and standard error bars) in five successional stages in a coastal heath. Parameters differed significantly among successional stages (ANOVA). Different letters indicate significant differences (Scheffé post-hoc test, $P < 0.05$). For abbreviation of successional stages, see Fig. 2

of the CA explained 66% of the variance of the species data.

Orthoptera response to environmental variables

Generalized linear models (GLM) showed significant relations for five species and two life forms (Table 3). Densities of *M. maculatus* were negatively associated with cover of grasses and density of field layer. Densities of *C. biguttulus*, *O. viridulus* and *C. dispar* were positively related to cover of tall *C. arenaria*. *O. viridulus*, *C. dispar* and *M. roeselii* showed a negative response to air temperature. Regarding life forms, the geobionts showed a negative response to cover of grasses and density of field layer, while the geo-chortobionts were positively associated with cover of tall *C. arenaria*. GLM indicated no significant response of densities of chortobionts and thamnobionts to environmental variables.

Patterns of threatened species

Threatened Orthoptera species occurred in grey dunes, dwarf-shrub heath and grassy heath and were absent in the oldest successional stages heath with shrubs and birch forest. The proportion of number of threatened species decreased from grey dunes (50%) over dwarf-shrub heath to grassy heath (Fig. 6).

Discussion

Vegetation characteristics and environmental parameters showed strong differences among the successional stages.

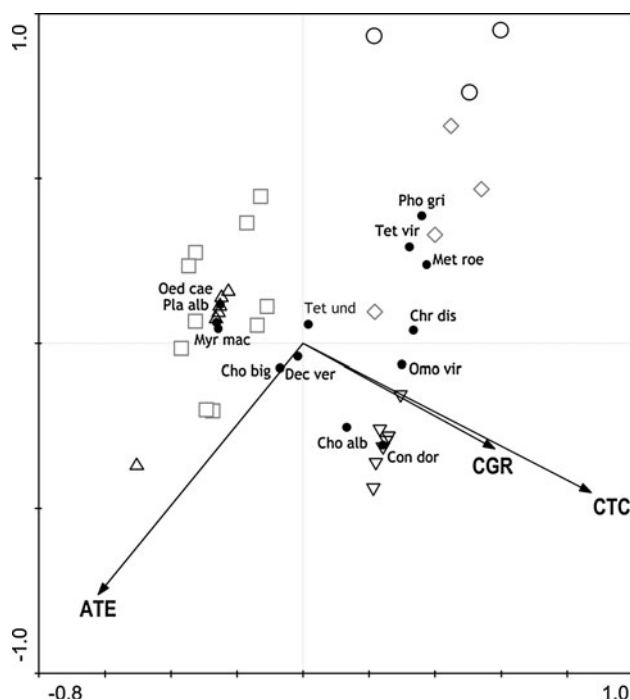


Fig. 5 CCA ordination (sum of all eigenvalues: 1.443) based on Orthoptera data and environmental parameters (*CTV* cover of total vegetation, *CGR* cover of grasses, *CTC* cover of tall *Carex arenaria*, *CBS* cover of bare soil, *DFL* density of field layer, *ATE* air temperature, *SHU* soil humidity). Only significant environmental parameters are shown (at $P < 0.05$, Monte-Carlo permutation test based on 499 permutations). Up-triangles = grey dunes (*GD*), square = dwarf-shrub heath (*DH*), down-triangle = heath encroached by grasses (*HG*), diamond = heath encroached by shrubs (*HS*), circles = birch forest (*BF*, one plot was excluded from the model, because no specimen was observed). Abbreviations of species names: Chr.dis, *Chrysochraon dispar*; Cho.alb, *Chorthippus albomarginatus*; Cho.big, *Chorthippus biguttulus*; Con.dor, *Conocephalus dorsalis*; Dec.ver, *Decticus verrucivorus*; Met.roe, *Metriopectera roeselii*; Myr.mac, *Myrmeleotettix maculatus*; Oed.cae, *Oedipoda caerulescens*; Omo.vir, *Omocestus viridulus*; Pho.gri, *Pholidoptera griseoaptera*; Pla.alb, *Platycleis albopunctata*; Tet.und, *Tetrix undulata*; Tet.vir, *Tettigonia viridissima*

