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Losing uniqueness – shifts in carabid species composition during dry grassland and heathland succession

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Abstract

Dry sand ecosystems, such as dry grasslands and heathlands, have suffered habitat loss and degradation due to land-use changes and are today among the most endangered habitats in Central Europe. To evaluate the impact of degradation processes on habitat quality, we investigated how succession from sparse vegetated sand ecosystems to grass-invaded and tree-dominated ecosystems and the environmental parameters associated with it influences carabid assemblages. We also determined to what extent typical xerophilic species assemblages still exist. Pitfall trapping at 28 study sites in northwestern Germany yielded 111 carabid species that were grouped using Kendall's W coefficient of concordance. Ordination revealed that the differences between the four species groups resulted from vegetation cover and soil humidity, indicating that carabid distribution clearly reflects degradation processes. Our results suggest that areas in which succession proceeds were unsuitable for assemblages typical of dry grasslands and heathlands. In all, 35 species are lost due to succession from dry grassland and heathland to grass-invaded and tree-dominated sites. We discuss implications for habitat management and restoration, since dry sand ecosystems comprise a very high number of specialized and endangered species.

Introduction

Habitat loss and degradation are among the most important threats to global diversity (Groom, Meffe & Carroll, 2006). To counteract species loss, the conservation of a broad range of natural and seminatural habitats in good quality – in line with the goals of the European Union Directive – is essential. For the maintenance of high diversity in Europe, the conservation of dry sand ecosystems is important. Dry sand ecosystems such as inland dunes, dry grasslands as well as dry *Calluna*-, *Genista*- and *Empetrum nigrum*-heathlands (excluding humid *Erica tetralix*-heathlands) are characterized by extreme habitat conditions including nutrient poverty, shifting sand, sparse vegetation and a dry and hot microclimate. Central European dry sand ecosystems are endangered habitats listed in Annex I of the European Habitats Directive (FFH 2310, 2320, 2330, 4030, 6110, 6120; Riecken *et al.*, 2006) which harbour a specialized flora and fauna, including a remarkable number of endangered species (Lehmann *et al.*, 2004*a*,*b*; Maes & Bonte, 2006; Buchholz, 2010).

In Central Europe dry sand ecosystems are mainly anthropo-zoogenic habitats that have developed as a result of traditional land management such as sheep grazing, sod cutting and burning (Webb, 1998). Over the last 50 years the number of such ecosystems has decreased, resulting in highly fragmented and isolated patches of low habitat quality (Verbücheln & Jöbges, 2000; Pardey, 2004). The main reasons for this reduction are the abandonment of traditional land use, intensive cultivation and afforestation. As a consequence, disturbance effects such as drifting sand, grazing and fire, which are the most important drivers of habitat dynamics, have decreased (White & Jentsch, 2001; Jentsch *et al.*, 2002), thus promoting succession towards shrub- and tree-dominated vegetation (Webb, 1998; Provoost, Jones & Edmondson, 2011). Succession is further enhanced by increasing amounts of atmospheric nitrogen deposition which cause eutrophication and grass encroachment (Roem, Klees & Berendse, 2002).

Many rare and dry-loving (xerophilic) arthropods depend on early and dynamic successional stages and are negatively affected by the development of dense vegetation and an increasing soil stabilization (De Vries, den Boer & van Dijk, 1996; Price, 2003; Buchholz, 2010; Drees *et al.*, 2011; Schirmel & Buchholz, 2011). The conservation of these habitats and their dynamics is therefore most urgently needed (Steven, 2004; Buchholz, 2010).

In this study, we analysed the current habitat quality of dry sand ecosystems in northwestern Germany using ground beetles as model organisms. Ground beetles

(Coleoptera: Carabidae) are known to be useful indicator taxa to analyse shifts in terrestrial ecosystems (Schirmel, 2010; Koivula, 2011; Kotze *et al*., 2011; Schirmel & Buchholz, 2011) including European dry grasslands and heathlands (e.g. Falke & Assmann, 1997, 2001; Mossakowski, Främbs & Baro, 1999; Irmler, 2004). Carabid species of dry and poor grasslands and heathlands – especially specialized and endangered ones – have decreased significantly in the past (Desender & Turin, 1989; Kotze & O'Hara, 2003) and thus it is imperative to evaluate current degradation processes in remaining dry sand ecosystems. In particular, we were interested in (1) how succession and the environmental parameters associated with it influence carabid assemblages, (2) to what extent typical xerophilic species assemblages still exist and (3) what is required for a successful habitat management.

