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Rejuvenation and restoration measures foster specialised and threatened carabid beetle species in montane heathland ecosystems

Thomas Fartmann[1,2] | Marco Drung[1] | Max Freienstein[1]

[1]Department of Biodiversity and Landscape Ecology, Faculty of Biology and Chemistry, Osnabrück University, Osnabrück, Germany

[2]Institute of Biodiversity and Landscape Ecology (IBL), Münster, Germany

Correspondence
Thomas Fartmann, Department of Biodiversity and Landscape Ecology, Faculty of Biology and Chemistry, Osnabrück University, Barbarastraße 11, 49076 Osnabrück, Germany.
Email: t.fartmann@uos.de

Abstract

1. Montane heathlands are among the most threatened semi-natural ecosystems across Central Europe. Nevertheless, empirical studies on the effects of rejuvenation and restoration of montane heathlands have been scarce thus far.

2. The aim of our study was to analyse the long-term effects of heathland rejuvenation and restoration on carabid beetle assemblages. Our study took place in the Rothaar Mountains, one of the most important strongholds of montane heathlands in Central Europe. We considered four different successional stages: (i) early-successional heathlands as a result of rejuvenation measures (EARLY), (ii) restored heathlands (RESTORED), (iii) late-successional heathlands (LATE) and (iv) windthrows (WIND).

3. Our study revealed that the composition of carabid beetle assemblages differed across the gradient. From the earlier to the later stages, beetle biomass, richness of macropterous, threatened and heathland species decreased, whereas moisture and shading indicator values increased. The number of indicator species peaked in EARLY and RESTORED. Solely brachypterous species had the highest species richness in the later seral stages.

4. Overall, rejuvenation and restoration measures fostered specialised and threatened carabid beetle species of montane heathlands. In contrast, carabid beetle assemblages of the two later and dense successional stages consisted mainly of non-threatened habitat generalists. Vegetation structure and the interrelated microclimate are assumed to be the key drivers of assemblage composition.

5. For the long-term conservation of montane heathlands and their specialised carabid beetle assemblages, we recommend rejuvenation by sod cutting and choppering in a mosaic-like manner and at intervals that clearly exceed more than two decades.

KEYWORDS
biodiversity conservation, ground beetle assemblage, insect biomass, semi-natural habitat, species richness, successional gradient

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INTRODUCTION

We are living in a time of continuous and dramatic biodiversity loss on a global scale (Butchart et al., 2010). Hence, scientists have already warned that we are heading towards a sixth global mass extinction (Barnosky et al., 2011; McCallum, 2015). In this context, the loss of insects has gained public attention, especially in the last few years, and international researchers are calling for urgent and increased efforts in habitat conservation and restoration (Cardoso et al., 2020; Harvey et al., 2020; Samways et al., 2020). In terrestrial biomes, land-use change is considered to be the main driver of this biodiversity crisis (Fartmann et al., 2021; Foley et al., 2005; IPBES, 2019; Stoate et al., 2009).

Semi-natural habitats shaped by traditional low-intensity management, such as the vast majority of European heathlands (Halada et al., 2011), have been particularly affected by land-use change and have dramatically declined since the mid-19th century (Keienburg & Prüter, 2004; Symes & Day, 2003). While many lowland heathlands have been converted to arable fields, montane heathlands have largely disappeared because of abandonment of traditional land use (Hahn, 2007; Schubert et al., 2008) and afforestation (Symes & Day, 2003; Walker et al., 2004). In general, heathlands are characterised by highly specialised and, thus, often threatened species (Buchholz et al., 2013; Schirmel & Fartmann, 2014). As a result, they are of great value for biodiversity conservation and are protected by the EU Habitats Directive (EC, 2007).