Table 2 Summary of CCA based on Orthoptera data

Environmental axis	1	2	3	4
Eigenvalues	0.642	0.123	0.041	0.177
Species-environment correlations	0.950	0.775	0.729	0.000
Cumulative % variance explained:				
of species data	44.5	53.0	55.9	68.2
of species-environment relation	79.6	94.9	100.0	0.0

Along the successional gradient from grey dunes towards birch forests an increase of vegetation height and density was observed. Due to the effect of vegetation, the microclimate becomes more balanced during this succession. Grey dunes showed the most extreme microclimate with high temperatures and low air humidity, while the

Table 3 Response of Orthoptera species and life forms to environmental variables (for abbreviation, see Table 1)

	CGR		CTC		DFL		ATE		R ²
	F	P	F	P	F	P	F	P	
Life form ^a									
Geobionts	18.75	—*			6.54	—*			86.71
Geo-chortobionts			21.80	+*					60.94
Species									
<i>Myrmeleotettix maculatus</i>	17.57	—*			6.44	—*			86.01
<i>Chorthippus biguttulus</i>			21.65	+*					66.95
<i>Omocestus viridulus</i>			19.03	+**			6.41	—*	79.46
<i>Chrysochraon dispar</i>			10.58	+***			19.01	—***	77.10
<i>Metrioptera roeselii</i>							21.67	—***	77.70

Only significant variables are shown. Positive effects of environmental parameters on species or life form type abundances are indicated as “+”, a negative effect as “—”. The goodness-of-fit of the model is shown as the residual deviance by calculating the pseudo R²

*** P < 0.001; ** P < 0.01; * P < 0.05

^a According to Racz (1998), Nagy et al. (2007) and Schirmel et al. (2010a)

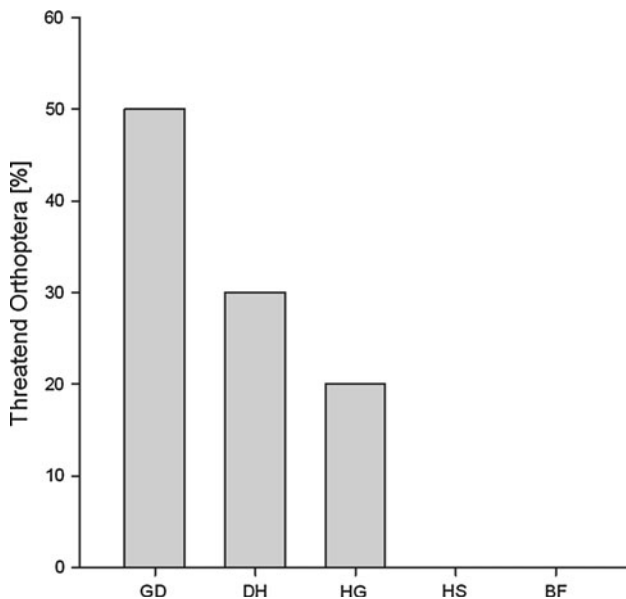


Fig. 6 Proportion of number of regionally scarce and threatened Orthoptera species (“Red list species”; Wranik et al. 2008) within each of the five successional stages. For abbreviation of successional stages, see Fig. 2

microclimatic conditions change continuously towards the successional stages to low temperatures and high air humidity in the birch forests.

Orthoptera strongly responded to these changes in vegetation and environmental conditions. As shown for grasslands (Fartmann and Mattes 1997; Köhler and Kopetz 1993; Marini et al. 2009), Orthoptera are negatively affected by succession, with lower species richness in old successional stages. In this study a similar pattern was observed for heathlands. The latest successional stage, the

