

Carabid beetles and spiders as bioindicators for the evaluation of montane heathland restoration on former spruce forests



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ABSTRACT

Semi-natural habitats such as heathland ecosystems are important for the conservation of biodiversity. Due to land use changes, these valuable ecosystems have become highly threatened. Nowadays, their management and restoration is of special relevance for nature conservation.

In this study, we used carabid beetles and spiders as bioindicators to evaluate the success of montane heathland restoration on former spruce forests. We compared three different treatments: (i) montane heathlands (MONHEATH), (ii) restoration (RESSITE) and (iii) control (CONTROL) sites.

Four to five years after conducting the restoration measures, all environmental variables, except soil moisture, significantly differed between MONHEATH on one hand and RESSITE and CONTROL on the other. MONHEATH was characterised by a high cover of dwarf shrubs; in contrast, RESSITE/CONTROL had a vegetation rich in herbs/grasses with some bare ground. Both carabid beetle and spider assemblage composition clearly reflected these differences in environmental conditions. Alpha-diversity (Simpson diversity, evenness) and niche positions were, however, only significantly different for spiders. Diversity as well as spider indicator values for shade and moisture were higher for MONHEATH.

Due to the cool and wet montane climate and the dense dwarf-shrub stands the carabid beetle and spider species characteristic of MONHEATH are typical woodland species. Four to five years after restoration, RESSITE and CONTROL still represent early successional stages with a low cover of the Ericaceae target dwarf shrubs (*Calluna vulgaris*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*), but are already home to some typical heathland carabid beetle and spider species that are missing in MONHEATH.

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1. Introduction

There is a broad consensus that global land use change has serious repercussions for biodiversity (Groom et al., 2006; Fischer and Lindenmayer, 2007). Agricultural intensification on the one hand (Koh et al., 2009) and cessation of traditional management on the other hand has resulted in loss, fragmentation and degradation of valued habitats (Bakker and Berendse, 1999; Cristofoli et al., 2010). Particular traditionally managed semi-natural habitats such as grassland and heathland ecosystems are of high importance for biodiversity conservation (Matson et al., 1997; Doxa et al., 2010). Due to long lasting and extensive management by humans, they are characterised by diverse and specialised flora and fauna (Littlewood et al., 2006c; Kleijn et al., 2009; Newton et al., 2009),

including many rare and threatened species (Buchholz, 2010; Buchholz et al., 2013; Fartmann et al., 2012).

Since the beginning of the 20th century, semi-natural habitats have started to decline in extent and quality (Rose et al., 2000; Watt et al., 2007). Among the main reasons contributing to this decline is a strong decrease in traditional management practices, such as sod cutting, grazing and burning, as well as the use of artificial fertiliser (Webb, 1998; Plieninger et al., 2006). Formerly unproductive grass- and heathlands were ploughed and subjected to agriculture. While grassland ecosystems suffered primarily from agricultural intensification, heathlands became abandoned or afforested and, hence, subjected to natural succession (Britton et al., 2001; Roem et al., 2002). Since the 1950s onwards, the high amounts of atmospheric nitrogen deposition have caused eutrophication and accelerated successional processes such as shrub encroachment and the expansion of perennial grasses (Bobbink et al., 1992; Härdtle et al., 2006).

In Central Europe, montane heathland ecosystems, in particular, are among the most threatened habitats, as they have been degraded

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to small and isolated patches (cf. Hoffmann, 1998). Our study area, the Rothaar Mountains ('Rothaargebirge') is considered to be one of the last regions within Germany where intact montane heathland ecosystems that harbour many rare, arctic-alpine and boreal-montane species still occur (cf. Usher, 1992; Geringhoff and Daniëls, 2003; Borchard and Fartmann, 2014). In order to protect these unique semi-natural habitats and their specialised wildlife, the European Union has supported the restoration and enlargement of montane heathlands in this region. Restoration measurements have included clear-cutting of planted conifer forests (*Picea abies*) and the subsequent transfer of montane heathland species (seed material) onto the restoration sites. All sites belong to the EU Natura 2000 network.

Restoration of habitats requires the evaluation of the conducted measures. Carabid beetles and spiders have been shown to be excellent indicator organisms (Dennis et al., 2001; Perner and Malt, 2003; Kotze et al., 2011; Buchholz et al., 2013): (i) they are taxonomically well known, abundant and inhabit a wide array of spatial and temporal niches (Kremen et al., 1993); (ii) their ecology has been widely studied and both organism groups respond significantly to abiotic and biotic variation, disturbance and management, even on small-scales (Thiele, 1977; Lövei and Sunderland, 1996; Rainio and Niemelä, 2003; Juen and Traugott, 2004) and (iii) carabid beetles and spiders can easily be collected using standardised sampling methods (Wise, 1993). Consequently, both groups are valuable and useful for monitoring habitat management and restoration practices (Huber et al., 2007; Buchholz, 2010).

To date, data on the success of montane heathland restoration (reseeded) are widely missing (Borchard et al., 2013; but see Littlewood et al., 2006a,b), particularly regarding former coniferous forests (cf. Pywell et al., 2002). Generally, the focus has been on the management and restoration of lowland heathlands (Gimingham, 1992; Usher, 1992; Symes and Day, 2003; Keienburg and Prüter, 2004). Thus, the overall aim of this study was to evaluate whether the previously conducted montane heathland restoration efforts have been successful. Accordingly, we have compared long-existing montane heathlands with restoration and control sites (clear-cut of spruce forests, no restoration). In particular, we were interested to see if:

- (i) Restoration is reflected by changes in alpha-diversity and community composition of carabid beetles and spiders?
- (ii) Management caused species specific responses and if certain species can be taken as target species for further monitoring studies?

