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The classification of insect communities: Lessons from orthopteran assemblages of semi-dry calcareous grasslands in central Germany

DOMINIK PONIATOWSKI and THOMAS FARTMANN*

Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Robert-Koch-Straße 26, 48149 Münster, Germany

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Abstract. Whereas the classification of plant communities has a long tradition that of animal assemblages remains poorly developed. Here we propose a classification scheme for orthopteran communities based on regional "character species", "differential species" and "attendant species" at different levels of habitat complexity, which is also applicable to other insect groups. In this context there are three main points of special importance: (i) the geographical reference area, (ii) the hierarchical spatial level (e.g. habitat complex, habitat and microhabitat) and (iii) precise constancy criteria for the definition of character species and differential species. We develop this new approach using a study on orthopteran communites of central German semi-dry calcareous grasslands. Within this habitat, we describe seven structural types that are characterized by specific orthopteran communities. For the arrangement of the structural types several environmental parameters (e.g. height and density of vegetation) were collected. Orthopteran densities were sampled at 80 sites using a biocoenometer (box quadrat). Regional character species of semi-dry grasslands include *Myrmeleotettix maculatus*, *Metrioptera brachyptera*, *Stenobothrus lineatus* and *Tetrix tenuicornis*. Within this habitat, *Chorthippus parallelus*, *Metrioptera roeselii*, *Omocestus viridulus*, *Pholidoptera griseoaptera* and *Tettigonia viridissima* were designated as differential species for particular structural types. Furthermore, *Tettigonia cantans* and *Tettigonia viridissima* act as altitudinal differential species. *Chorthippus biguttulus* is the only attendant species with high constancy values in all structural types. This classification is a powerful tool for arthropod conservation, since it allows one to determine community completeness of very important and threatened habitats, like semi-dry calcareous grasslands.

INTRODUCTION

A major goal of synecology is to analyse the composition and structure of plant and animal communities. The composition of plant communities attracted considerable interest during the past century, leading to the development of various global and regional classification approaches. In central Europe, vegetation synecology is dominated by the floristic-sociological or Braun-Blanquet (Zürich-Montpellier) approach (Mucina, 1997). As a basic principle, this approach classifies communities by the absence or presence of species with highly specific ecological niches, so called diagnostic species. Identification of diagnostic species is based on the constancy (fidelity) with which they occur in an array of plots that share important abiotic and biotic conditions. Nowadays, classification rules for plant communities allow highly differentiated characterizations of local ecological conditions (Bruelheide, 2000; Chytrý et al., 2002; Dengler, 2003).

There are no comparable standards for the characterization of terrestrial animal communities. Recently, some studies in central Europe attempted to make the classification of animal communities more transparent. Similar to phytosociology, they defined character species and differential species based on their fidelity to study plots with shared environmental conditions as the two diagnostic groups (Seitz, 1989; Flade, 1994; Fartmann, 1997; Schultz & Finch, 1997; Behrens & Fartmann, 2004a). However, the definitions of the diagnostic species in these studies were arbitrary. A unified classification system also needs to take into account at which spatial level animal communities are studied. Studies on animal communities typically occur at three spatial levels: (i) the level of habitat complexes or plant-community complexes, often coinciding with a landscape-level approach; (ii) the level of single habitats or single plant-communities; and (iii) the level of structural habitat composition, which may vary within a habitat or plant community (Kratochwil & Schwabe, 2001). Here we develop a method for the assignment of regional character, differential and attendant species to structural types that is applicable to a wide array of other insect groups and other hierarchical levels.

Habitat selection in Orthoptera is the result of their responding to a complex combination of different and often interrelated environmental factors (see review in Ingrisch & Köhler, 1998). Within these parameters, the microclimate at oviposition sites, which is often affected by vegetation structure, plays a crucial role (Oschmann, 1973; Uvarov, 1977; Anderson et al., 1979; Willott & Hassall, 1998). As cold-blooded organisms, most Orthoptera require high ambient temperatures for optimal growth and development (Chappell & Whitman, 1990). Because of their high diversity, functional importance and sensitivity to environmental change (Báldi & Kisbenedek,