birch forest, had by far the lowest species richness and it was highest in the transitional stages of succession grassy heath and heath with shrubs. In these stages chorto- and thamnobiont species and in particular graminivorous Acrididae had their highest species richness. This might be explained by the broad food supply offered in these habitats for many of these Orthoptera species. Heath encroached by graminoids and by shrubs had a relatively high plant biomass. Both successional stages are characterized by a high cover of grasses and tall *C. arenaria*, respectively, reaching a height of more than 70 cm. Besides the high species richness, food supply could also explain the high densities of chortobiont Orthoptera. In the present study these are mainly the chortobiont Acrididae species *C. biguttulus*, *C. dispar* and *O. viridulus*. Particularly, cover of tall *C. arenaria* was significantly positively correlated with densities of these Acrididae, especially in grass-encroached heath. In addition, food quality (content of N) might be enhanced due to eutrophication. In general, abundances of herbivores (Berdowski 1993; Whittaker 1988) and grasshopper growth rate (Strengbom et al. 2008) seem to increase with an increased N content. Besides food supply, grassy heath and heath with shrubs might offer favorable egg-laying substrates to species that oviposit in plants such as the chortobiont species *M. roeselii*, *C. dispar* and *C. dorsalis* (Fartmann and Mattes 1997; Ingrisch and Köhler 1998; Lehmann and Haacks 2006). This explains why *C. dorsalis* which normally occurs in wet habitats with pithy Juncaceae, Cyperaceae and Poaceae (Detzel 1998; Lehmann and Haacks 2006) occurs in the dry habitat of grass-encroached heath. Especially in the transitional stage heath with shrubs, also the thamnobiont species *T. viridissima* and *P. griseopatera* were common, which might be

explained by the occurrence of suitable singing sites in higher vegetation (*T. viridissima*; Arak and Eiriksson 1992) and moderate microclimate conditions with lower temperatures and a higher air humidity (*P. griseoptera*; Detzel 1998). In general, Ensifera species are less negatively affected by the presence of shrubs or trees (Bieringer and Zulka 2003), as many species are thamnobiont and inhabiting forest edges (Racz 1998).

Compared to the transitional stages grassy heath and heath with shrubs, species richness was remarkably lower in the younger and less productive grey dunes and dwarf-shrub heath. Since microclimate conditions of dwarf-shrub heath were similar to grassy heath (Fig. 3), differences in Orthoptera species richness, densities and composition have to be based on vegetation composition. The dwarf-shrub heath was almost free of grasses and therefore offers only a slender food supply for species specialized on grasses, which might explain the low overall densities of Orthoptera and the occurrence of other than graminivorous species such as *D. verrucivorus* (omnivorous), *P. albopunctata* (partly phytophagous) and *M. maculatus* (only partly graminivorous) in this stage. Dwarf-shrub heath therefore seems to have only a low relevance for Orthoptera (Schirmel et al. 2010b). In contrast, the sparsely vegetated grey dunes showed the highest total Orthoptera densities of all studied successional stages which is mainly caused by high abundances of the heat-loving grasshoppers *M. maculatus* and *C. biguttulus* (Schirmel et al. 2010a, b). This is especially true for the geobiont *M. maculatus* (40% of the total catch), which prefers habitats with scarce vegetation (Willot and Hassall 1998), indicated by a negative response to density of field layer and cover of grasses in this study. Although the grey dunes might also offer an adequate food supply (grass cover about 40%) the occurring grasses in grey dunes (*Corynephorus canescens*, small *Carex arenaria*) possibly have a reduced food quality (Zehm 1997). Due to the extreme microclimatic conditions in open grey dunes and dwarf-shrub heath a high proportion of specialised, xero- and thermophilic species occurred. Within the study area of the coastal heathland, regionally scarce and threatened species such as *O. caerulea* and *P. albopunctata* occurred exclusively in open grey dunes and dwarf-shrub heath. With the presence of (tall grasses and) shrubs, these specialised species quickly disappear.

In order to maintain a high diversity of Orthoptera in heathlands, the presence of different successional stages is of outstanding importance. While younger stages (grey dunes and dwarf-shrub heath) offer favorable conditions to specialised (xero and thermophilic) and regionally threatened species (Schirmel et al. 2010a), transitional stages are important for several chortobiont and graminivorous species as well as for thamnobionts (mostly Ensifera).