2. Materials and methods

2.1. Study area

The study was conducted in the Rothaar Mountains, a low mountain range on the border of the Federal States of North Rhine-Westphalia and Hesse, Germany (51°28'N, 7°33'E) (Fig. 1). The study area stretches 40 km from north to south and 30 km from east to west. It is characterised by a montane climate with a mean annual temperature of 5 °C, an average annual precipitation of 1450 millimetre and a prolonged snow cover of 100 day/annum (Deutscher Wetterdienst, pers. comm.). The main habitat types are woodland, in particular spruce forests (*Picea abies*), arable land and improved grassland. Montane heathlands are restricted to mountain peaks.

2.2. Study sites

The study sites were located in the highest parts of the Rothaar Mountains, with altitudes ranging from 540 to 831 m a.s.l.

(mean \pm SE = 705 \pm 39.8). In total, we established 19 permanent plots each with an area size of 500 m² (20 m \times 25 m). We analysed the following three treatments: (i) montane heathlands (MON-HEATH) that were characterised by dwarf shrub vegetation with a high cover of *Calluna vulgaris*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea* ($N = 7$), (ii) restoration sites (RESSITE) dominated by *Agrostis capillaris*, *Rubus idaeus* and young *Calluna vulgaris* ($N = 7$) and (iii) clear-cut sites (CONTROL) of spruce forests that were covered by a high proportion of *Cytisus scoparius*, *Deschampsia flexuosa* and *Rubus idaeus* ($N = 5$). While MONHEATH and RESSITE were grazed by sheep or goats, CONTROL sites were kept ungrazed (cf. Borchard et al., 2013).

2.3. Restoration methods

The restoration measurements were conducted in 2008 and 2009 in the direct vicinity of existing montane heathlands (Borchard et al., 2013). Until the beginning of the 20th century, all restoration and control sites were used as montane heathlands. In the following decades they were afforested with *Picea abies*. Hence, the soil seed bank on both treatments (RESSITE, CONTROL) should be similar (cf. Walker et al., 2004; Eycott et al., 2006). The restoration was conducted in three steps: (i) deforestation of the spruce forests, (ii) clearing of remaining branches and (iii) transfer of seed material (hydroseeding, application of chopper material). The seed material was harvested on the largest heathland in the study area ('Neuer Hagen', 73.9 ha).

2.4. Sampling design

Carabid beetles and spiders were sampled using pitfall traps. Three traps spaced at least 10 m apart (to minimise interference) and away from the boundaries of the treatment (to avoid edge effects) were randomly set out in each plot. Pitfall traps consisted of 7.5 cm deep and 9 cm diameter polypropylene cups filled with Renner solution (40% ethanol, 30% water, 20% glycerine, 10% acetic acid) and a few drops of detergent. In order to avoid losses of pitfall trap catches, all traps were protected with a 20 cm \times 20 cm wire netting (15 cm above each trap) and a roof (10 cm diameter, 3 cm above each trap) to prevent trampling and overflow. Pitfall traps were opened continuously from mid-August until mid-October 2011 and from mid-May until the beginning of July 2012. The traps were emptied every three weeks during the sampling period. For subsequent analyses, pitfall trap catches were pooled for each individual plot, thus producing one dataset per plot.

We determined all carabid beetles to species level according to Müller-Motzfeld (2006) and Trautner and Geigenmüller (1988). The nomenclature follows Müller-Motzfeld (2006). Spiders were identified according to Roberts (1987, 1998) and Nentwig et al. (2013). Only adult spiders were included in the analysis. Nomenclature follows Platnick (2013).

2.5. Environmental variables

We sampled environmental variables from three randomly established subplots (replicates) within each plot. The size of the subplots was 16 m² (4 m \times 4 m). Sampling took place in June/July 2011 and September 2012. We recorded vegetation cover (5% steps) for the shrub, dwarf shrub, herb and moss layer. Furthermore, we recorded the percentage of bare soil and soil moisture using the Theta probe ML2 (Delta-T Devices Ltd, 128 Low Road, Burwell, Cambridge CB5 0EJ, England). For statistical evaluation, we computed mean values of the subplot data, considering both sampling periods (2011 and 2012).

Air temperature and humidity were recorded during the whole study period from August 2011 to September 2012 on all plots. We