Plant and insect communities of montane heathlands differ strongly from those of lowland heathlands due to a wet and cold mountain climate (Britton et al., 2005). However, nowadays, the remaining montane heathlands mostly consist of small and isolated patches with species-poor old-growth heath (Borchard et al., 2013; Streitberger et al., 2021a). Therefore, they are among the most threatened ecosystems across Central Europe (Finck et al., 2017; Hoffmann, 1998). Nevertheless, empirical studies on the effects of rejuvenation and restoration measures in montane heathlands have been scarce thus far. The few available Central European studies solely investigated choppering (removal of biomass and the organic layer) as a rejuvenation measure (Fartmann et al., 2015) or only studied the short-term effects of restoration (4–5 years after application of the measures) (Borchard et al., 2013, 2014, 2017; Borchard & Fartmann, 2014). Recently, however, research on the long-term effects of rejuvenation and restoration of montane heathlands on phytodiversity (vascular plants, bryophytes and lichens) has been conducted (Streitberger et al., 2021a, 2021b).

The aim of our study was to analyse the long-term effects of montane heathland rejuvenation and restoration on carabid beetle assemblages (Coleoptera: Carabidae). Carabid beetles are excellent bioindicators for environmental alterations in heathland ecosystems (Buchholz et al., 2013; Bargmann et al., 2016). They (i) feature typical heathland species, (ii) respond rapidly to environmental change, (iii) are abundant, (iv) are easy to sample and (v) represent essential elements of the food chain (Borchard et al., 2014; Kotze et al., 2011; Rainio & Niemelä, 2003). Our study took place in the Rothaar Mountains, one of the most important strongholds of montane heathlands in Central Europe (Borchard & Fartmann, 2014). We compared carabid beetle assemblages across a gradient from early- to late-successional stages. These successional stages contained (i) rejuvenated heathlands that originated either from sod cutting 10–20 years ago or regular disturbance by skiing, (ii) restored heathlands with the application of seed transfer on former spruce forests 9–10 years after restoration, (iii) old-growth heathlands without any rejuvenation measures for at least 30 years and (iv) windthrows of spruce forests with salvage logging as a reference for vegetation development without seed transfer (cf. Streitberger et al., 2021a).

In particular, we addressed the following questions:

- How do the four successional stages differ in environmental conditions?
- What were the effects of rejuvenation and restoration measures on species richness and biomass of carabid beetles, and how did assemblage composition differ between the four successional stages?
- What management recommendations can be derived from our findings for rejuvenation and restoration of montane heathlands?

MATERIALS AND METHODS

Study area

The study area is located in the Rothaar Mountains, a low mountain range at the border of the German Federal States of North Rhine-Westphalia and Hesse (51°09′N, 8°24′O to 51°17′N, 8°40′O, 540–830 m a.s.l.). It is characterised by a cool (mean annual temperature: 5°C) and wet (mean annual precipitation: 1.450 mm) montane climate (Borchard et al., 2013) with snowy winters (mean snow-cover duration: 100 days/year) (German Weather Service, pers. comm.). The prevailing soils are nutrient-poor cambisols on acidic bedrock (Geologisches Landesamt NRW, 1998). The landscape is dominated by woodland, especially non-native spruce forests (*Picea abies*) and grassland (Borchard et al., 2014). However, on many mountain peaks, remnants of montane heathlands still regularly occur (Streitberger et al., 2021a, 2021b). Altogether, we examined eight different subareas with occurrences of montane heathlands having a minimum size of 4.6 ha per subarea (cf. Streitberger et al., 2021b).

In the years 2008–2009, large-scale heathland restoration adjacent to the remaining heathlands was conducted in the study area (Borchard et al., 2013; Streitberger et al., 2021a). Spruce forests on former heathlands were deforested and, additionally, remaining branches and most of the organic layer were removed. Subsequently, seeds from a nearby nature reserve ('Neuer Hagen') with representative montane heathland vegetation were transferred to the restoration sites. For this purpose, two different procedures were applied: (i) hydroseeding and (ii) the spreading of choppered material. Hydroseeding involves the even distribution of a homogeneous suspension composed of threshed montane heathland species mixed with water and erosion control agents using a syringe. Choppered material

contains crushed aboveground biomass from the donor heathland including seeds.