Methods

Study area

The study sites were scattered throughout the Westphalian Bay in NW Germany. Maximum distances between the sites were 125 km (W-E) and 75 km (N-S), respectively. The landscape was glacially formed with fluvial and aeolic ice-age top layers showing dry soil conditions (Dinter, 1999). The climate is sub-Atlantic with a mean annual temperature of 9.5 to 10°C and an annual precipitation between 700 and 750 mm. The lowlands are mainly managed for agricultural use (Dinter, 1999). Open sand habitats occur mostly on military training sites which significantly contribute to the preservation of these habitats (e.g. the military training area 'Senne' comprises about 2000 ha *Calluna* heathland and about 350 ha dry grassland) (Pardey, 2004). Due to the shutdown of most military training sites in the last years the open sand habitats undergo succession. This is the same in the cultivated landscape where traditional land-use forms were abandoned many years ago (Pardey, 2004; Steven, 2004).

Sampling design

Sampling was done in 28 study sites (Supporting Information Appendix S1). Four uncovered pitfall traps were installed randomly at each site and were open from August 2006 to July 2008. Minimum distance between traps was 5 m. Pitfall trap catches can be biased by numerous factors, for example trap design, sampling protocol (Buchholz *et al*., 2010; Schirmel *et al*., 2010) as well as differing habitat structure and activity rates (Topping & Sunderland, 1992). Pitfall trapping is a selective method yielding activity rather than true densities of ground-dwelling arthropods (Lang, 2000). Nevertheless, the method is commonly applied for sampling epigeic invertebrates as it provides large data sets that allow statistically sound analyses (Southwood & Henderson, 2000).

Traps consisted of 500 mL plastic cups (9 cm diameter, 12 cm depth) one-fourth filled with a 4% formalin-detergent solution. They were emptied every 4 weeks. All arthropods were removed, sorted and transferred to 75% ethanol. Carabid beetles were identified using the standard keys of Müller-Motzfeld (2006).

The endangerment status of carabid beetles was based on Hannig & Kaiser (2011). Species were classified as endangered when listed as '1' (= in imminent danger of becoming extinct), '2' (= highly endangered), '3' (= endangered), or 'V' (= endangerment may be assumed). Values of eurytopy – a measure for the range of settled habitat types by species – were taken from Turin (2000) and ranged from '0' (occurrence in one single or very few habitat types = stenotopic) to '10' (occurrence in a broad spectrum of habitat types = eurytopic). Indicator values of moisture preferences were taken from Irmler & Gürlich (2004). Species with values ≤'1' strongly prefer dry conditions (= euxerophilic), ≤'2' prefer dry conditions (xerophilic), >'2–6' prefer moderate conditions (mesophilic), >'6' prefer moist conditions (hygrophilic) and ≥'7' strongly prefer moist conditions (euhygrophilic).

The study sites differed in vegetation structure and size and covered a broad range of dry sand ecosystems. Open and dry sand habitat types included drift sand without vegetation (DS), dry grassland (= Spergulo-Corynephoretum, including patches of Agrostietum coarctatae; DG), and *Calluna* heathland (= Genisto-Callunetum; CH). Furthermore, habitat types that represented degraded or tree-invaded stages of succession were semi-dry grasslands (= Diantho-Armerietum, *Deschampsia*-grassland; SG), *Juniperus* heath (= Dicrano scoparii-Juniperetum; JH), and surrounding forests (Betulo-Quercetum roboris, *Pinus sylvestris*-forests; FO) (Table 1, Supporting Information Appendix S1). Our study covered all dry sand ecosystems

Table 1 Site characteristics showing the total number of sites per habitat type (no. sites) and the means (±SE) of the vegetation structure [c.hl, coverage of herb layer; c.cl, coverage of *Calluna vulgaris*; c.mo, coverage of mosses (percentage of cover in %); sha, shading (percentage of canopy density in %)] and soil humidity (hum) (categories: 1 = dry, 2 = slightly humid, 3 = humid, 4 = very humid, 5 = wet)

Habitat type (site IDs)	no. sites	c.hl***	c.cl***	c.mo	sha***	hum***
Drift sand (7, 16)	2	1	–	1	–	1
Dry grassland (1, 2, 3, 5, 12, 14, 15, 19, 28)	9	13 ± 2	–	30 ± 6	–	1.2 ± 0.1
Calluna heath (6, 8, 17, 22, 24, 25, 27)	7	13 ± 6	44 ± 11	39 ± 9	–	1.6 ± 0.3
Semi-dry grassland (18, 21, 23)	3	73 ± 18	–	27 ± 14	–	1.7 ± 0.6
Juniperus heath (4, 9, 10)	3	57 ± 19	10 ± 6	1 ± 1	10	3
Forest (11, 13, 20, 26)	4	55 ± 16	–	43 ± 20	66 ± 6	4 ± 0.4

***significantly different among habitat types ($P < 0.001$, analysis of variance).

accessible in the study area and it should be stressed that as a result, the number of study sites per habitat type was uneven (Supporting Information Appendix S1).