* Corresponding author; e-mail: fartmann@uni-muenster.de

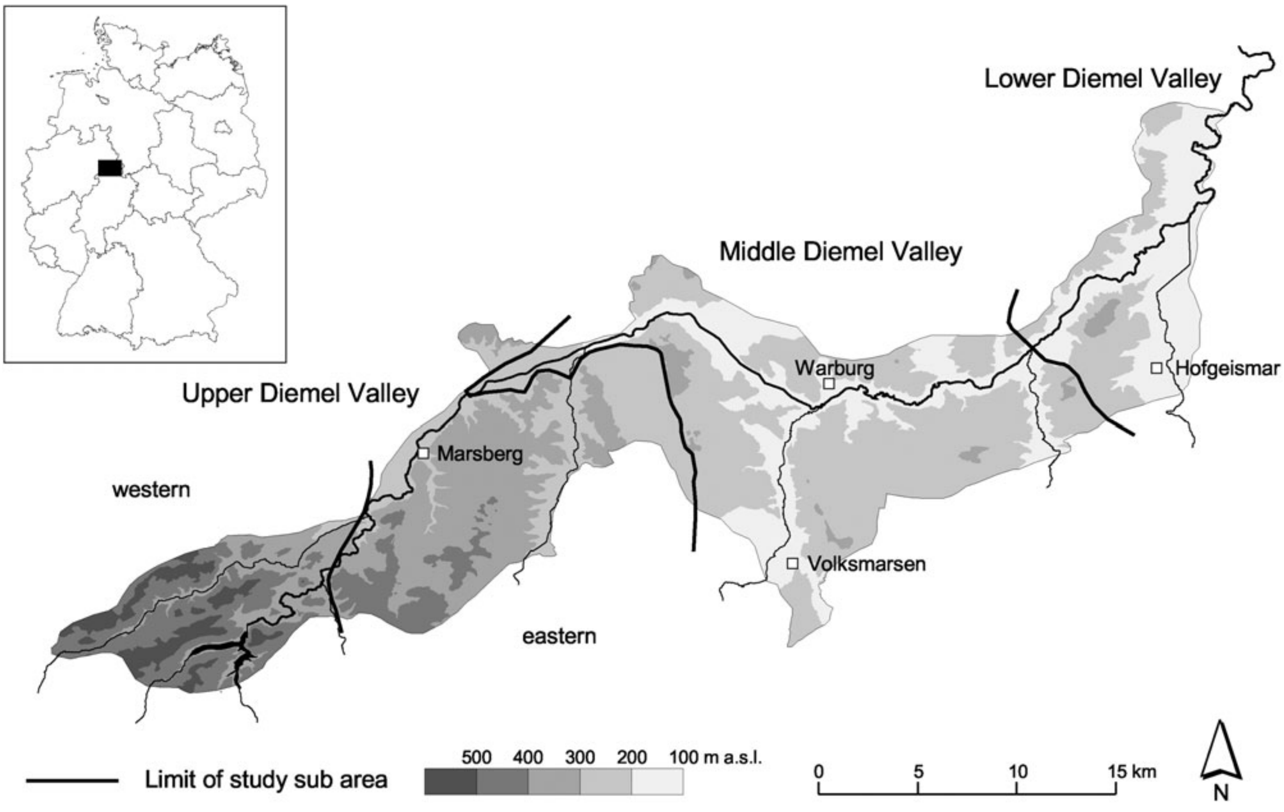

Fig. 1. The study area; the Diemel Valley and its sub areas in northwestern Germany (inlay).

1997; Samways, 1997; Andersen et al., 2001; Szövényi, 2002; Bieringer & Zulka, 2003), we expect Orthoptera to be highly indicative of grassland characteristics. The relatively good knowledge of their taxonomy and distribution as well as the ease with which they can be sampled make Orthoptera suitable subjects for ecological and biogeographical community studies (Sergeev, 1997; Lockwood & Sergeev, 2000). In recent decades, there have been several studies on orthopteran assemblages in the northern hemisphere; especially in North America, where different aspects of rangeland grasshopper communities have been studied in detail (e.g. Kemp et al., 1990; Kemp 1992a, b; Fielding & Brusven, 1993; 1995; Joern, 2004, 2005; Jonas & Joern, 2007). Most of the community studies done in the Palaearctic are for central Europe and address dry and semi-dry grassland habitats (e.g. Sänger, 1977; Fartmann, 1997; Zehm, 1997; Hemp & Hemp, 2000; Behrens & Fartmann, 2004a).

The current study was conducted in semi-dry calcareous grasslands in the Diemel Valley (central Germany). Despite a recent decrease in area, the size of these calcareous grasslands in Germany is only matched by some regions in the south (Fartmann, 2004, 2006). An important attribute of these semi-natural habitats is their structural and floristic diversity and species-rich fauna (WallisDeVries et al., 2002; van Swaay, 2002; Fartmann, 2004). Thus, these open habitats are important for many orthopteran species (Detzel, 1998; Schlumprecht, 2003). Due to their importance calcareous grasslands are listed in the Habitats Directive of the European Union and the orchid-rich stands are priority habitats (Ssymank et al., 1998).

A biogeographic study on the grasshopper and cricket fauna of the semi-dry grasslands of the Diemel Valley was recently published by Poniatowski & Fartmann (2006). However, there is no description of the orthopteran communities of the largest continuous area of calcareous grassland in Northwest Germany. Therefore, the objective of this investigation of the orthopteran communities in the semi-dry calcareous grasslands of the Diemel Valley was to (i) investigate orthopteran species composition of sites that are broadly similar in plant community but differ in vegetation structure, (ii) define character and differential species for the classification of the communities, (iii) analyse orthopteran habitat requirements in relation to habitat structure and microclimate.

MATERIAL AND METHODS

Study area

The study area (hereafter called Diemel Valley) of about 500 km² is located in central Germany along the border between the federal states of North Rhine-Westphalia and Hesse (51°22´N/8°38´E and 51°38´N/9°25´E) at an elevation of 160 to 480 m a.s.l. (Fig. 1). The climate is subatlantic and varies greatly according to altitude (Müller-Wille, 1981). The Upper Diemel Valley (300–500 m a.s.l.) is the coldest and wettest section with mean temperatures of 6.5–8°C and an annual precipitation of 700–1,000 mm (Table 1). The Middle and Lower Diemel Valley (< 300 m a.s.l.) in the eastern part of the study area have a relatively mild climate with less than 800 mm annual precipitation and an average annual temperature of up to

TABLE 1. Characteristic environmental factors of sub areas of the Diemel Valley (modified after Fartmann, 2004).

	Diemel Valley			
	Upper		Middle	Lower
	Western	Eastern		
Biogeographic region	Bergisch-Sauer-ländisches Gebirge	Bergisch-Sauerländisches Gebirge, Hessisches Berg- and Senkenland	Hessisches Berg- and Senkenland, Oberes Weserbergland	Hessisches Berg- and Senkenland, Oberes Weserbergland
Bedrock	Shale, quartzite and diabas	Zechstein limestone and brownstone	Shell limestone, keuper and loess	Shell limestone, brown-stone and fluviatile sedi-ments
Soil	Base-rich brown earth and ranker brown earth	Rendzina, base-rich and base-poor brown earth	Rendzina and lessivé	Rendzina and lessivé
Altitude (m a.s.l.)	400–500	300–400	200–300	100–200
Annual precipitation (mm)	850–1,000	700–850	600–800	650–800
Annual temperature (°C)	6.5–8	7.5–8	8–8.5	7.5–9

9°C (Müller-Temme, 1986; MURL NRW, 1989; Fartmann, 2004).

For a detailed description of the study sites see Poniatowski (2006). Further information on geology, soils, climate, vegetation and nature conservation is available in Fartmann (2004, 2006).

Study design

A total of 80 plots at 26 sites on calcareous soils were analysed in order to characterize orthopteran communities of the semi-dry grasslands of the Diemel Valley. For each plot, we recorded the following environmental parameters (Table 2).

Climate

Aspect and slope of the plots were recorded by using a compass with an inclinometer. Maximal average sunshine duration for August was determined using a horizontoscope (Tonne, 1954).

Plant communities

For assessing the plant community at each plot a mapping key was prepared, based on character and differential species and/or dominant species (Dierschke, 1994). Fartmann (2004) acted as a phytosociological reference. Nomenclature of plant species and plant communities follow Wisskirchen & Haeupler (1998) and Rennwald (2000), respectively.

Vegetation structure

All study plots, each with a minimum size of 500 m² (e.g. Behrens & Fartmann, 2004a; Poniatowski & Fartmann, 2005), had a homogenous vegetation structure (Sänger, 1977). This means that the vegetation height, density and cover were more or less uniform. The measurement of structural parameters took place after the quantitative sampling of Orthoptera (see below) in an undisturbed section of the plot. Based on these structural parameters, plots with a similar structure were grouped in structural types (e.g. Fartmann, 1997; Behrens & Fartmann, 2004a; Poniatowski & Fartmann, 2005) (see below, data analysis).