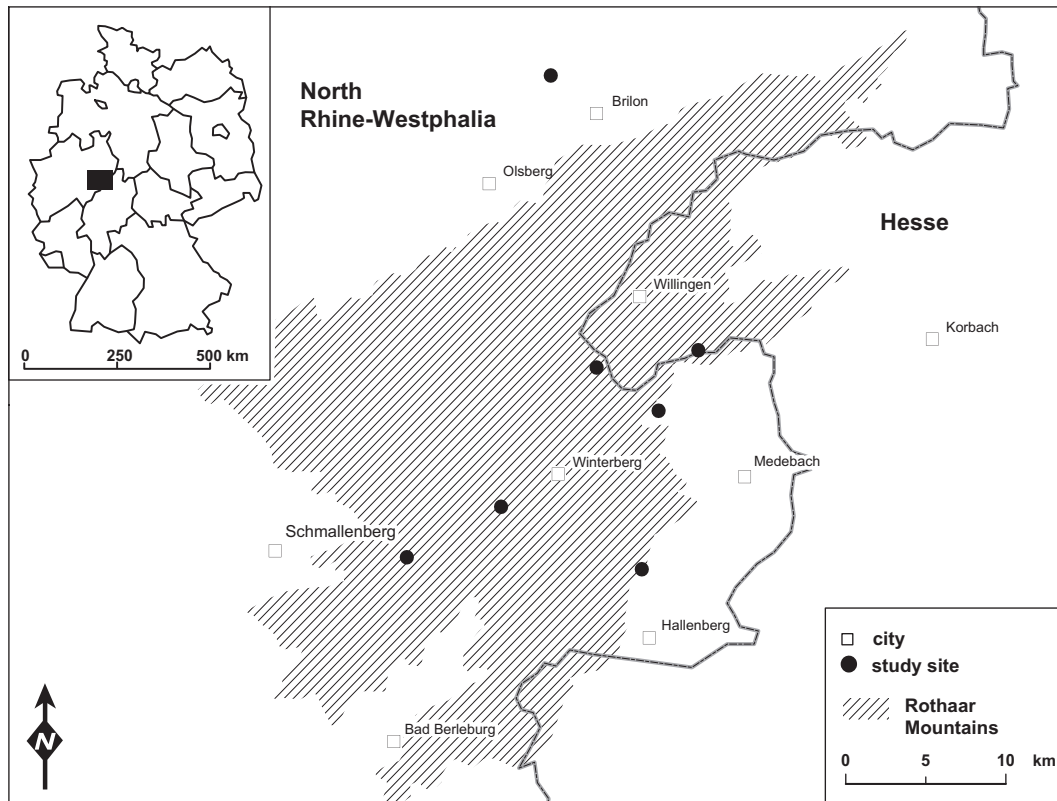


Fig. 1. Location of the study area and the study sites in Central Germany.

set up a Hygrochron Temperature/humidity data-logger (iButton, Maxim/Dallas, DS1923, USA) 10 cm above the ground and measured air temperature and humidity every hour. We protected the data-logger from direct sunlight and precipitation with help of a self-constructed radiation shield (cf. Borchard and Fartmann, 2014).

2.6. Data analysis

The applied restoration procedures did not show any differences in the composition of carabid beetles and spiders, nor the sampled environmental variables, and were thus analysed together (cf. Section 2.3). Further details of the applied restoration measurements are given in Borchard et al. (2013).

Differences between environmental variables and carabid beetle as well as spider diversity (Simpson index of diversity 1-D), among the analysed treatments MONHEATH, RESSITE and CONTROL, were tested using one-way analysis of variance (ANOVA) followed by Holm-Sidak tests. If data did not show normal distribution and homogeneity of variance, we performed a Kruskal–Wallis ANOVA on ranks with Dunn's test as a post hoc test.

Assemblage structure of carabid beetles and spiders were analysed ecologically using a non-metric multidimensional scaling (NMDS) (R packages: VEGAN, MASS). NMDS ordination was based on the Bray–Curtis distance measure and a maximum number of 100 random starts were used to search for a stable solution. In order to reduce noise of the NMDS ordination we omitted all carabid and spider species occurring with less than three individuals in our data set. To avoid multicollinearity, we only included environmental variables with correlations of $|r_s| < 0.7$. The environmental variables were fitted afterwards onto the ordination and only significant variables ($P < 0.05$) are shown. Mantel tests, based on Spearman's rank correlation and 999 permutations were used to

test for correlations between the carabid and spider species and environmental variables.

We determined the ecological preferences of carabids and spiders using niche positions (shading, moisture) provided by Irmeler and Gürlich (2004) and Entling et al. (2007). In order to detect the most influential carabid and spider species for each of the three treatments, we applied a simpler analysis (similarity percentages). The simpler analysis performs pairwise comparisons of groups of sampling units and finds the average contribution of each species to the average overall Bray–Curtis dissimilarity. The function displays the most important species, which contribute to at least 70% of the differences between groups. That is, such a species is overwhelmingly more important than all other species detected.

The data analysis was conducted using the free software package R-3.0.1 (R Development Core Team, 2010), including the libraries VEGAN (Oksanen et al., 2008) and MASS (Venables and Ripley, 2008), and SigmaPlot 11.0.

3. Results

3.1. Environmental variables

All environmental variables differed significantly between the three treatments, except soil moisture (Table 1). The cover of shrubs was lowest on MONHEATH, differing significantly from RESSITE and CONTROL. Dwarf shrubs such as *Calluna vulgaris*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea* had a significantly higher cover on MONHEATH than on either RESSITE or CONTROL. The cover of herbs and grasses, as well as bare soil, was significantly lower on MONHEATH than on the other two treatments. In contrast, the moss cover was highest on MONHEATH whereas RESSITE and CONTROL had significantly lower values. Plant species richness

Table 1
Environmental variables (mean values \pm SE) of montane heathlands (MONHEATH), restoration sites (RESSITE) and control sites (CONTROL). Differences among treatments were tested by applying One-Way ANOVA or Kruskal–Wallis ANOVA on ranks, respectively. In case of normal distribution and equal variance differences between groups were tested using the Holm–Sidak method; otherwise, we used Dunn’s test as a post hoc test. Different letters indicate significant differences between treatments ($P < 0.05$). n.s. not significant.