Successional stages

Altogether, we considered four different seral stages along a successional gradient (Streitberger et al., 2021a): (i) early-successional heathlands (EARLY), (ii) restored heathlands (RESTORED), (iii) late-successional heathlands (LATE) and (iv) windthrows (WIND). EARLY emerged either from sod cutting 10–20 years ago or on ski pistes through regular disturbance by skiing in winter and mulching in late summer. Sod cutting involves the removal of the complete aboveground biomass, the organic layer and parts of the mineral soil. EARLY was characterised by very open habitat structures, namely sparse and short vegetation rich in bare ground, and *Calluna vulgaris* as the dominant plant species. Since environmental parameters and species data did not differ between sod cutting and ski pistes, they were merged to one successional stage. At RESTORED, the restoration measures mentioned in the Section 'Study area' had been applied 9–10 years ago. These mid-successional stages were rich in typical heathland and acidic grassland plant species. However, *Calluna vulgaris* was also the dominant dwarf shrub here. LATE comprised late-successional stages of montane heathlands, where no rejuvenation measures had been carried out during the last 30 years and dwarf shrubs of the genus *Vaccinium* (*V. myrtillus* and *V. vitis-idaea*) were dominant. Within the heathland remnants of the study area, this stage dominated. All three successional stages were managed by grazing. WIND served as a reference for natural vegetation development without seed transfer. This successional stage comprised windthrows of former spruce forests adjacent to heathland remnants, which were caused by the storm Kyrill in 2007. Except salvage logging, they have been unmanaged since then. After 11 years of succession, they were characterised by a dense and tall vegetation, rich in species of clear cuts and forests such as *Digitalis purpurea*, *Luzula luzuloides*, *Picea abies*, *Rubus idaeus* and *Senecio ovatus*.

Sampling design

For each of the four successional stages, we randomly selected eight plots ($N = 32$). Each plot had a size of 20 m × 25 m (500 m²). The number of studied successional stages within a subarea corresponded to their occurrence and was at least two. The minimum distance between two plots ranged between 105 and 535 m (mean distance to nearest plot: 168 m). Subareas were 2660 to 6410 m apart (mean distance to nearest subarea: 4080 m).

Environmental parameters

For each plot, we sampled different parameters of habitat structure and macro−/mesoclimate (Table 1). During mid-June 2018, we surveyed habitat structure and sunshine duration. The cover of vegetation in the plot was estimated in 5% steps (2.5% steps below 10% and

TABLE 1 Mean values [± standard error (SE)] of environmental parameters in the four different successional stages

Parameter	Successional stage				p
	EARLY	RESTORED	LATE	WIND	
Macro- and mesoclimate					
Elevation (m a. s. l.)	700 ± 18.2	720 ± 18.5	752 ± 22	798 ± 12.6	n.s.
Mean summer temperature (°C)	11.4 ± 0.2	11.3 ± 0.1	11.0 ± 0.2	10.8 ± 0.1	n.s.
Heatload index	0.74 ± 0.06	0.82 ± 0.02	0.83 ± 0.01	0.89 ± 0.01	n.s.
Sunshine duration (h)	14.6 ± 0.2	13.7 ± 0.3	14.3 ± 0.3	12.3 ± 0.3	n.s.
Habitat structure					
Cover (%)					
Trees	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.1 ± 1.9	n.s.
Shrubs	0.0 ± 0.0[a]	0.0 ± 0.0[a]	4.4 ± 2.1[ab]	23.8 ± 3.8[b]	***
Field layer	58.1 ± 1.6[a]	94.1 ± 2.1[c]	91.6 ± 3.4[c]	78.8 ± 3.4[b]	***
Grass	20.0 ± 3.3[a]	65.9 ± 6.8[b]	17.5 ± 4.2[a]	49.4 ± 6.2[b]	***
Litter	14.4 ± 2.8[a]	42.8 ± 13.2[ab]	40.0 ± 8.6[ab]	85.0 ± 2.3[b]	***
Moss	17.2 ± 7.1[a]	57.5 ± 10.6[b]	76.9 ± 4.2[b]	26.9 ± 4.6[a]	***
Bare ground	35.9 ± 4.9[b]	2.2 ± 0.6[a]	2.8 ± 1.8[a]	4.7 ± 0.7[a]	***
Height (cm)					
Shrubs	0.0 ± 0.0 [a]	0.0 ± 0.0 [a]	131.3 ± 60.6[ab]	305.0 ± 19.6[b]	***
Field layer	10.0 ± 1.3[a]	37.5 ± 8.9[b]	25.6 ± 2.9[b]	36.3 ± 2.1[b]	***