Horizontal structure: We recorded (in 5% steps) total vegetation cover, the cover of litter, mosses/lichens, grasses/herbs, shrubs as well as bare ground, gravel, stones and rocks. In cases where cover was above 95% or below 5%, according to Behrens & Fartmann (2004a) 2.5% steps were used.

Vertical structure: The average vegetation height, the vegetation layer with the highest solar-irradiation conversion, was ascertained with an accuracy of 2.5 cm. Horizontal vegetation density (Sundermeier, 1998) was estimated using a 50 cm wide and 30 cm deep wire framed box (Mühlenberg, 1993), which was open on all sites except the back. Horizontal wires on the

TABLE 2. The parameters used in the Detrended Correspondence Analysis (DCA) and structural type (st) characterization.

	Type	Study part
Climate		
Aspect (“eastness”, “northness”)[1]	(°)	DCA*
Inclination	(°)	DCA*
Potential daily sunshine duration[2]	(h)	DCA
Altitude	(m a.s.l.)	DCA
Vegetation structure		
Cover of different layers[3]	(%)	DCA**, st
Vegetation height	(cm)	DCA*, st
Horizontal vegetation density[4]	(%)	DCA, st
Habitat characteristics		
Vegetation type	nominal	st

[1]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°); [2]measured using a horizontoscope (Tonne, 1954) for August, accuracy: ½ h; [3]for categories (s. text), the sum of bare ground and stony surface (gravel, stones and rocks) is used in DCA; [4]different layers (s. text), the sum of all layers is used in DCA; *parameters that did not have a significant influence on total variance (forward selection, Monte-Carlo permutation test); **only bare ground/ stony surface, shrubs and cryptogams (mosses and lichens) had a significant influence on total variance (forward selection, Monte-Carlo permutation test).

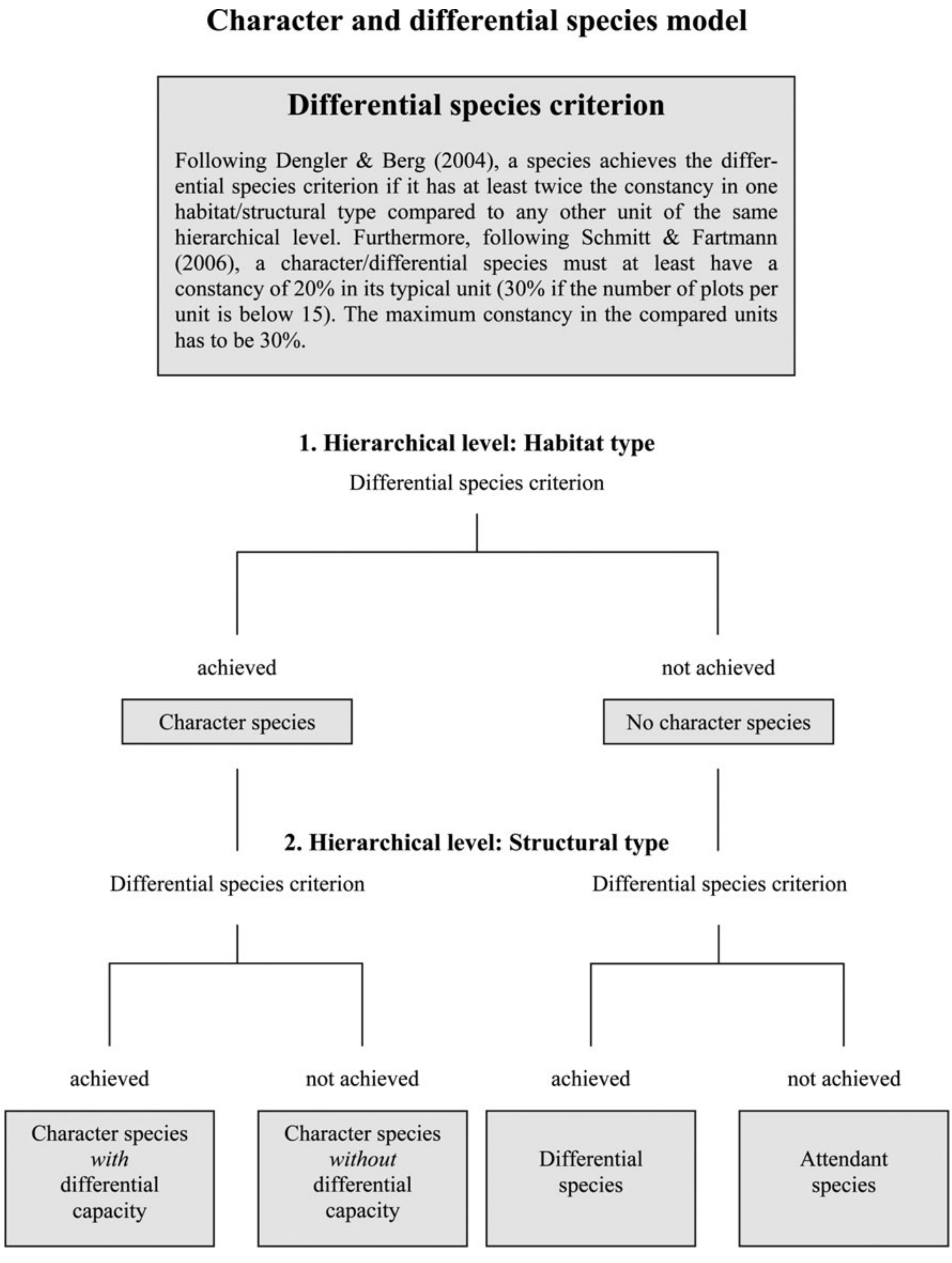

Fig. 2. Character and differential species for the classification of insect communities.

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 (the reciprocal value is the horizontal vegetation density) against the bright back of the box, using same classes as for the horizontal structure.

Orthopteran sampling

For orthopteran sampling every plot was visited twice: The first survey (between the end of April and beginning of June) was used to detect tetrigids, which reach their population peaks during this period (Fartmann, 1997). For this purpose the sites with bare ground were searched visually. Quantitative sampling of all orthopteran species in open habitats took place during mid–July and the beginning of August. Orthopteran densities were recorded using a biocoenometer (box quadrat) with sides of 0.8 m (Behrens & Fartmann, 2004a; Gardiner et al., 2005; Poniatowski & Fartmann, 2005; Fartmann et al., 2008). The mobile 0.5 m² box quadrat was randomly placed at forty different points per plot (= 20 m² surveyed area per plot).