	Treatment			Statistical test	P
	MONHEATH	RESSITE	CONTROL		
Cover (%) of					
Shrubs	0.1 \pm 0.1 ^a	5.8 \pm 5.3 ^b	11.5 \pm 6.3 ^b	8.3 [*]	-
Dwarf shrubs	81.5 \pm 4.5 ^a	15.8 \pm 6.6 ^b	1.9 \pm 1.2 ^b	67.5	***
Herbs/grasses	9.9 \pm 3.9 ^a	62.0 \pm 5.4 ^b	68.9 \pm 6.2 ^b	40.6	***
Mosses	9.5 \pm 0.9 ^a	2.1 \pm 1.0 ^b	1.5 \pm 0.7 ^b	25.4	***
Bare soil	0.0 \pm 0.0 ^a	5.5 \pm 0.9 ^b	2.8 \pm 1.2 ^b	11.9	***
Soil moisture (%)	25.1 \pm 2.4	20.3 \pm 1.5	26.8 \pm 5.1	1.3	n.s.
No. of plant species	10.0 \pm 1.6 ^a	34.6 \pm 4.1 ^b	33.8 \pm 7.4 ^b	10.8	***

^{*} $P < 0.05$.

^{**} $P < 0.01$.

^{***} $P < 0.001$.

was highest on RESSITE and CONTROL, differing significantly from MONHEATH.

3.2. Capture statistics

In total, we recorded 5303 carabid beetles of 57 species and 5837 spiders of 129 species in our plots (Appendix A). The number of carabid individuals was highest on RESSITE ($N = 2478$), followed by CONTROL ($N = 1653$) and MONHEATH ($N = 1172$). The most frequent species was *Poecilus versicolor*, representing 37% of the total catch, followed by *Carabus problematicus* (17%) and *Pterostichus burmeisteri* (10%).

The highest number of spiders was also found on RESSITE ($N = 3079$), followed by CONTROL ($N = 1444$) and MONHEATH ($N = 1314$). The lycosid spider *Pardosa pullata* was the most abundant species, representing 36% of the total catch. Also frequent were *Pardosa palustris* (18%) and *Alopecosa pulverulenta* (5%).

3.3. Carabid and spider diversity

With respect to the alpha-diversity measurements, differences between the three treatments were only found in Simpson diversity and species evenness for spiders (Fig. 2). Simpson diversity was highest on MONHEATH, differing significantly from RESSITE