Note: Comparisons between groups were made by generalised linear mixed models with Tukey's contrasts (see Statistical analysis for details). The absence of concurrent letters indicates significant differences between successional stages ($p < 0.05$). Statistical differences are indicated as follows: ***$p < 0.001$, n.s. not significant.

above 90%). Vegetation height was measured with a folding rule at five randomly selected spots within each plot and then averaged. The duration of sunshine in June was recorded using a horizontoscope (Scherer et al., 2021). Data on mean annual temperature were derived from 1-km^2 grid datasets of Germany's National Meteorological Service (personal communication), which contain 10-year (2010–2019) mean values. The mean elevation (m a.s.l.) of the patches was calculated from topographic maps using ArcGIS 10.2. We calculated the heat load index according to McCune and Keon (2002) as a measure of radiation influx, based on the aspect and slope of each plot.

Carabid beetles

Carabid beetles were sampled from the beginning of May until mid-June 2018 and from the end of August until the beginning of October 2018 using pitfall traps. In each plot, three traps were randomly placed with a distance of 10 m to each other and to the boundaries of the plot in order to minimise interference and edge effects. The traps consisted of cups (7.5 cm deep and 9 cm wide) half filled with Renner solution (40% ethanol, 30% water, 20% glycerin, 10% acetic acid and a few drops of detergent). To avoid catch loss by overflow and trampling, we installed a plastic roof (2 cm above each trap) and wire netting (15 cm above each trap). The traps were emptied every 3 weeks during the sampling period resulting in 252 trap days per plot.

Carabid beetles were determined according to Trautner et al. (1987) and Müller-Motzfeld (2006). Nomenclature follows Trautner et al. (2014). For statistical analyses, pitfall catches were pooled, rendering one dataset per plot.

Classifications

Classification of heathland species were based on GAC (2009) and Trautner (2017). Accordingly, all species for which heathlands are among the main habitats were considered heathland specialists. Threatened species were assigned according to the red data book of North Rhine-Westphalia (Hannig & Kaiser, 2011). Biomass of carabid beetles was calculated for each plot based on body length of the species using the formula provided by Szyszko (1983). Body length of each species was averaged based on minimum and maximum values extracted from Klaiber et al. (2017). Additionally, we determined the wing length (macropterous vs. brachypterous, dimorphic species were considered macropterous; Klaiber et al., 2017) as a measure for the dispersal ability of the species (Kotze & O'Hara, 2003; Ng et al., 2018). Ecological preferences of carabid beetle assemblages were analysed by averaging indicator values for moisture and shading (Irmler & Gürlich, 2004) across all species of a plot.

Statistical analysis

Shannon diversity and evenness were calculated for each plot (Fedor & Zvaríková, 2019). In order to detect significant differences in environmental conditions and species data among the successional stages, (generalised) linear mixed-effect models (LMM; GLMM) were applied (R package lme4; Bates et al., 2021) with subarea as a random factor to account for potential spatial autocorrelation. *Successional stage* was used as a nominal fixed factor and the analysed parameters were used as dependent variables. Depending on the distribution of the variables, either proportional binomial (percentage data), Poisson or linear (for normally distributed and square-root- or log-transformed variables with normal distribution) models were applied. To reduce overdispersion within the models (binomial/Poisson), observation-level random effects were added as a random factor (Harrison, 2014, 2015). The overall effect of the dependent variables on successional type was analysed by comparing the full models with reduced models without successional type as the fixed factor and applying likelihood-ratio tests. Pairwise differences between the successional types were detected by applying Tukey's contrasts (glht function, R package multcomp; Hothorn et al., 2021).