The habitat conditions of the study sites were characterized using five environmental parameters: vegetation structure [cover of herb layer, dwarf-shrubs (*Calluna vulgaris*) and mosses (%)], soil humidity and shading. Vegetation structure was estimated in an area of 1 m^2 around each pitfall trap. The four measurements per study site were averaged for statistical analysis. Following the method of AG Boden (1994), soil humidity was estimated in the field and categorized into five classes: '1' = dry, '2' = slightly humid, '3' = humid, '4' = very humid, '5' = wet. Shading was estimated as a percentage of canopy density.

Data analysis

To ensure valid comparisons between study sites, data were standardized using the following formula: individual activity densities/sampling days/pitfall trap number. Standardizations were necessary to compensate for artificial effects due to damaged or dried up pitfall traps.

Since deleting rarely detected species is recommended to enhance accuracy of statistical analyses, a species was omitted from multivariate analyses if less than four individuals per site were found (McCune & Grace, 2002). To identify species associations in the data set, we first used Kendall's W coefficient of concordance, which aims to find the smallest number of groups containing the largest number of positively and significantly associated species (Legendre, 2005).

In a second step, species groups were analysed ecologically using a nonmetric multidimensional scaling (NMDS) as multivariate analysis. The results were drawn in a plot which illustrates the association between species groups and environmental parameters (vegetation structure, soil humidity, shading). To test if species groups and their habitat were related we ran a Mantel test. We analysed species responses to environmental parameters by means of Poisson generalized linear models (GLM).

Comparisons of values of eurytopy and moisture preferences among the species associations obtained from the prior analysis described above (which resulted in four species groups) were performed using one-way analysis of variance (ANOVA).

The free software package R (R Development Core Team, 2010) including library VEGAN (Oksanen *et al*., 2008) was used for all statistics. Detailed explanations of the statistics applied are given in Supporting Information Appendix S2.

Results

General results

A total of 20 420 individuals belonging to 111 species were sampled (Supporting Information Appendix S3). Among these three species are in imminent danger of becoming extinct, seven species are highly endangered and 19 species are endangered. The most abundant species were *Cicindela hybrida* ($n = 4118$), *Poecilus versicolor* ($n = 2338$), *Nebria salina* ($n = 2320$), *Po. lepidus* ($n = 1959$), *Calathus fuscipes* ($n = 1440$) and *Cala. erratus* ($n = 1282$).

Dry grasslands and *Calluna* heathland had the highest species numbers (88 and 70, respectively) as well as the highest numbers of endangered and unique species (30, 15 and 18, 6, respectively). Unique to open and dry sand habitat types (DS, DG, CH) were for example *Amara spreta, Bradycellus caucasicus, Broscus cephalotes, Cala. ambiguus, Harpalus distinguendus* and *H. flavescens*. *Bra. ruficollis* was exclusive for *Calluna* heathland. *Juniperus* heathland contained 55 species (12 endangered, three unique), followed by drift sands (42, 13, 2) and semi-dry grasslands (41, 10, 2). Finally, forests had the fewest species number (33) with only two endangered and no unique species.

Species assemblages

Four groups comprising 52 significantly concordant species were identified and subjected to NMDS (Fig. 1). Group distribution and habitat matrix were significantly correlated ($r = 0.20$, $P < 0.05$, Mantel test). Soil humidity ($P < 0.001$) and herb layer cover ($P < 0.01$) contributed significantly to the ordination model. Both environmental parameters determined the group distribution along two main environmental gradients with humid and densely vegetated habitats in the upper left, densely vegetated but drier patches in the lower, and dry and sparsely vegetated sites in the upper right part of the ordination diagram. The NMDS ordination showed that the four groups were separated. Species of group 1 were restricted to more humid and shaded forest habitats (FO). Species of group 2 and 3 were arranged closely together and occurred mainly in open habitats with a high cover of herbs or dwarf-shrubs (SG, DG, CH), whereby species of group 2 were clearly related to a higher humidity. Group 4 species inhabited the driest grassland and drift sand sites (DG, DS). *Juniperus* heath sites (JH) were clearly separated from all other sites and seemed to be related to the cover of herb layer. However, these sites were not inhabited by a distinctive species group but showing some intergrading between forests and *Calluna* heathland.

A trend towards lower mean values of eurytopy was observed in group 4 ($F = 2.97$, $P = 0.091$, one-way ANOVA, Fig. 2). Mean indicator values of moisture preferences were highly significant among the four groups and were clearly lowest (i.e. most xerophilic) in groups 3 and 4 ($F = 32.51$, $P < 0.001$, Fig. 2). The proportion of endangered species varied among groups and was clearly highest in groups 4 (53%) and 3 (50%). In group 3, 15% of all species were endangered, while no endangered species occurred in group 1.