Implication for conservation

Based on our results, conservation practice should aim at maintaining a heterogeneous heathland mosaic with open grey dunes and *Calluna* stands in addition to scattered grassy and shrub-encroached heath for the survival of species-rich heathland Orthoptera assemblages with high densities (Schirmel et al. 2010a). Sheep grazing, reintroduced a few years ago, seems to be a positive measure to preserve the coastal dune heath. However, grazing and trampling can have negative impacts on some (threatened) dune animals (Maes and Bonte 2006, Bonte and Maes 2008). In contrast, the restoration of eolian dynamics, which enhances sand dynamics, might be a more successful conservation measure (Bonte et al. 2003; Maes and Bonte 2006). In addition, the regular but moderate use of paths and dunes by people seeking for recreation might be beneficial for the protection of dynamic grey dunes (Bonte and Maes 2008). Also modern and intensive management measurements such as sod-cutting, choppering or mowing are known to preserve heathlands on a long-term basis (Niemeyer et al. 2007; Power et al. 2001). These measurements could counteract high nutrient loads (eutrophication) and the appropriate application of these measures might contribute to a heathland mosaic consisting of different successional stages. Especially the creation of disturbed and highly dynamic habitats (e.g. sand blow) similar to younger and more pristine successional stages might be of great importance for oviposition and thermo-regulation of threatened species (Maes et al. 2006).

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References

- Arak A, Eiriksson T (1992) Choice of singing sites by male bushcrickets (*Tettigonia viridissima*) in relation to signal propagation. *Behav Ecol Sociobiol* 30:365–372
- Báldi A, Kisbenedek T (1997) Orthopteran assemblages as indicators of grassland naturalness in Hungary. *Agric Ecosyst Environ* 66:121–129. doi:10.1016/S0167-8809(97)00068-6
- Balmer O, Erhardt A (2000) Consequences of succession on extensively grazed grasslands for central European butterfly communities: rethinking conservation practices. *Conserv Biol* 14:746–757
- Baur B, Cremene C, Groza G, Rakosy L, Schileyko AA, Baur A, Stoll P, Erhardt A (2006) Effects of abandonment of subalpine hay meadows on plant and invertebrate diversity in Transylvania, Romania. *Biol Conserv* 132:261–273
- Bellmann H (2006) *Der Kosmos Heuschreckenführer. Die Arten Mitteleuropas sicher bestimmen*, Kosmos, Stuttgart