Orthoptera species were identified in the field and then released. Species, sex and stage (nymph or imago) were noted for all specimens. Adults were identified using Bellmann (1993) and Horstkotte et al. (1994), for nymphs we used Oschmann (1969) and Ingrisch (1977). Identification of nymphs of the sibling species *Chorthippus biguttulus* and *C. brunneus* was not possible. They were merged in the *C. bigutullus* group. Due to the rarity of *C. brunneus* in the semi-dry grasslands of the study area (Poniatowski & Fartmann, 2006), nearly all nymphs of the group are likely to belong to *C. biguttulus*. Tetrigids (adults and nymphs) were identified using the key in Schulte (2003). Scientific nomenclature followed Coray & Lehmann (1998).

Data analysis

Plots with similar vegetation structure (structural types) were classified using Ward's method of agglomerative clustering based on Euclidean distance (Bacher, 1994; Jongman et al., 1995). Eight variables were imported to the statistical package SPSS 11.0: Total vegetation cover, cover of the field layer, cover of gravel, stones and rocks (from now on called stony surface), cover of bare ground, height of the field layer and horizontal vegetation density at three heights (0–5 cm, 5–10 cm and 10–15 cm). Prior to the analysis values were z-tranformed.

Classification of orthopteran communities follows a method that is based on the assignment of character and/or differential species to a habitat (here: semi-dry calcareous grasslands) and every structural type within this habitat (Fig. 2). The validity of every diagnostic species is restricted to distinct biogeographical regions (here: the Diemel Valley). Furthermore, the method can be used for the determination of altitudinal differential species.

As the basic unit for the evaluation of character and differential species we use the differential species criterion after Dengler & Berg (2004) with additions by Schmitt & Fartmann (2006) (Fig. 2). The basis for this is the percentage constancy of the species in a habitat or structural type (calculated using the results of the quantitative orthopteran sampling). For the identification of character and differential species we take into account that the different developmental stages (nymphs, adults) have different phenologies. Thus, only one of the stages has to fulfil the differential species criterion.

There are generally two hierarchical levels:

Habitat type

First, we check at the level of a biogeographic region, if a species is restricted to a single habitat (regional character species) or occurs in several distinct habitats (not a character species) (for exact constancy definitions see Fig. 2). This evaluation requires knowledge of the constancy values of this species in all potentially suitable habitats (Seitz, 1989). Community studies rarely provide both the constancy of species in an array of habitats and different structural types within each habitat. However, the large-scale relationship between a certain species and habitats are much better documented than the preferences for structures within each habitat. Because of the lack of constancy values at the habitat level we classified character species on the basis of information in the literature (for the study area and its vicinity: Ingrisch, 1981, 1982; Schulte, 1997, 2003; Hill & Beinlich, 2001; Poniatowski & Fartmann, 2005, 2006, 2007).

Structural types

This step analyses the orthopteran communities in different structural types within a habitat (here: semi-dry calcareous grassland) (for the classification of the structural type see above). If a species meets the differential species criterion (see above) it is classified – depending on the initial position (character species or not) – a "character species with differential capacity" or a "differential species" (Fig. 2). In both cases, the species indicates certain qualities of the structural types (e.g. high vegetation cover). A differential species, unlike a character species with differential capacity, can also be found in other habitats in a particular biogeographic region. If the differential species criterion does not apply, the considered species is – depending on the initial position (character species or not) – either a "character species without differential capacity" or an "attendant species" (Fig. 2). The latter shows no preference for certain structural types, this means that the constancy is high in all structural types or the species is generally very rare (Fartmann, 1997).

Besides the presence of a species (here constancy), the dominance within a community is a further criterion of the suitability of a structural type for the species (Ingrisch & Köhler, 1998). Thus, for every structure the dominance of every species was calculated and classified according to the dominance classes of Engelmann (1978) (eudominant ≥ 32%, dominant = 10.0–31.9%, subdominant = 3.2–9.9%).

Detrended Correspondence Analysis (DCA) (using CANOCO 4.51; Hill, 1979; Hill & Gauch, 1980; ter Braak & Šmilauer, 2002), an indirect gradient ordination technique, was used to examine orthopteran community trends and relations between habitat structure and species composition (Fielding & Brusven, 1993, 1995; Torrusio et al., 2002; Gebeyehu & Samways, 2003, 2006). DCA is commonly used in vegetation and community ecology (Kratochwil & Schwabe, 2001) and requires a unimodal distribution of the species. The following adjustments were carried out: Detrending by segments, no transformation.

RESULTS

Orthopteran communities and structural types

Based on the structural parameters the 80 plots could be placed in one of seven structural types characterized by increasing vegetation height and density (= productivity and biomass gradient) from type 1 to type 7 (Table 3). Each structural type was characterized by a specific set of character species, differential species and attendant species and thus a specific orthopteran community.

Information in the literature (e.g. Ingrisch, 1981; Schulte, 1997, 2003; Poniatowski & Fartmann, 2006) indicates, that four species fulfill the criterion of a regional character species for the semi-dry calcareous grasslands in the Diemel Valley: *Myrmeleotettix maculatus*, *Tetrix tenuicornis*, *Stenobothrus lineatus* and *Metrioptera brachyptera*.

The findings of the current study show that *Chorthippus parallelus, Pholidoptera griseoaptera*, *Omocestus viridulus*, *Metrioptera roeselii* and *Tettigonia viridissima* are differential species for some structural types. Furthermore, *Tettigonia viridissima* and *T. cantans*, which are allopatric in the study area (Poniatowski & Fartmann, 2006), are altitudinal differential species. *T. cantans* was present at all sites studied ($N = 4$) in the western Upper Diemel Valley and absent from the sites in the other three subareas. In contrast, there was an increase in the constancy of *T. viridissima* with decrease in altitude: western Upper Diemel Valley (25%, $N = 4$), eastern Upper Diemel Valley (60%, $N = 5$), Middle Diemel Valley (86%, $N = 7$) and Lower Diemel Valley (80%, $N = 10$). Among the ten attendant species, *Chorthippus biguttulus*

TABLE 3. The orthopteran assemblages of the semi-dry calcareous grasslands in the Diemel Valley. Constancy table for seven structural types (plant communities and land-use, see text); percentage constancy values are given; classification of character species (CS) and differential species (DS) based on the differential species criterion (Fig. 2); Ny = Nymphs, Im = Imago; superscript: range in the number of Orthoptera individuals/20 m²: q = qualitative detection, r = 1 individual (ind.), + = 2–5 ind., 1 = 6–10 ind., 2 = 11–20 ind., 3 = 21–50 ind., 4 = 51–100 ind., 5 >100 ind.; if not stated otherwise the values are medians; for further explanation see text.