In order to identify indicator species for each successional stage, we conducted an indicator species analysis (ISA) (Dufrêne & Legendre, 1997). All statistical analyses were performed using R 3.6.2 (R Development Core Team, 2021).

RESULTS

Environmental conditions

Macro- and mesoclimatic parameters did not differ between the four studied successional stages (Table 1). In contrast, all habitat-structure variables differed – except trees, which only occurred in WIND at low cover. Shrubs were only present in LATE and WIND. Therefore, the cover and height of shrubs increased from EARLY/RESTORED to LATE to WIND. The cover of the field layer and of mosses were lowest in EARLY/WIND and highest in RESTORED/LATE. Additionally, EARLY had the highest cover of bare ground and the shortest swards compared to the three other successional stages. The cover of grasses peaked in RESTORED/WIND compared to EARLY/LATE. Litter cover increased across the successional gradient from EARLY to RESTORED/LATE to WIND.

Response of carabid beetle assemblages to environmental conditions

In total, we collected 3283 individuals from 58 species of carabid beetles on the 32 plots (Table A1). Ten of these species were considered threatened, and seven were typical heathland species. The most common species were *Poecilus versicolor* (34% of all individuals), *Carabus problematicus* (14%) and *Pterostichus burmeisteri* (13%). Among threatened species, *Cicindela campestris* (3%) and *Carabus arvensis* (2%) were the most frequent ones.

Overall species richness, Shannon diversity and evenness did not differ between the four successional stages (Figure 1). In contrast, beetle biomass peaked in RESTORED, differing from WIND, while EARLY and LATE had an intermediate position. The number of
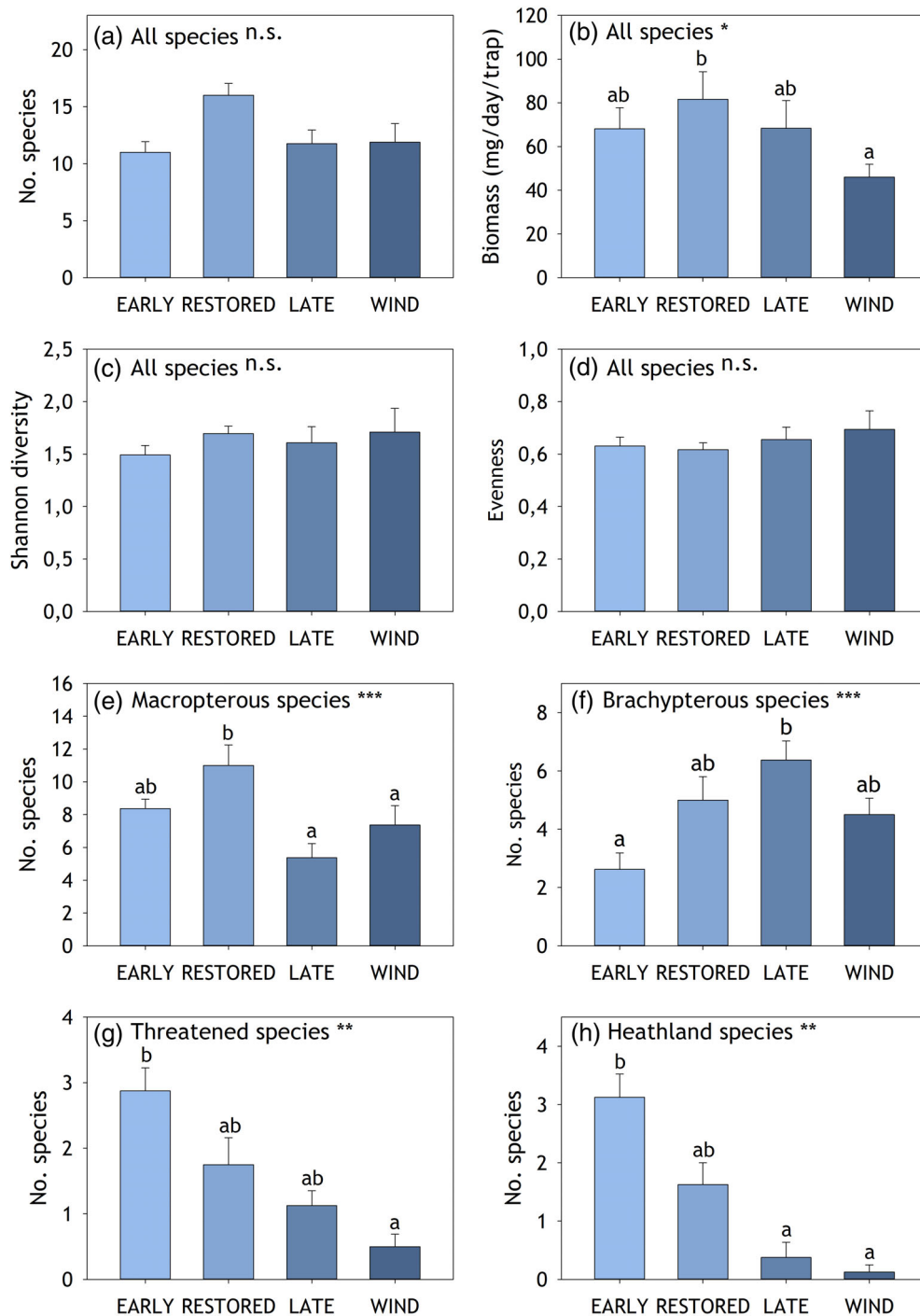
FIGURE 1 Mean values [± standard error (SE)] of total species richness (a), biomass (b), Shannon diversity (c), evenness (d), number of macropterous species (e), number of brachypterous species (f), number of threatened species (g) and heathland species (h) in the four different successional stages. Comparisons between groups were made by generalised linear mixed models with Tukey's contrasts (see Statistical analysis for details). The absence of concurrent letters indicates significant differences between successional stages $p < 0.05$. Statistical differences are indicated as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, n.s. not significant