- Berdowski JJM (1993) The effects of external stress and disturbance factors on *Calluna*-dominated heathland vegetation. In: Aerts RH, Heil GW (eds) Heathlands: patterns and processes in a changing environment. Kluwer, Dordrecht, pp 85–124
- Bieringer G, Zulka KP (2003) Shading out species richness: edge effect of a pine plantation on the Orthoptera (Tettigoniidae and Acrididae) assemblage of an adjacent dry grassland. *Biodivers Conserv* 12:1481–1495. doi:10.1023/A:1023633911828
- Bonte D, Maes D (2008) Trampling affects the distribution of specialized coastal dune arthropods. *Basic Appl Ecol* 9:726–734
- Bonte D, Criel P, Van Thournout I, Maelfait J-P (2003) Regional and local variation of spider assemblages (Araneae) from coastal grey dunes along the North Sea. *J Biogeogr* 30:901–911
- Britton AJ, Pakeman RJ, Carey PD, Marrs RH (2001) Impacts of climate, management and nitrogen deposition on the dynamics of lowland heathland. *J Veg Sci* 12:797–806
- Coray A, Lehmann AW (1998) Taxonomie der Heuschrecken Deutschlands (Orthoptera): Formale Aspekte der wissenschaftlichen Namen. *Articulata*, Beiheft 7:63–152
- Cuesta D, Taboada A, Calvo L, Salgado JM (2008) Short- and medium-term effects of experimental nitrogen fertilization on arthropods associated with *Calluna vulgaris* heathlands in north-west Spain. *Environ Pollut* 152:394–402
- Curry JP (1994) Grassland Invertebrates—Ecology, influence on soil fertility and effects on plant growth. Chapman and Hall, London
- Detzel P (1998) Die Heuschrecken Baden-Württembergs. Ulmer, Stuttgart
- Dobson AJ (2002) Introduction to generalized linear models, 2nd edn. Chapman and Hall, London
- Fartmann T, Mattes M (1997) Heuschreckenfauna und Grünland—Bewirtschaftungsmaßnahmen und Biotopmanagement. *Arbeiten aus dem Institut für Landschaftsökologie* 3:179–188
- Fielding AH, Haworth PF (1995) Testing the generality of bird-habitat models. *Conserv Biol* 9:1466–1481
- Gardiner T, Hill J, Chesmore D (2005) Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. *J Insect Conserv* 9:151–173. doi:10.1007/s10841-005-2854-1
- Gimingham CH (1972) Ecology of heathlands. Chapman Hall, London
- Heil GW, Diemont WH (1983) Raised nutrient levels change heathland into grassland. *Vegetatio* 53:113–120
- Ingrisch S, Köhler G (1998) Die Heuschrecken Mitteleuropas. Westarp-Wissenschaften, Magdeburg
- Köhler G, Kopetz A (1993) Veränderungen in Heuschrecken (Saltatoria)-Assoziationen als Folgen der Verbuschung von Kalktrockenrasen. *Arch Nat Lands* 32:147–159
- Kruess A, Tschamtker T (2002a) Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biol Conserv* 106:293–302
- Kruess A, Tschamtker T (2002b) Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv Biol* 16:1570–1580
- Lehmann AW, Haacks M (2006) Vorkommen von *Conocephalus dorsalis* (Latreille, [1804]) in vom Salzwasser beeinflussten Habitaten der schleswig-holsteinischen Nord- und Ostseeküste. *Articulata* 21:161–167
- Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University press, New York
- Leuschner C, Lenzion J (2009) Air humidity, soil moisture and soil chemistry as determinants of the herb layer composition in European beech forests. *J Veg Sci* 20:288–298
- Leyer I, Wesche K (2007) Multivariate Statistik in der Ökologie. Springer, Berlin
- Londo G (1976) Scale for relevés of permanent quadrats. *Vegetatio* 33:61–64
- Londo G (1984) The decimal scale for relevés of permanent quadrats. In: Knapp R (ed) Sampling methods and taxon analysis in vegetation science. Handbook of vegetation science. Springer, The Hague, pp 45–49
- Maes D, Bonte D (2006) Using distribution patterns of five threatened invertebrates in a highly fragmented dune landscape to develop a multispecies conservation approach. *Biol Conserv* 133:490–499
- Maes D, Ghesquiere A, Logie M, Bonte D (2006) Habitat use and mobility of two threatened coastal dune insects: implications for conservation. *J Insect Conserv* 10:105–115
- Marini L, Fontana P, Battisti A, Gaston KJ (2009) Response of orthopteran diversity to abandonment of semi-natural meadows. *Agric Ecosyst Environ* 132:232–236
- Marrs RH (1993) An assessment of changes in *Calluna* heathlands in Breckland, Eastern England, between 1983 and 1991. *Biol Conserv* 65:133–139
- Nagy A, Sólymos P, Rácz IA (2007) A test on the effectiveness and selectivity of three sampling methods frequently used in orthopterological field studies. *Entomol Fennica* 18:149–159
- Niemeyer M, Niemeyer T, Fottner S, Härdtle W, Mohamed A (2007) Impact of sod-cutting and choppering on nutrients budgets of dry heathlands. *Biol Conserv* 134:344–353. doi:10.1016/j.biocon.2006.07.013
- Öckinger E, Eriksson AK, Smith HG (2006) Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biol Conserv* 133:291–300
- Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MH, Wagner H (2008) The vegan package version 1.15-0. Online at: <http://cran.r-project.org/>, [http://vegan.r-forge.r-project.org/\(27.04.2009\)](http://vegan.r-forge.r-project.org/(27.04.2009))
- Power SA, Barker CG, Allchin EA, Ashmore MR, Bell JNB (2001) Habitat Management: a tool to modify ecosystem impacts of nitrogen deposition. *Sci World J* 1:714–721. doi:10.1100/tsw.2001.379
- Racz IA (1998) Biogeographical survey of the Orthoptera fauna in central part of the Carpathian Basin (Hungary): fauna types and community types. *Articulata* 13:53–69
- Reinhard H (1962) Klimatologie. Atlas der Bezirke Rostock, Schwerin und Neubrandenburg. VEB Topographischer Dienst, Schwerin
- Remke E (2003) Vegetationsökologischer Vergleich von Heidegebieten der Insel Hiddensee, Mecklenburg-Vorpommern. Diploma thesis, University of Greifswald
- Remke E, Brouwer E, Kooijman A, Blindow I, Esselink H, Roelofs JGM (2009a) Even low to medium nitrogen deposition impacts vegetation of dry, coastal dunes around the Baltic Sea. *Environ Pollut* 157:792–800
- Remke E, Brouwer E, Kooijman A, Blindow I, Roelofs JGM (2009b) Low Atmospheric nitrogen loads lead to grass encroachment in coastal dunes, but only on acid soils. *Ecosystems* 12:1173–1188
- Roem WJ, Klees H, Berendse F (2002) Effects of nutrient addition and acidification on plant species diversity and seed germination in heathland. *J Appl Ecol* 39:937–948
- Rose RJ, Webb NR, Clarke RT, Traynor CH (2000) Changes on the heathlands in Dorset, England, between 1987 and 1996. *Biol Conserv* 93:117–125
- Samways MJ (1997) Conservation biology of Orthoptera. In: Gangwere SK, Muralirangan MC, Muralirangan M (eds) The Bionomics of Grasshoppers. Katydid and their Kin. CAB International, Wallingford, pp 481–496
- Schirmel J, Buchholz S, Fartmann T (2010a) Is pitfall trapping a valuable sampling method for grassland Orthoptera? *J Insect Conserv* 14:289–296. doi:10.1007/s10841-009-9258-6
- Schirmel J, Blindow I, Fartmann T (2010b) The importance of habitat mosaics for Orthoptera (Caelifera and Ensifera) in dry heathlands. *Eur J Entomol* 107:129–132