Structural type	1	2	3	4	5	6	7
N Study plots	5	8	18	8	11	21	9
Median cover (%)							
Total vegetation	40	75	90	85	95	95	100
Field layer	40	70	80	80	90	90	95
Cryptogam layer	3	13	23	5	15	50	0
Litter layer	5	5	5	10	25	40	90
Bare ground	30	18	5	13	3	0	0
Stony surface (= gravel, stones and rocks)	30	9	0	1	0	0	0
Median vegetation height (cm)	2.5	5	5	10	10	20	30
Median horizontal vegetation density (%)							
0–5 cm	20	95	96	100	100	100	100
5–10 cm	3	5	10	70	95	98	100
10–15 cm	3	3	3	4	20	80	100
15–20 cm	0	0	3	3	5	20	95
20–25 cm	0	0	0	3	3	3	90
25–30 cm	0	0	0	0	0	3	70
Nymphs/20 m²	19	14	25	23	31	24	7
Adults/20 m²	16	10	11	22	17	23	15
Species number per plot (median and range)	$4^{2–4}$	$3^{1–5}$	$3^{2–5}$	$4.5^{4–9}$	$4^{2–6}$	$5^{3–8}$	$4^{3–8}$
Total species number	4	7	8	11	10	16	13
CS of gravel-rich grassland							
Myrmeleotettix maculatus Im	$80^{r–1}$	·	·	13^{r}	·	·	·
Myrmeleotettix maculatus Ny	20^{r}	·	·	·	·	·	·
CS of gap-rich semi-dry grassland							
Tetrix tenuicornis Im	$100^{q–2}$	$88^{q–1}$	$28^{q–+}$	$75^{q–1}$	$27^{q–r}$	10^{r}	·
Tetrix tenuicornis Ny	$60^{q–+}$	$75^{q–+}$	$22^{q–r}$	$75^{q–+}$	·	·	·
CS of low-growing semi-dry grassland							
Stenobothrus lineatus Im	$60^{r–+}$	$88^{+–2}$	$94^{q–1}$	$100^{r–3}$	$91^{q–2}$	$57^{q–3}$	11^{q}
Stenobothrus lineatus Ny	$60^{r–+}$	$50^{r–+}$	$61^{r–2}$	$38^{r–+}$	$64^{r–+}$	$33^{r–1}$	11^{+}
DS of semi-dry grassland with high vegetation cover							
Chorthippus parallelus Im	·	13^{+}	$44^{q–+}$	$63^{r–1}$	$64^{q–3}$	$71^{r–3}$	$89^{+–3}$
Chorthippus parallelus Ny	·	·	11^{1}	13^{+}	$27^{r–3}$	$57^{r–3}$	$78^{+–3}$
CS of semi-dry grassland with little or no land use							
Metrioptera brachyptera Im	·	·	6^{r}	$63^{q–3}$	$36^{r–1}$	$95^{q–3}$	$67^{r–+}$
Metrioptera brachyptera Ny	·	·	·	$25^{r–+}$	9^{r}	$52^{q–1}$	11^{r}
DS of semi-dry grassland with very little or no land use							
Pholidoptera griseoaptera Im	·	13^{r}	·	25^{+}	$18^{r–+}$	$52^{q–1}$	$67^{q–1}$
Pholidoptera griseoaptera Ny	·	·	·	13^{q}	9^{r}	$33^{r–+}$	·
DS of medium- to high-growing semi-dry grassland at high altitude							
Omocestus viridulus Im	·	·	·	·	9^{+}	$52^{q–2}$	$44^{r–1}$
Omocestus viridulus Ny	·	·	·	·	9^{r}	·	·
DS of high-growing and dense semi-dry grassland							
Metrioptera roeselii Im	·	·	·	13^{r}	·	$14^{q–+}$	$56^{q–2}$
Altitudinal DS of semi-dry grassland							
Lower to eastern Upper Diemel Valley							
Tettigonia viridissima Im	·	·	·	·	9^{+}	$14^{r–+}$	$33^{q–r}$
Tettigonia viridissima Ny	·	·	·	13^{q}	18^{q}	·	11^{q}
western Upper Diemel Valley							
Tettigonia cantans Im	·	·	·	·	·	$14^{q–r}$	22^{r}
Attendant species							
Chorthippus biguttulus Im	$100^{r–2}$	$88^{r–2}$	$89^{r–4}$	$75^{+–3}$	$82^{r–2}$	$57^{r–3}$	$33^{r–+}$
Chorthippus biguttulus group Ny	$100^{1–3}$	$100^{+–4}$	$100^{r–3}$	$100^{r–3}$	$100^{+–4}$	$95^{r–5}$	$78^{+–1}$
Tetrix bipunctata ssp. *bipunctata* Im	·	13^{q}	$22^{r–+}$	13^{+}	$27^{r–+}$	14^{+}	11^{+}
Tetrix bipunctata ssp. *krausii* Im	·	·	6^{+}	·	·	·	·
Tetrix bipunctata Ny	·	13^{q}	$11^{r–+}$	·	9^{q}	5^{r}	·
Stenobothrus stigmaticus Im	·	13^{+}	6^{3}	·	·	·	·
Stenobothrus stigmaticus Ny	·	·	6^{3}	·	·	·	·
Chorthippus albomarginatus Im	·	·	6^{+}	·	·	·	11^{q}
Gomphocerippus rufus Im	·	·	·	·	·	5^{q}	·
Gomphocerippus rufus Ny	·	·	·	13^{+}	·	5^{q}	·
Phaneroptera falcata Im	·	·	·	·	·	5^{r}	·
Phaneroptera falcata Ny	·	·	·	·	·	·	11^{q}
Tetrix undulata Im	·	·	·	·	9^{r}	·	·
Tetrix undulata Ny	·	·	·	·	·	·	11^{+}
Chorthippus brunneus Im	·	·	·	·	·	5^{q}	·
Decticus verrucivorus Im	·	·	·	·	·	5^{q}	·
Leptophyes punctatissima Im	·	·	·	·	·	5^{r}	·

TABLE 4. Dominance of the Orthoptera species in the structural types. Percentage values, sum of individuals = number of individuals per structural type = 100%, 0 = single specimen (= 0.3% and/or qualitative detection), . = absence; for further explanation see table 3 and text.