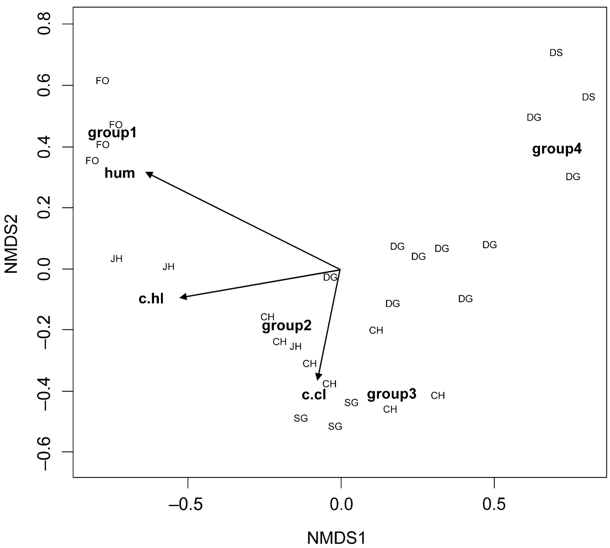

Figure 1 Nonmetric multidimensional scaling (NMDS) ordination (stress = 2.96) of four carabid beetle associations and six habitat types (DS, drift sand; DG, dry grassland; CH, *Calluna* heathland; SG, semi-dry grassland; JH, *Juniperus* heathland; FO, forests) based on the Bray-Curtis distance. Environmental variables fitted onto the ordination plot: hum, soil humidity ($P < 0.001$); c.hl, cover of herb layer [%] ($P < 0.01$) and c.cl = cover of *Calluna vulgaris* [%] (n.s.) (correlation of group distribution and habitat matrix r = 0.20, Mantel test, $P < 0.05$).

Groups were assessed using Kendall's W coefficient of concordance and included the following significant species:

group 1: *Abax parallelepidus*, *Carabus auronitens*, *C. nemoralis*, *C. problematicus*, *C. violaceus* ssp. *purpurascens*, *Leistus rufomarginatus*, *Notiophilus biguttatus*, *N. rufipes*, *Pterostichus oblongopunctatus*;

group 2: *Agonum muelleri*, *Amara curta*, *A. lunicollis*, *A. makolskii*, *A. plebeja*, *A. similata*, *Anisodactylus binotatus*, *Bembidion lampros*, *Bradycellus harpalinus*, *Carabus cancellatus*, *Harpalus latus*, *Poecilus cupreus*, *Pterostichus niger*, *Syntomus truncatellus*;

group 3: *Amara aenea*, *A. tibialis*, *Bembidion nigricorne*, *Calathus erratus*, *C. fuscipes*, *C. melanocephalus*, *Cicindela campestris*, *Harpalus anxius*, *H. autumnalis*, *H. rubripes*, *H. rufipes*, *H. tardus*, *Poecilus lepidus*, *P. versicolor*, *Syntomus foveatus*;

group 4: *Amara bifrons*, *A. fulva*, *A. spreta*, *Bembidion femoratum*, *Broscus cephalotes*, *Calathus ambiguus*, *C. cinctus*, *Cicindela hybrida*, *Harpalus affinis*, *H. distinguendus*, *H. flavescens*, *H. griseus*, *H. rufipalpis*, *H. smaragdinus*.

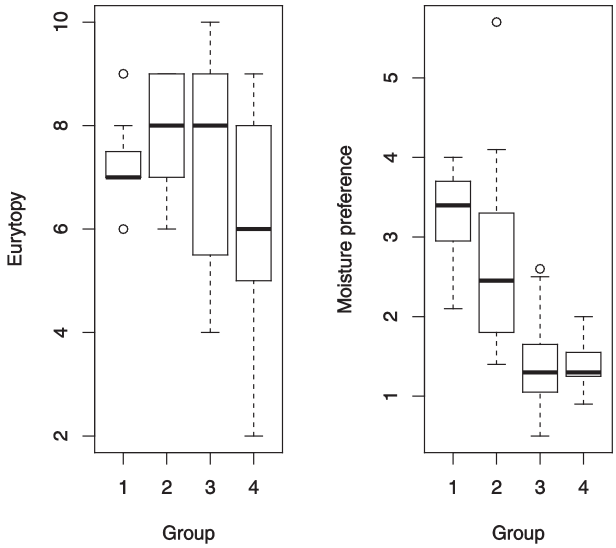

Figure 2 Values of eurytopy (left) and moisture preferences (right) of carabids in the four species groups. Values of eurytopy range from 0 (stenotopic) to 10 (most eurytopic) following Turin (2000). Indicator values of moisture preferences (≤1 = euxerophilic, ≤2 = xerophilic, >2–6 = mesophilic, >6 = hygrophilic, ≥7 = euhygrophilic) were taken from Irmler & Gürlich (2004). Differences of eurytopy and moisture values among the four groups were tested using one-way analysis of variance (eurytopy: F = 2.97, $P = 0.091$; moisture preferences: F = 32.51, $P < 0.001$).