- Sjursen H, Michelsen A, Jonasson S (2005) Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems. *Appl Soil Ecol* 30:148–161
- Skórka P, Settele J, Woyciechowski M (2007) Effects of management cessation on grassland butterflies in southern Poland. *Agric Ecosyst Environ* 121:319–324
- Ssymank A, Hauke U, Rückriem C, Schröder E (1998) Das europäische Schutzgebietssystem NATURA 2000–BfNHandbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie und der Vogelschutz-Richtlinie. *Schriftenr Landschaftspfl Natursch* 53:1–560
- Strengbom J, Reich PB, Ritchie ME (2008) High plant species diversity indirectly mitigates CO₂- and N-induced effects on grasshopper growth. *Acta Oecologia* 34:194–201
- Sundermeier A (1998) Methoden zur Analyse der Vegetationsstruktur. In: Traxler A (ed) *Handbuch des vegetationsökologischen Monitorings*. Teil A: Methoden. Umweltbundesamt Wien:123–158
- Venables WN, Ripley B (2008) The VR package version 7.2-45. Online at: [http://www.stats.ox.ac.uk/pub/MASS4/\(27.04.2009\)](http://www.stats.ox.ac.uk/pub/MASS4/(27.04.2009))
- Webb NR (1998) The traditional management of European heathlands. *J Appl Ecol* 35:987–990
- Whittaker JB (1988) Response of the heather psyllid, *Strophingia ericae* to addition of fertiliser to *Calluna* on heath and moorland. *Bull Br Ecol Soc* 16:102–104
- Willot SJ, Hassall M (1998) Life-history responses of British grasshoppers (Orthoptera: Acrididae) to temperature change. *Func Ecol* 12:232–241
- Wranik W, Meitzner V, Martschei T (2008) Verbreitungsatlas der Heuschrecken Mecklenburg-Vorpommerns. Beiträge zur floristischen und faunistischen Erforschung des Landes Mecklenburg-Vorpommern, LUNG M-V
- Zehm A (1997) Untersuchungen zur Nahrungswahl von Heuschrecken (Orthoptera) in zwei Sand-Pioniergesellschaften der nördlichen Oberrheinebene. *Articulata* 12:131–140
- Zuur AF, Ieno IN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, Berlin