macropterous species was also highest in RESTORED and differed from LATE/WIND but not from EARLY. In contrast, the number of brachypterous species increased from EARLY to LATE but was not different from RESTORED and WIND. For threatened and heathland species, the patterns were very similar: species richness was highest in EARLY and lowest in WIND; figures of RESTORED and LATE were intermediate (between both). On the contrary, mean indicator values for moisture and shading increased from EARLY to RESTORED to LATE/WIND (Figure 2).

All four successional stages were characterised by at least one indicator species (Table 2). However, the number of indicative species was highest in EARLY and RESTORED; in each case, three species were
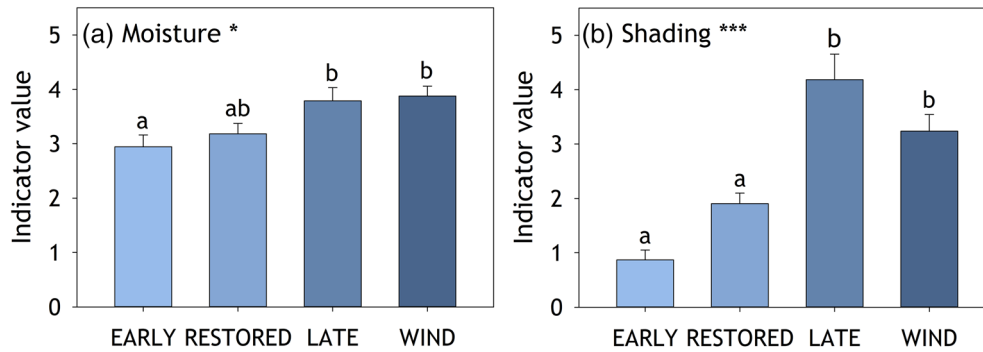
FIGURE 2 Mean indicator values [± standard error (SE)] for moisture (a) and shading (b) in the four different successional stages. Comparisons between groups were made by generalised linear mixed models with Tukey's contrasts (see Statistical analysis for details). The absence of concurrent letters indicates significant differences between successional stages ($p < 0.05$). Statistical differences are indicated as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, n.s. not significant