Species responses to environmental parameters

The GLM results indicated that 23 carabid species responded significantly to environmental parameters (Table 2). Group 1 comprised eight species that were positively associated with increasing soil humidity. Of these, *Abax parallelepidus* and *Carabus nemoralis* were also positively correlated with dense herb layer and dwarf-shrubs, respectively. Species of groups 2 and 3 both showed positive correlations with an increasing density of herbal layer or dwarf-shrub cover. Finally, activity densities of *Am. fulva*, *Am. spreta*, *Cala. ambiguus* and *Cici. hybrida* (all classified as euxerophilic or xerophilic; group 4) significantly decreased with increasing herb layer cover.

Discussion

Carabid assemblages of dry sand habitats

Formerly a typical and widespread landscape component, open dry grasslands and heathlands are nowadays restricted to few and small areas as most sites have undergone succession towards grass- and shrub-dominated vegetation (Pardey, 2004; Steven, 2004). These degradation processes are clearly reflected in the ground beetle distribution found in this study. Although typical dry grassland and drift sand species still occur on a few sites, the habitat conditions of most sites have deteriorated (Pardey, 2004). The representatives of xerophilic carabid species were *Am. fulva*, *Am. spreta*, *Cala. ambiguus*, *Cici. hybrida* and *H. rufipalpis* (species of group 4) and *Bro. cephalotes* and *H. flavescens* (unique to DS and DG). These species are characteristic for young, dynamic habitats with low and sparse vegetation (Turin, 2000) and formed a unique assemblage of xerophilic habitat specialists with a high proportion of endangered species (Figs 1 and 2). All these species responded negatively to increasing vegetation cover and humidity and are particularly threatened by succession. Carabid species turnover during dry grassland succession is symptomatic not only for

Table 2 Responses of carabid beetle species to environmental parameters (c.hl, coverage of herb layer; c.cl, coverage of *Calluna vulgaris*; hum, soil humidity) were analysed using generalised linear models (GLM)

	Environmental variables									
	c.hl			c.cl			hum			
Species	est.	stde.	t	est.	stde.	t	est.	stde.	t	R^2 [%]
Group 1										
Abax parallelepidus	**0.03**	**0.01**	**2.8***	0.02	0.02	1.1	**0.80**	**0.28**	**2.9****	59
Carabus auronitens	–0.05	0.05	–1.2	–0.07	0.08	–0.9	**1.50**	**0.55**	**2.8****	54
Carabus nemoralis	0.01	0.01	1.2	**0.04**	**0.01**	**2.9****	**0.77**	**0.29**	**2.7***	49
Carabus violaceus ssp. purpurascens	0.00	0.01	0.3	–0.02	0.03	–0.6	**0.70**	**0.31**	**2.2***	35
Leistus rufomarginatus	–0.03	0.02	–1.8	–14.25	2505	–0.01	**2.17**	**0.30**	**8.1*****	92
Notiophilus biguttatus	–0.04	0.02	–1.6	–0.13	0.16	–0.8	**1.16**	**0.32**	**3.7****	58
Notiophilus rufipes	–0.02	0.02	–1.0	–17.17	4216	0.0	**0.83**	**0.35**	**2.3***	43
Pterostichus oblongopunctatus	0.00	0.01	0.3	–0.11	0.11	–1.0	**0.91**	**0.25**	**3.6****	55
Group 2										
Amara lunicollis	**0.03**	**0.01**	**3.4****	0.00	0.02	0.0	–0.15	0.29	–0.5	50
Anisodactylus binotatus	0.02	0.01	1.3	**0.03**	**0.01**	**2.8***	–0.52	0.40	–1.3	29
Bradycellus harpalinus	0.00	0.01	–0.4	**0.01**	**0.01**	**2.1***	–0.25	0.31	–0.8	25
Harpalus latus	**0.02**	**0.01**	**2.1***	0.01	0.01	0.5	0.02	0.30	0.1	24
Pterostichus niger	0.03	0.01	1.7	**0.04**	**0.02**	**2.4***	–0.56	0.53	–1.1	29
Syntomus truncatellus	**0.07**	**0.03**	**2.7***	0.01	0.05	0.3	–0.20	0.43	–0.5	71
Group 3										
Amara tibialis	–0.01	0.02	–0.4	**0.03**	**0.01**	**2.3***	–0.58	0.63	–0.9	33
Cicindela campestris	–0.03	0.03	–0.9	**0.03**	**0.01**	**2.6***	0.41	0.56	0.7	37
Harpalus rufipes	0.00	0.01	0.7	0.00	0.01	–0.1	**–0.68**	**0.29**	**–2.3***	22
Poecilus versicolor	**0.04**	**0.01**	**3.8*****	**0.05**	**0.01**	**3.8*****	–0.11	0.28	–0.4	55
Group 4										
Amara fulva	**–0.07**	**0.03**	**–2.5***	–0.08	0.06	–1.4	–18.08	3 535	0.0	64
Amara spreta	**–0.12**	**0.03**	**–3.7****	**–4.34**	**2.02**	**–2.1***	–17.66	2 943	0.0	78
Calathus ambiguus	**–0.16**	**0.05**	**–3.2****	–19.33	2546	0.0	–19.45	12 980	0.0	68
Cicindela hybrida	**–0.05**	**0.02**	**–2.4***	–0.04	0.03	–1.8	–1.11	0.84	–1.3	43
Harpalus rufipalpis	0.00	0.01	0.6	0.00	0.01	–0.1	**–0.68**	**0.29**	**–2.3***	22