Structural type	1	2	3	4	5	6	7
Number of study plots	5	8	18	8	11	21	9
Sum of individuals	168	245	717	419	577	1.353	286
Character and differential species							
Myrmeleotettix maculatus	10	·	·	0	·	·	·
Tetrix tenuicornis	19	5	1	5	0	0	·
Stenobothrus lineatus	6	18	18	18	12	6	1
Chorthippus parallelus	·	1	2	7	17	21	62
Metrioptera brachyptera	·	·	0	12	3	18	7
Pholidoptera griseoaptera	·	1	·	2	1	3	4
Omocestus viridulus	·	·	·	·	1	3	6
Metrioptera roeselii	·	·	·	0	·	1	9
Tettigonia viridissima	·	·	·	0	1	1	1
Tettigonia cantans	·	·	·	·	·	0	1
Attendant species							
Chorthippus biguttulus	65	75	68	55	65	47	9
Tetrix bipunctata	·	0	3	1	1	1	1
Stenobothrus stigmaticus	·	1	9	·	·	·	·
Chorthippus albomarginatus	·	·	1	·	·	·	0
Gomphocerippus rufus	·	·	·	1	·	0	·
Phaneroptera falcata	·	·	·	·	·	0	0
Tetrix undulata	·	·	·	·	0	·	1
Chorthippus brunneus	·	·	·	·	·	0	·
Decticus verrucivorus	·	·	·	·	·	0	·
Leptophyes punctatissima	·	·	·	·	·	0	·

is the only one with a high constancy in all structural types.

Structural type 1: Community of gravel-rich calcareous grasslands

The sites have predominantly shallow soils and are south-facing on steep (20–24°) slopes with sparse vegetation (median cover: 40%; Table 3). The percentage of both stony surfaces and bare ground are high (median: 30%). All plots of this structural type belong to the *Gentiano-Koelerietum typicum*, gravel-rich subtype. The majority of these sites were sheep grazed.

The occurrence of *Myrmeleotettix maculatus* is largely restricted to this structural type. Furthermore, *Tetrix tenuicornis* has a high constancy in the gravel-rich calcareous grasslands, whereas *Stenobothrus lineatus* regularly occurs in this sparsely vegetated structural type, but at a low density (Table 3).

TABLE 5. Eigenvalues of the first two axes of the Detrended Correspondence Analysis (DCA) and the intraset correlations between DCA axes and the major environmental variables.

Axes	1	2
Eigenvalues	0.63	0.31
Sunshine duration	–0.63	0.24
Altitude	0.43	0.49
Bare ground and stony surface	–0.67	0.00
Cryptogams	0.25	–0.35
Shrubs	0.13	–0.03
Vegetation density	0.81	0.12

Structural type 2: Community of gap-rich, short-growing semi-dry grasslands

The percentage of bare ground in structural type 2 is still high (median: 18%, Table 3). Calcareous gravel covers only up to 15% of the soil surface. Moreover, the turf cover is greater (55–85%) than in type 1. The plots of this structural type belong to the *Gentiano-Koelerietum typicum*, gravel-rich and gravel-poor subtype and the *Gentiano-Koelerietum cladonietosum*. All sites are grazed by sheep and goats.

The regional character species of this community are *Tetrix tenuicornis* (sub-dominant) and *Stenobothrus lineatus* (dominant) (Table 4). Both species have high constancy values (Table 3). Hence, in contrast to structural type 1, the orthopteran community of this structural type is largely characterized by the absence of *M. maculatus*.

Structural type 3: Community of dense, short-growing semi-dry grasslands

In contrast to the two previous structural types, this one is characterized by a nearly complete coverage of turf (median cover: 90%). Due to intensive grazing, the sward is still very short (median: 5 cm; Table 3). This structural type belongs to the *Gentiano-Koelerietum typicum*, gravel-poor subtype and the *Gentiano-Koelerietum trifolietosum*.

Tetrix tenuicornis is quite rare in these swards. However, *Chorthippus parallelus* is more frequent in this community and differentiates this community from struc-

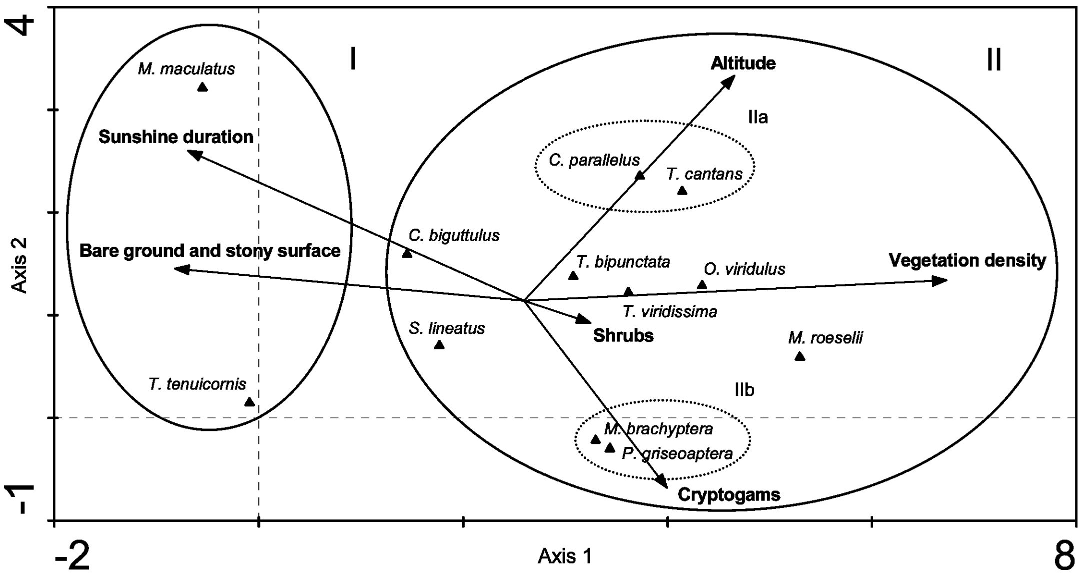

Fig. 3. Detrended Correspondence Analysis (DCA) of the most frequent orthopteran species of the semi-dry calcareous grasslands in the Diemel Valley. The length of the gradient on 1st axis is 4.495; the 1st axis explains 21% and the 1st and 2nd axes 32% of total variance; the sum of all eigenvalues is 2.978. For more information see Table 2 and 5. Species with an absolute constancy < 3 were excluded from the analysis. Arrows denote major environmental gradients (overlay). Group I: species of bare ground-rich semi-dry grasslands; Group II: species of semi-dry grassland with a high incidence of cover, subgroup IIa: species at high altidudes and subgroup IIb: species of cryptogam-rich semi-dry grassland. Data basis: box quadrat captures (only adults) and environmental parameters of 80 plots; density range: 1–61 adults/20 m². The complete orthopteran names are given in Table 3 and 4.

tural type 2. The only character species is the highly constant *Stenobothrus lineatus* (Table 3).