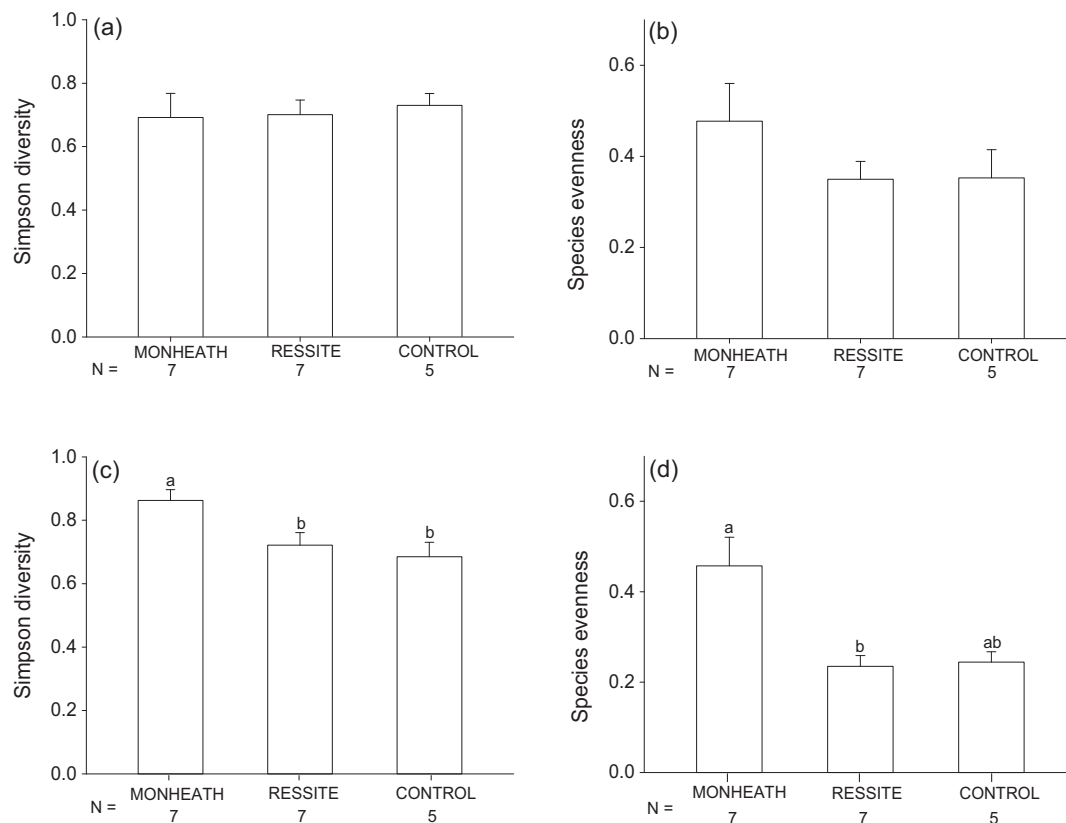


Fig. 2. Comparison of species diversity (Simpson diversity, 1-D) and relative abundance (species evenness) (mean values \pm SE) of carabid beetles (a and b) and spiders (c and d) among the analysed treatments. Statistics: (a) Kruskal–Wallis ANOVA on ranks, $H = 0.065$, $df = 2$, $P = 0.96$; (b) ANOVA, $F = 1.31$, $df = 2$, $P = 0.29$; (c) ANOVA, $F = 5.69$, $df = 2$, $P < 0.05$; (d) Kruskal–Wallis ANOVA on ranks, $H = 7.78$, $df = 2$, $P < 0.05$. In case of normal distribution and equal variance, differences between groups were tested using the Holm–Sidak method; otherwise, we used Dunn’s test as a post hoc test. Different letters indicate significant differences between treatments ($P < 0.05$).

and CONTROL. Species evenness was highest on MONHEATH, differing significantly from RESSITE, but not from CONTROL.

3.4. Assemblage structure and species response to environmental variables

NMDS ordination revealed that the environmental conditions, as well as the carabid and spider assemblages of MONHEATH and RESSITE/CONTROL, were distinctly different from each other (Figs. 3 and 4). RESSITE and CONTROL, however, were not separated in the carabid and spider ordination. In both ordinations, MONHEATH was associated with a dense vegetation of dwarf shrubs and RESSITE/CONTROL with open conditions, having a higher cover of bare ground and herbs/grasses.

The results of the simpler analysis supported this: *Abax parallelepipedus*, *Pterostichus burmeisteri* as well as *Pocadicnemis pumila* and *Tenuiphantes mengei* had high contribution values for MONHEATH, while *Amara lunicollis*, *Bembidion lampros*, *Notiophilus aquaticus* and *Poecilus versicolor* as well as *Alopecosa cuneata*, *A. pulverulenta*, *Drassyllus pusillus*, *Erigone atra*, *Pardosa amentata*, *P. palustris*, *P. pullata*, *Xerolycosa nemoralis* and *Xysticus kochi* were characteristic of RESSITE/CONTROL. Overall, montane heathlands comprised fewer characteristic species compared to the two other treatments.

Carabid and spider species data were significantly correlated with environmental variables (Mantel test, carabid species:

$r = 0.45, P < 0.001$; spider species: $r = 0.49, P < 0.001$). All variables contributed significantly to both ordination models. In particular, the cover of dwarf shrubs and herbs/grasses showed a highly significant contribution to the spider ordination ($P < 0.001$), whereas the cover of bare soil was of less importance ($P < 0.01$).

The evaluation of the carabid and spider ecology, expressed by their niche positions (mean values \pm SE), revealed significant differences in shade and moisture indicator values for spiders among MONHEATH and RESSITE/CONTROL (Table 2). MONHEATH were characterised by many spider species that prefer a cool, moist microclimate whereas RESSITE/CONTROL had a higher proportion of spider species with clear preferences for a warmer and drier microclimate. Carabid indicator values for water and tree cover showed a trend towards higher values on MONHEATH, compared to RESSITE/CONTROL. However, the values did not differ significantly.

4. Discussion

Four to five years after conducting the restoration measures, all environmental variables, except soil moisture, differed considerably between MONHEATH on one hand and RESSITE and CONTROL on the other. MONHEATH was characterised by a high cover of dwarf shrubs; in contrast, RESSITE/CONTROL had a vegetation rich in herbs/grasses with some bare ground. Both carabid beetle and spider assemblage composition clearly reflected these differences