The results include the estimated slopes (est.) (positive values indicate a positive effect on activity densities, negative values vice versa), standard error (stde.) and *t*-values (t.). Significant results (*** = $P < 0.001$, ** = $P < 0.01$ and * = $P < 0.05$) are printed in bold. Only species with significant responses are displayed.

the investigated area but also for the lowlands of northern and northwestern Germany (Falke & Assmann, 1997, 2001; Lehmann *et al*., 2004*a*) and Western Europe (Desender & Turin, 1989; Kotze & O'Hara, 2003). Similar patterns were observed for a multiplicity of other rare xerophilic arthropods (Ingrisch & Köhler, 1998; Hochkirch *et al*., 2006; Buchholz, 2008, 2010).

In contrast, heathland and semi-dry grassland species assemblages were difficult to differentiate. This could already reflect a heathland degradation process towards *Deschampsia flexuosa* dominated grasslands. *D. flexuosa* usually invades heathlands due to eutrophication (Mickel, Brunschön & Fangmeier, 1991; Steubing, 1993). Carabid distribution reflected these habitat shifts by the increased occurrence of mesophilic grassland species (e.g. *Am. lunicollis*). Moisture was the main environmental factor for structuring assemblages of semi-dry grasslands and heathlands. Typical species more related to dry conditions were *Am. tibialis*, *Bembidion nigricorne, Cici. campestris,* and *H. anxius* (group 3), while *Agonum muelleri*, *Ansiodactylus binotatus*, *Bembidion lampros* and *Bra. harpalinus* were typical in habitats with higher humidity (group 2). *Bra. ruficollis* was a unique species to *Calluna* heathland. Heathland species are favoured by the (at least scattered) occurrence of dwarf-shrub vegetation (*Call. vulgaris*) which, for example provides shelter, food and adequate microclimate (Mossakowski *et al*., 1999). Dwarf-shrubs depend on habitat dynamics (e.g. grazing or burning) and therefore heathland carabid species should generally benefit from habitat dynamics, too.

Habitat degradation is especially striking if sites undergo succession towards shrub and tree encroachment. Open habitat species from dry or semi-dry grassland and heathlands (groups 2–4) are replaced by (hygrophilic) woodland species like *Abax parallelepidus*, *Leistus rufomarginatus* and *Pterostichus oblongopunctatus* or by eurytopic species tolerating shade and a higher soil humidity like *Carabus nemoralis* and *Notiophilus biguttatus* (group 1).

Conservation value of open dry sand habitats and heathlands

Dry sand ecosystems are characterized by specific carabid species assemblages. The importance of these habitats with respect to species conservation is additionally highlighted by the occurrence of a very high proportion of endangered species. More than 50% of the typical species found in drift sands, dry grasslands and heathlands (group 3 and 4) are classified as endangered. Species occurring in these ecosystems are mainly xerophilic and tended to be more stenotopic (Fig. 2). As also described in earlier studies xerophilic carabid species are highly threatened by succession and habitat decline (Desender & Turin, 1989; Mathiak, Schultz & Ringel, 2004). This might be most critical since, firstly, some dry grassland carabid species have a low dispersal potential (Lehmann *et al*., 2004*b*) and thus are not able to migrate, secondly, these species are dependent on sufficient habitat size (Falke & Assmann, 1997, 2001; Drees *et al*., 2011), and, finally, negative succession effects are most pronounced in small-sized habitats (Webb & Hopkins, 1984). Typical assemblages of open dry sand ecosystems therefore run the risk of going extinct or at least losing their uniqueness as specialized xerophilic species fail to appear (Price, 2003).