Structural type 4: Community of sparse, low-growing semi-dry grasslands

In terms of the horizontal vegetation structure there are similarities with structural type 2. This structural type has a higher and denser vegetation than type 2 (Table 3). All plots studied of this structural type belong to the *Gentiano-Koelerietum typicum*, gravel-poor subtype. One half each was sheep grazed and abandoned.

Differences in vertical vegetation structure have an impact on the composition of the orthopteran community: First, phytophilous species such as *Metrioptera brachyptera* and *Chorthippus parallelus*, that are absent from structural type 2, reach high constancy values. Second, *Tetrix tenuicornis* benefits from the abundance of bare ground. *Stenobothrus lineatus* has very high constancy values and is dominant (18%) (Table 3 and Table 4).

Structural type 5: Community of dense, low-growing semi-dry grasslands

Compared to the previous type, this type has a higher vegetation cover (median: 95%). Bare ground is rare (median: 3%) and there is a more extensive litter layer (median: 25%). The plant communities making up this structural type are the *Gentiano-Koelerietum typicum*, gravel-poor subtype and the *Gentiano-Koelerietum trifolietosum*. All but three sites were grazed sheeply.

Only *Chorthippus parallelus*, *Stenobothrus lineatus* and *Metrioptera brachyptera* could be classified as differential or character species of this structural type (Table 3).

Structural type 6: Community of medium-growing semi-dry grasslands

As in structural type 5, the vegetation cover is nearly complete (median: 95%). But, as a consequence of the twofold higher field layer (median: 20 cm), the vegetation is denser at 10–15 cm (median: 80%) and this type overlaps to the next type. The moss layer has the highest value (median: 50%). The *Gentiano-Koelerietum typicum*, gravel-poor subtype with *Sesleria* facies and the *Gentiano-Koelerietum trifolietosum* form this structural type. The majority of these sites are abandoned ($N = 13$).

This type is colonised by *Chorthippus parallelus* and *Metrioptera brachyptera* as dominant differential and character species, respectively. For the first time, *Omocestus viridulus* and *Pholidoptera griseoaptera* have high constancy values whereas the frequency of *Stenobothrus lineatus* decreases (Table 3 and Table 4).

Structural type 7: Community of high-growing semi-dry grasslands

What is characteristic of this structural type is a complete cover of vegetation (median: 100%) with field layer heights of 25–35 cm. The litter layer reaches its highest values at 95%. The composition of the plant communities in this structural type is very heterogeneous: *Brachypodium pinnatum*-dominance stands, *Gentiano-Koelerietum trifolietosum* with crossover to *Cynosuretum* and *Arrhenatheretum*, *Trifolio-Agrimonietum*, respectively. All but two sites have not been managed for years.

Compared to the former type the composition of differential and character species is very different: *Stenobothrus lineatus* is very rare, two bush-crickets *Metrioptera roeselii* (constancy: 56%) and *Tettigonia vir-*

idissima (constancy: 33%) occur more frequently and *Chorthippus parallelus* is eudominant (Table 3 and Table 4).

Ordination

The DCA with a gradient-length of 4.495 for the first axis (unimodal model) shows a clear separation of species along the first axis (species-environment correlation: r = 0.907, Table 5), largely falling into two groups (Fig. 3): Taxa that were recorded only on bare ground-rich sites with a high sunshine duration (*Myrmeleotettix maculates* and *Tetrix tenuicornis*) and species of sites with denser vegetation (e.g. *Metrioptera roeselii* and *Omocestus viridulus*). The second canonical axis is positively correlated with altitude and negatively with cryptogam cover (Fig. 3, Table 5): Some orthopteran species have a strong positive association (in particular *Chorthippus parallelus* and *Tettigonia cantans*) and others a negative association (in particular *Pholidoptera griseoaptera* and *Metrioptera brachyptera*) with this axis.

DISCUSSION

Classification of insect communities

For the classification of insect communities by character and differential species three points are of special importance: (i) the geographical reference area, (ii) the hierarchical level (e.g. habitat complex, habitat and microhabitat) and (iii) clear constancy criteria for the definition of character and differential species. Ecological niches of animal or plant species can vary across latitudinal and altitudinal gradients (Thomas et al., 1998; McPherson & Jetz, 2007). Hence, the diagnostic character of a species within communities can differ across the range of the species (Kratochwil & Schwabe, 2001). As a consequence, it is important to mention the biogeographic reference area for which the classification is valid.

Insect communities can be classified at several hierarchical levels. The one chosen depends mainly on the home range of the animals considered. This study deals with two hierarchical levels (habitat and structural type), whereas former studies mostly address only one level (Seitz, 1989; Flade, 1994; Schultz & Finch, 1997).

Until now, classification of insect communities by character and differential species was mainly intuitive (Seitz, 1989; Flade, 1994; Fartmann, 1997; Schultz & Finch, 1997; Behrens & Fartmann, 2004a). Based on Flade (1994) most authors defined character species as species with significantly higher constancy values in one or several units and mostly higher densities than in all other units (Schultz & Finch, 1997; Kratochwil & Schwabe, 2001).

The method described in the current paper is the first one that specifies precise constancy criteria for the classification of terrestrial insect communities and is applicable at different hierarchical levels. Since the early 1990s ordination techniques have become more important in orthopteran community analysis (e.g. Kemp et al., 1990; Fielding & Brusven, 1993; Andersen et al., 2001; Torrusio et al., 2002; Gebeyehu & Samways, 2003, 2006). For example functional groups (guilds) can be arranged along ecological gradients (e.g. Szövényi, 2002; Gavlas et al., 2007). In this study, the results of the DCA (Fig. 3) indicate that vegetation structure and the interlinked microclimate strongly accounts for habitat selection in Orthoptera (see also Joern, 1982; Ingrisch & Köhler, 1998).