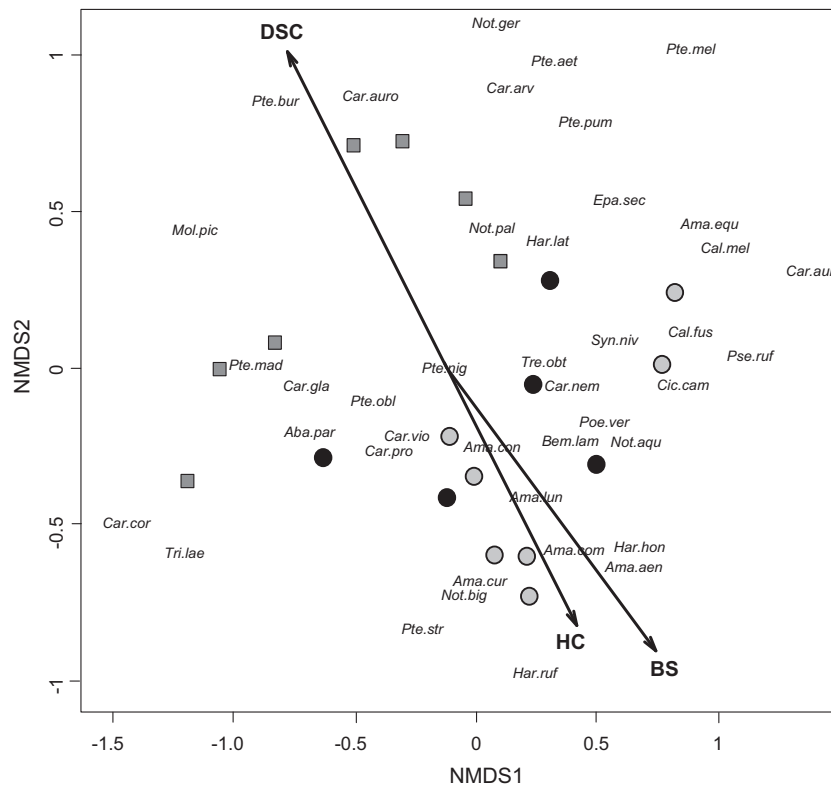


Fig. 3. Results of NMDS ordination (stress = 10.58, 3 dimensions, Bray–Curtis distance) based on carabid beetle data and environmental variables (BS, cover of bare soil ($P < 0.01$); DSC, cover of dwarf shrubs ($P < 0.01$); HC, cover of herbs and grasses ($P < 0.01$)). Dark grey squares = montane heathlands, light grey circles = restoration sites and black circles = control sites. Correlation of environmental variables and carabid beetle data ($r = 0.45$, Mantel test, $P < 0.001$). Abbreviations of species names and contribution values of conducted simpler analysis for the corresponding treatment in parentheses: *Aba.par* = *Abax parallelepipedus* (MONHEATH: 16.4), *Ama.aen* = *Amara aenea*, *Ama.com* = *Amara communis*, *Ama.con* = *Amara convexior*, *Ama.cur* = *Amara curta*, *Ama.equ* = *Amara equestris*, *Ama.lun* = *Amara lunicollis* (RESSITE: 6.1), *Bem.lam* = *Bembidion lampros* (RESSITE: 11.7; CONTROL: 18.2), *Cal.fus* = *Calathus fuscipes*, *Cal.mel* = *Calathus melanocephalus*, *Car.arv* = *Carabus arvensis*, *Car.aur* = *Carabus auratus*, *Car.auro* = *Carabus auronitens*, *Car.cor* = *Carabus coriaceus*, *Car.gla* = *Carabus glabratus*, *Car.nem* = *Carabus nemoralis*, *Car.pro* = *Carabus problematicus*, *Car.vio* = *Carabus violaceus*, *Cic.cam* = *Cicindela campestris*, *Epa.sec* = *Epaphius secalis*, *Har.hon* = *Harpalus honestus*, *Har.lat* = *Harpalus latus*, *Har.ruf* = *Harpalus rufipalpis*, *Mol.pic* = *Molops piceus*, *Not.aqu* = *Notiophilus aquaticus* (RESSITE: 21.9; CONTROL: 7.2), *Not.big* = *Notiophilus biguttatus*, *Not.ger* = *Notiophilus germyini*, *Not.pal* = *Notiophilus palustris*, *Poe.ver* = *Poecilus versicolor* (RESSITE: 164.1; CONTROL: 139.6), *Pse.ruf* = *Pseudophonus rufipes*, *Pte.aet* = *Pterostichus aethiops*, *Pte.bur* = *Pterostichus burmeisteri* (MONHEATH: 70.6), *Pte.mad* = *Pterostichus madidus*, *Pte.mel* = *Pterostichus melanarius*, *Pte.nig* = *Pterostichus niger*, *Pte.obl* = *Pterostichus oblopnctatus*, *Pte.pum* = *Pterostichus pumilio*, *Pte.str* = *Pterostichus strenuus*, *Syn.niv* = *Synuchus nivalis*, *Tre.obt* = *Trechus obtusus*, *Tri.lae* = *Trichotichnus laevicollis*.