Implications for habitat management and restoration

For the conservation of open dry sand habitats and heathlands and their flora and fauna, appropriate management is needed. Achieving a good conservation status of these habitats is moreover requested by the European Habitats Directive. Most important is the creation of habitat dynamics and early successional stages (shifting sand, sparse vegetation, dry and hot microclimate) which are basic requirement for many specialized and endangered species (Supporting Information Appendix S4). In earlier times, these habitat conditions were maintained by anthropogenic disturbance due to traditional land use (Härdtle *et al*., 2009; Schwabe & Kratochwil, 2009). Nowadays, it is in the hand of conservationists, land managers and policy makers to seek for appropriate management and restoration strategies (Schwabe & Kratochwil, 2009; Brooks *et al*., 2012). Therefore, precise knowledge of species habitat preferences – as provided for carabids in the present study – is fundamental. Based on our results and together with literature data, we review implications for habitat management to maintain or improve degraded dry sand habitats and heathlands.

Grazing is a fundamental and attractive option for dry grassland and heathland management (Gimingham, 1992) although it is difficult to organize on small patches (Webb, 1998). The impact varies depending on herbivore-based factors (e.g. digestive morphology, body size, incisor morphology, foraging and herding behaviour), plant-based factors (e.g. plant quality and quantity, plant distribution, interaction between plant quality and quantity and livestock behaviour) and site-based factors (e.g. shelter, water, site characteristics) (for extensive descriptions see Lake, Bullock & Hartley, 2001 or Brunzel-Drüke *et al*., 2008). For example, cattle and ponies are less suitable for *Calluna* heathlands and play only a minor role in scrub management, but can be effective in reducing invasive grasses or creating bare sand patches by trampling in dry grasslands (Lake *et al*., 2001; Tschöpe *et al*., 2004). Sheep are usually best for heath grazing as they feed on grasses in summer and on dwarf-shrubs in winter (Gimingham, 1992; Lake *et al*., 2001). Goats can play a major role in scrub management (Lake *et al*., 2001). Apart from livestock species, stocking rates and flock management as well as frequency (e.g. annual, one year in three), timing and duration affect grazing impacts (van Wieren, 1998; Lake *et al*., 2001; Offer, Edwards & Edgar, 2003; Schwabe & Kratochwil, 2009) and it has to be considered that these effects may vary between seasons, sites and years (Lake *et al*., 2001). In general, stocking rates should not be too high and several authors suggest a moderate or extensive grazing intensity (Kirby, 1992; Dennis *et al*., 1997; van Wieren, 1998; Bell, Wheater & Cullen, 2001; Wurth, 2002). In this context, Lake *et al*. (2001) emphasize that both, over or undergrazing, should be avoided and they estimate the current stocking rates for lowland heathland management at 0.03 up to 0.50 LU ha^{-1} yr^{-1} [(no. of livestock × livestock unit equivalence × proportion of year grazed)/grazing unit area]. In contrast, Offer *et al*. (2003) recommend high grazing densities over short periods in localized areas to periodically reset succession since long-term extensive systems are often unrewarding. They state that populations of most organisms can better cope with occasional, localized catastrophic events than regular, individually small but widespread, disruptive events (as provided by low-density, year-round grazing). However, although applying a reasonable and well-conceived grazing system, grazing impacts are negative on habitat features (e.g. vegetation cover) certain invertebrates depend on (Newton *et al*., 2009). This may lead to declines in overall diversity and ecological types (e.g. group 1 species in this study). Thus, even within reserves, conflicts can arise as a result of the management requirements of different taxa (Bakker & Berendse, 1999).