For the classification of orthopteran communities we used a method based on constancy criteria because it is (i) more transparent than multivariate techniques and (ii) the habitat requirements of the species can be shown in more detail. Similar approaches have been successfully used in vegetation science for decades (Dierschke, 1994), and continuously improved (Dengler, 2003; Dengler & Berg, 2004; Schmitt & Fartmann, 2006). This methodology has the advantage that in addition to the ecological optima the whole niche breadth of a species is revealed, assuming that the sample size is big enough and representative.

Habitat requirements

Arthropod assemblages in general (Schaffers et al., 2008), and particularly in host-specified insects, like butterflies (Benes et al., 2006), might be best predicted by plant species composition, however, as shown here, orthopteran communities are closely associated with structural types within certain habitats (see also Fartmann, 1997; Morgen, 1998; Behrens & Fartmann, 2004a). Not only do the stenotopic species (character species) have very specific habitat requirements of special relevance but some eurytopic species have very distinct structural preferences (differential species). Below the habitat requirements of these orthopteran species are discussed (following Table 3 and Fig. 3, see also Poniatowski & Fartmann, 2006).

Of the character species, *Myrmeleotettix maculatus* is typical of habitats with little vegetation cover (e.g. Sänger, 1977; Ingrisch, 1984; Zehm, 1997), and a dry and warm microclimate (Detzel, 1998). In the Diemel Valley, the occurrence of *M. maculatus* is restricted to sparsely vegetated *Calluna* heaths at high altitudes and to calcareous gravel-rich plant communities at low altitudes (Poniatowski & Fartmann, 2006). In contrast the geophilous *Tetrix tenuicornis* occurs in several structural types with some bare ground (Schulte, 2003). Occurrence of *Stenobothrus lineatus* is restricted to semi-natural grasslands in Germany (e.g. Detzel, 1998). In accordance with other studies, *S. lineatus* prefers low-growing but mostly dense swards within these habitats (Wallaschek, 1995; Behrens & Fartmann, 2004b). In the Diemel Valley *Metrioptera brachyptera* is a character species of dwarf-shrub-rich upland heath (Poniatowski & Fartmann, 2007) and semi-dry calcareous grassland (Poniatowski & Fartmann, 2006). Occurrence of this phytophilous species (Ingrisch & Köhler, 1998) within the calcareous grasslands is largely restricted to the structural types 4–7, which develop in the absence of grazing (Poniatowski, 2006).

Of the differential species, *Chorthippus parallelus* colonizes a wide array of habitat types (Ingrisch, 1982) and is one of the most common grasshopper species in

Germany (Glück & Ingrisch, 1990). Because of its preferences for the herbaceous layer (Sänger, 1977) and the high moisture requirements of the eggs (Ingrisch, 1983) this species avoids, as in the study area, vegetation-poor sites (Froehlich, 1994; Fartmann, 1997). These sites are too dry and do not fit the vegetation structural requirements of the species (Behrens & Fartmann, 2004a). The habitat preference of *Pholidoptera griseoaptera* is one with sufficient hiding places and moisture for the development of its eggs (Ingrisch, 1988). Hence, *P. griseoaptera* predominantly colonizes abandoned or less intensively used semi-dry calcareous grasslands, often with some shrubs (Morgen, 1998). The medium- to high-growing herbaceous layer provides a good windbreak in this habitat and reduces the risk of the eggs dehydrating in the soil (Ingrisch, 1988; Detzel, 1998). The mesophilous *Omocestus viridulus* is typical of calcareous grasslands in regions with an atlantic and subatlantic climate (Ingrisch, 1984). In regions with a low annual precipitation it is restricted to mesic and wet habitats (e.g. Ingrisch, 1981; Fartmann, 1997). The eggs of *Metrioptera roeselii* are laid in plant stems and are sensitive to desiccation (Ingrisch, 1988). In the semi-dry calcareous grasslands of the Diemel Valley this species is restricted to high-growing and dense swards, which provide the fresh-moist microclimate necessary for successful embryonic development (Poniatowski, 2006). Because *M. roeselii* also colonizes other habitats in the Diemel Valley (e.g. Hill & Beinlich, 2001) it is a differential species (see Behrens & Fartmann, 2004a). The sibling species *Tettigonia viridissima* and *T. cantans* occur allopatrically as they have different habitat requirements in the study area (Poniatowski & Fartmann, 2006).

Chorthippus biguttulus, the only attendant species with high constancy values, is slightly xerophilous (Glück & Ingrisch, 1990) and colonizes differently structured types of the semi-dry calcareous grasslands with high constancy (Schulte, 1997). Intermediate and high-growing swards are poorly colonised (Morgen, 1998), presumably because of an adverse microclimate (van Wingerden et al., 1993) and a deficit of egg-laying sites. For egg-laying *C. biguttulus* requires bare ground (Ingrisch & Boekholt, 1983), that is lacking in the structural types 6–7. Because *C. biguttulus* is also comparatively abundant in these semi-dry calcareous grasslands it is a typical attendant species (Fartmann, 1997; Morgen, 1998; Behrens & Fartmann, 2004a).

CONCLUSION

Comparison of the ordination and constancy table (hierarchical classification) indicate that the habitat requirements of the species can be illustrated more condensed and clearly using ordination (Fig. 3). However, the constancy table gives a more detailed insight into the ecology of the species (Table 3) and is undispensable for the successful conservation of the species and their habitats (e.g. Hein et al., 2007). Moreover, the hierarchical classification of insect assemblages by defined criteria provides an indication of environmental changes. For a distinct biogeographic region and hierarchical level reference communities can be specified (c.f. Cam et al., 2000). Gains and losses of species relative to reference communities can thus be analysed. Inventory completeness (in our case: observed species richness relative to expected richness of the community) is an important criterion in ecology, biogeography and nature conservation (Soberón et al., 2007; Mora et al., 2008) and is nowadays incorporated in conservation policy (e.g. Gómez de Silva & Medellín, 2001; Greenbaum & Komar, 2005; Baselga & Novoa, 2008). But, surveys of typical communities of most regions and habitats of high conservation concern are still lacking (Bernotat et al., 2002). The classification presented is a powerful tool for arthropod conservation, since it allows one to determine the community completeness of very important and threatened habitats, like semi-dry calcareous grasslands. In future, changes in orthopteran species composition due to climate change may require some adjustments in this classification.

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