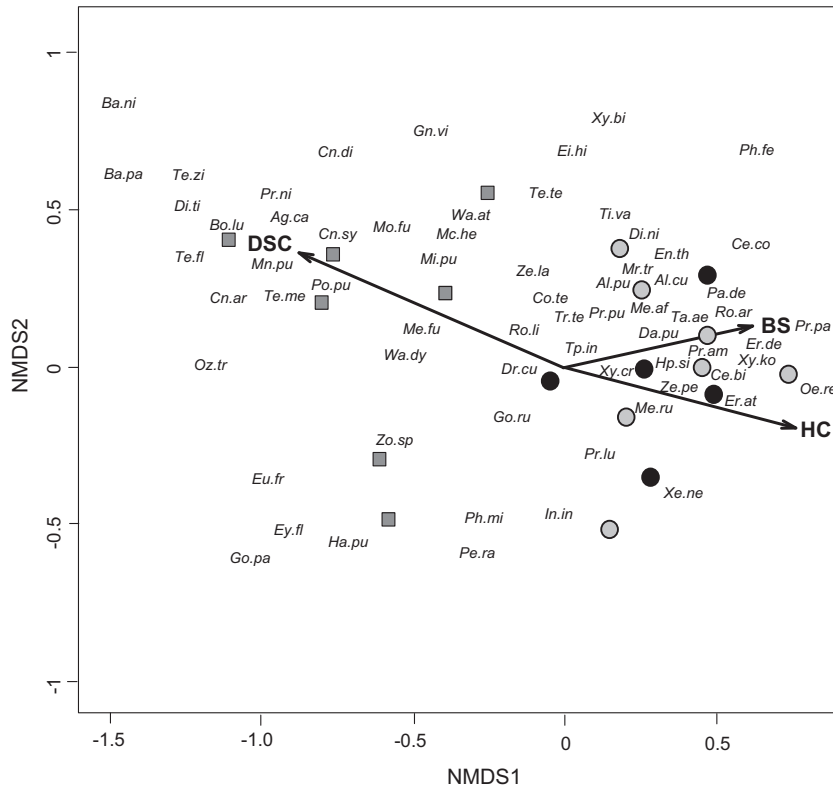


Fig. 4. Results of NMS ordination (stress = 10.01, 3 dimensions, Bray–Curtis distance) based on spider data and environmental variables (BS, cover of bare soil ($P < 0.01$); DSC, cover of dwarf shrubs ($P < 0.001$); HC, cover of herbs and grasses ($P < 0.001$)). Dark grey squares = montane heathlands, light grey circles = restoration sites and black circles = control sites. Correlation of environmental variables and carabid beetle data ($r = 0.49$, Mantel test, $P < 0.001$). Abbreviations of species names and contribution values of conducted simpler analysis for the corresponding treatment in parentheses: Ag.ca = *Agyneta cauta*, Al.cu = *Alopecosa cuneata* (RESSITE: 11.3), Al.pu = *Alopecosa pulverulenta* (RESSITE: 27.6), Ba.ni = *Bathyphantes nigrinus*, Ba.pa = *Bathyphantes parvulus*, Bo.lu = *Bolyphantes luteolus*, Ce.bi = *Centromerita bicolor*, Ce.co = *Centromerita concinna*, Cn.ar = *Centromerus arcanus*, Cn.di = *Centromerus dilutus*, Cn.sy = *Centromerus sylvaticus*, Co.te = *Coelotes terrestris*, Da.pu = *Drassyllus pusillus* (RESSITE: 9.1), Di.ni = *Dicymbium nigrum brevisetosum*, Di.ti = *Dicymbium tibiale*, Dr.cu = *Drassodes cupreus*, Ei.hi = *Erigonella hiemalis*, En.th = *Enoplognatha thoracica*, Er.at = *Erigone atra* (RESSITE: 9.0), Er.de = *Erigone dentipalpis*, Eu.fr = *Euophrys frontalis*, Ey.fl = *Euryopis flavomaculata*, Gn.vi = *Gongylidiellum vivum*, Go.pa = *Gonatium paradoxum*, Go.ru = *Gonatium rubens*, Ha.pu = *Hahnina pusilla*, Hp.si = *Haplodrassus signifer*, In.in = *Inermocoelotes inermis*, Mc.he = *Micrargus herbigradus*, Me.af = *Meioneta affinis*, Me.ru = *Meioneta rurestris*, Mi.fu = *Micaria fulgens*, Mi.pu = *Micaria pulicaria*, Mn.pu = *Minyriolus pusillus*, Mo.fu = *Monocephalus fuscipes*, Mr.tr = *Mermessus trilobatus*, Oe.re = *Oedothorax retusus*, Oz.tr = *Ozyptila trux*, Pa.de = *Pachygnatha degeeri*, Pe.ra = *Pelecopsis radicolica*, Ph.fe = *Phrurolithus festinus*, Ph.mi = *Phrurolithus minimus*, Po.pu = *Pocadicnemis pumila* (MONHEATH: 10.9), Pr.am = *Pardosa amentata* (CONTROL: 19.2), Pr.lu = *Pardosa lugubris*, Pr.ni = *Pardosa nigriceps*, Pr.pa = *Pardosa palustris* (RESSITE: 132.6), Pr.pu = *Pardosa pullata* (CONTROL: 145.4), Ro.ar = *Robertus arundineti*, Ro.li = *Robertus lividus*, Ta.ae = *Talavera aequipes*, Te.fl = *Tenuiphantes flavipes*, Te.me = *Tenuiphantes mengi* (MONHEATH: 9.9), Te.te = *Tenuiphantes tenuis*, Te.zi = *Tenuiphantes zimmermanni*, Ti.va = *Tiso vagans*, Tp.in = *Tapinocyba insecta*, Tr.te = *Trochosa terricola*, Wa.at = *Walckenaeria atrotibialis*, Wa.dy = *Walckenaeria dysderoides*, Xe.ne = *Xerolycosa nemoralis* (CONTROL: 6.6), Xy.bi = *Xysticus bifasciatus*, Xy.cr = *Xysticus cristatus*, Xy.ko = *Xysticus kochi* (RESSITE: 24.4), Ze.la = *Zelotes latreillei*, Ze.pe = *Zelotes petrensis*, Zo.sp = *Zora spinimana*.

Table 2 Niche positions (mean values \pm SE) of carabid beetles and spiders for montane heathlands (MONHEATH), restoration sites (RESSITE) and control sites (CONTROL). Differences among treatments were tested by applying One-Way ANOVA or Kruskal–Wallis ANOVA on ranks, respectively. In case of normal distribution and equal variance differences between groups were tested using the Holm–Sidak method; otherwise, we used Dunn’s test as a post hoc test. Different letters indicate significant differences between treatments ($P < 0.05$). n.s. not significant.

	Treatment			Statistical test	P
	MONHEATH	RESSITE	CONTROL		
Carabids					
Water	3.779 \pm 0.247	3.271 \pm 0.093	3.381 \pm 0.134	2.3*	n.s.
Tree cover	6.334 \pm 1.135	3.469 \pm 0.586	4.439 \pm 0.753	2.9	n.s.
Spiders					
Shade	0.42 \pm 0.01 ^a	0.35 \pm 0.01 ^b	0.37 \pm 0.01 ^b	14.5	***
Moisture	0.167 \pm 0.003 ^a	0.180 \pm 0.002 ^b	0.182 \pm 0.001 ^b	9.7	**

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

in environmental conditions. Alpha-diversity (Simpson diversity, evenness) and niche positions, however, were only different for spiders. Diversity as well as spider indicator values for shade and moisture were higher for MONHEATH.