One should consider that domestic grazers may not (alone) be able to eliminate or open up the dense shrub vegetation in heavily degenerated *Calluna* and *Juniperus* heaths. In fact, problems may arise when using grazing for scrub management; in that case, overly high stocking rates or long grazing periods are likely to produce excessive disruption to features important for invertebrates (Offer *et al*., 2003). Thus, in highly degraded dry sand ecosystems it might be more promising to remove the herb and topsoil layers mechanically prior to grazing (Diemont & Lindhorst Homan, 1989; Jansen *et al*., 2004; Maes & Bonte, 2006). Although topsoil removal represents a very intense intervention in the soil structure, it is a valuable initial management technique leading to redynamization that benefits habitat specialists in contrast to many eurytopic species (Den Boer & van Dijk, 1994; Sieren & Fischer, 2002; Schirmel, 2010). Cutting (including choppering) is well suited to reduce grasses and herbs in heathland (Prochnow, Brunk & Segert, 2004). Cutting can be a useful alternative to burning in small areas or where burning is unacceptable but the impact depends on cutting technique (pedestrian-operated machines, tractor drawn machines), cutting intensity and timing as well as storage of debris (Gimingham, 1992). The rapid change of site conditions (reduction of vegetation height, higher temperature and lower humidity and shading) caused by cutting may have a drastic impact on invertebrates (Bell *et al*., 2001). While loss of plant architecture is more important for phytophagous species and spiders, carabid species may be affected by a reduced prey availability since cutting can reduce Collembola densities (Purvis & Curry, 1981). However, given that an extensive cutting is applied during midsummer in patches, it is suitable to preserve typical heathland carabid assemblages (Melber, 1993; Prochnow *et al*., 2004; Schirmel, 2010).

Burning has been widely used for heathland management as it is an effective method to deplete nutrients and to maintain succession (Webb, 1997, 1998). However, burning is very complex and many factors have to be considered before and while applying this technique (e.g. local climate and weather conditions, size, water content and chemistry of the burn material, fire behaviour, burning season) (Warren, Scifres & Teel, 1987; Gimingham, 1992). Post-burn grasslands and heathlands often encourage invertebrate diversity and it has been proven that the amount of xerophilic and stenotopic species increases while eurytopic species decline (Gardner & Usher, 1989; Usher, 1992; Bell *et al*., 2001; Schmidt & Melber, 2004). Although many mobile species can escape to neighbouring habitats or burrows (the moss, litter and upper soil layers provide excellent insulation) burning may negatively affect the invertebrate fauna more especially phytophagous species (Warren *et al*., 1987; Bell *et al*., 2001). It is therefore, important that unburned refuges are left and that the time between burns is long enough to ensure a recolonization (Harper *et al*., 2000).

Conclusion

Our findings highlight that a successful conservation will preserve not only endangered habitats but also a distinct carabid fauna. It is most important to consider possible advantages and disadvantages of the management techniques described above from a carabidologists perspective. Carabids (and so other invertebrates) have very specific habitat requirements and to maximize carabid diversity, dry sand ecosystems should have a range of vegetation types and a variety of habitat structure. Thus, successful habitat management must consider spatially and temporally heterogeneous habitat mosaics. Patches of bare ground are essential to provide a dry and hot microclimate and shifting sand dynamics. Cameron & Leather (2012) suggested a broad variety of patch sizes whereas patch size should extend with increasing grass density at patch edges. However, apart from bare patches – which undoubtedly promote euxerophilic or xerophilic dry grassland species (see group 4 species) – a side by side existence of different successional stages will have a big benefit for invertebrate conservation as it increases overall diversity and promotes heathland species (see group 2 and 3 species) (Lake *et al*., 2001; Schirmel, Blindow & Fartmann, 2010; Woodcock & Pywell, 2010; Schirmel & Buchholz, 2011; Cameron & Leather, 2012). Grazing is preferable to cutting and burning, and from an carabidologists perspective, we suggest an initial short-term rotational high density grazing with cattle in degenerated sites – maybe combined with topsoil removing or cutting – to promote xerophilic dry grassland species and a low or moderate density grazing by sheep and goats that benefits heathland species (Supporting Information Appendix S5). It is most important to weigh up the pros and cons of burning. Burning is expensive, labour-intensive and rather unsuitable for small dry grassland and heathland patches.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Further information on the characteristics of each site (Site no.): north (N) and east (E) coordinates, surface in hectares [area (ha)], vegetation structure [coverage of herbal layer (c.hl.) and *Calluna vulgaris* (c.cl.)], soil humidity (s.hu.), number of species (no. spec.), number of individuals (no. indiv.) and number of endangered species (no. end. spec.).

Appendix S2. Further explanations of statistical methods applied during the analyses.

Appendix S3. List of species (mean activity density ± standard deviation) collected in each habitat type (DS = drift sand, DG = dry grassland, CH = *Calluna* heathland, SG = semi-dry grassland, JH = *Juniperus* heathland, FO = forests). Abbreviations: end., endangerment category according to Hannig & Kaiser, 2011; * , not endangered; D, insufficient data; V, endangerment may be assumed; 3, endangered; 2, highly endangered; 1, in imminent danger of becoming extinct; eury./moist., eurytopy and moisture values according to Turin (2000); *[1], 35 species were unique to open sand and heathland habitat types.

Appendix S4. Habitat restoration and management strategies for dry grasslands and heathlands from a carabidologists perspective.

Appendix S5. Grazing suggestions to enhance habitat suitability for dry grassland and heathland carabid species and assemblages.