Restoration of heathlands is a time-demanding process as heathland plant species, especially the target dwarf shrubs (*Calluna*

vulgaris, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*), are known to establish slowly (Walker et al., 2004; Diaz et al., 2008; Borchard et al., 2013). Although the cover of Ericaceae dwarf shrubs is already higher on RESSITE (Borchard et al., 2014) there were no general differences in vegetation structure between RESSITE and CONTROL. Consequently, assemblage composition,

alpha-diversity (Simpson diversity, evenness) and niche positions of both carabid beetles and spiders did not differ between the two treatments. For Orthoptera (Borchard et al., 2013) and Auchenorrhyncha (Borchard and Fartmann, 2014) there were also no differences found in assemblage composition between RESSITE and CONTROL. However, if the observed stronger rejuvenation of Ericaceae dwarf shrubs on RESSITE (Borchard et al., 2014) continues, differences in habitat structure and in carabid and spider community composition are very likely to occur.

Four to five years after restoration, RESSITE and CONTROL still represent early successional stages and are much more open and heterogeneous than the dense dwarf shrub stands of MONHEATH (cf. Borchard et al., 2013). While alpha-diversity of carabid beetles was already as high in these early seral stages as on MONHEATH, Simpson diversity and, partly, evenness (RESSITE) of spiders were lower. Differences in dispersal ability (cf. Baur, 2014) or habitat requirements are possible explanations for the observed discrepancy in the diversity patterns among the two arthropod groups. Both carabid beetles (Martay et al., 2012) and spiders (Bell et al., 2001) are known to be relatively effective dispersers. Moreover, RESSITE and CONTROL were directly adjacent to MONHEATH. Consequently, we assume that dispersal limitation can hardly explain the different patterns (cf. Borchard et al., 2013; Borchard and Fartmann, 2014). In contrast, several studies highlighted that open habitats containing bare ground are generally characterised by relatively species-poor spider communities where r-selected lycosids and linyphiids dominate (Bell et al., 2001; Perner and Malt, 2003; Buchholz, 2010; Negro et al., 2013). Seven of the nine species characteristic of RESSITE/CONTROL belonged to these two families (Lycosidae: *Alopecosa cuneata*, *A. pulverulenta*, *Pardosa amentata*, *P. palustris*, *P. pullata* and *Xerolycosa nemoralis*; Linyphiidae: *Erigone atra*). As ground-welling hunters, lycosids depend on open vegetation that allows running on the ground, and the linyphiid *Erigone atra* builds its webs over depressions in the soil (Alderweireldt, 1994). With increasing vegetation cover, open habitats become more attractive for web spiders; as a consequence, species richness increases (Bell et al., 2001). Carabid beetles, however, are able to form species-rich assemblages in both early and later stages of heathland succession (Schirmel et al., 2012). Accordingly, we assume that the contrasting responses of carabid beetles and spiders to heathland restoration reflect their general differences in habitat requirements.

Surprisingly, all species that were due to the simpler analysis characteristic of MONHEATH (carabid beetles: *Abax parallelepipedus* and *Pterostichus burmeisteri*; spiders: *Pocadicnemis pumila* and *Tenuiphantes mengei*) are usually considered as woodland, not heathland species (Kreuels and Buchholz, 2006; Gesellschaft für angewandte Carabidologie, 2009). The regular occurrence of typical woodland species in montane heathlands of our study area can be explained by (i) the cool montane climate with high precipitation (cf. Grosseschallau, 1981; Hannig and Hartmann, 2006), and additionally by (ii) the dense dwarf shrub stands of MONHEATH, which favour cool and moist microclimatic conditions. Consequently, shade and moisture indicator values for spiders differed between MONHEATH and RESSITE/CONTROL. However, typical heathland species such as *Amara equestris*, *Cicindela campestris*, *Notiophilous aquaticus* or *Harpalus rufipalpis* (Gesellschaft für angewandte Carabidologie, 2009) as well as *Xysticus kochi* (Kreuels and Buchholz, 2006) occurred on the warmer and drier RESSITE and CONTROL.

5. Conclusions

The evaluation of montane heathland restoration on former spruce forests showed that carabid beetles and spiders are useful

bioindicators. Both arthropod groups reflected the different environmental conditions between old montane heathlands on one hand and restoration and control sites on the other. Thus, due to the cool and wet montane climate and the dense dwarf-shrub stands, the carabid beetle and spider species characteristic of MONHEATH were typical woodland species. In contrast, four to five years after restoration, RESSITE and CONTROL still represent early successional stages with a low cover of Ericaceae dwarf shrubs, but were already home to some typical heathland carabid beetle and spider species that were missing in MONHEATH.

In conclusion, restoration of complete heathland ecosystems with their typical flora and fauna is a time-consuming process (Borchard et al., 2013) that will take much more time than covered by this study. Thereby the harsh climatic conditions of our study area (cf. Borchard et al., 2013) and the resultant short growing season might even slow down heathland establishment processes, too. There is a possibility that only further management of restoration sites will ensure the long term development towards the existing montane heathlands.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.08.006>.

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