TABLE 2 Results of ISA (Dufrêne & Legendre, 1997) for the four different successional stages (see Statistical analysis for details)

Species	HS	p	EARLY	RESTORED	LATE	WIND
Calathus fuscipes		***	92.7			
Cicindela campestris	x	***	88.5			
Notiophilus aquaticus	x	***	92.3			
Amara lunicollis		***		84.5		
Harpalus latus		**		75.4		
Syntomus truncatellus		*		61.2		
Pterostichus aethiops		*			64.0	
Harpalus laevipes		**				70.7
Trichotichnus laevicollis		***				91.4

Note: Only significant species with an indicator value (IV) ≥ 60 are shown. Indicator species are sorted by "IV" for the respective successional stage. The threatened species is highlighted in bold type. $N = 8$ per successional stage. Statistical differences of Monte-Carlo tests are indicated as follows: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Abbreviations: HS, heathland species; ISA, indicator species analysis.

identified as indicator species. Two of the indicator species of EARLY, *C. campestris* and *Notiophilus aquaticus*, were heathland species. Additionally, *C. campestris* was also a threatened species.

DISCUSSION

Our study revealed that the composition of carabid beetle assemblages clearly differed across the successional gradient in montane heathlands. From the earlier to the later successional stages, beetle biomass, richness of macropterous, threatened and heathland species decreased, whereas the indicator values for moisture and shading increased. The number of indicator species also peaked in EARLY and RESTORED. Solely brachypterous species had the highest species richness in the later seral stages. Since macro- and mesoclimatic conditions did not differ between the successional stages, the differences in habitat structure and the interrelated microclimate have to be considered as the main drivers of assemblage composition.

Habitat structure is an important proxy for microclimatic conditions since it greatly modifies temperature and humidity of the near-ground air

layer (Kennedy, 1997; Stoutjesdijk & Barkman, 1992). Short swards with a sparse vegetation rich in bare ground, which mainly occurred in EARLY (see also Streitberger et al., 2021a), exhibit extraordinarily warm microclimates (Stoutjesdijk & Barkman, 1992; Streitberger & Fartmann, 2015). Threatened and specialised ground beetle species of heathlands are known to vitally depend on such conditions (Desender et al., 2010; Cameron & Leather, 2012; Bargmann et al., 2016). This is especially true for regions that are characterised by a cool climate, like the study area (Borchard et al., 2014; Fartmann et al., 2015). In line with this, among the indicator species, heathland specialists were only detected in EARLY (*C. campestris*, *N. aquaticus*) and the number of threatened and heathland species was highest in EARLY and lowest in WIND. The microclimatic gradient was also reflected by increasing moisture and shading indicator values within carabid beetle assemblages from earlier to later successional stages.

In RESTORED, bare ground had widely disappeared 9–10 years after restoration and swards were taller compared to EARLY. Nevertheless, in contrast to LATE and WIND, the number of heathland species still did not differ from EARLY. Characteristic of LATE was a homogeneous vegetation consisting of a dense and tall dwarf-shrub layer mainly structured by *V. myrtillus* but also by *C. vulagris* and *V. vitis-idaea* (see also

Streitberger et al., 2021a). Dense dwarf-shrub stands, especially those of the broad-leaved *Vaccinium* species, build close canopies that hamper solar radiation to reach the near-ground layer; the result is a cool and moist microclimate (Stoutjesdijk & Barkman, 1992). At WIND, even some trees and a shrub layer had established. In contrast, RESTORED had the most heterogeneous vegetation of all four successional stages. The diversity of vascular plants was highest (Streitberger et al., 2021a) and it exhibited an intermediate cover of grasses, dwarf shrubs (*C. vulgaris*) and mosses, and also some herbs (see also Streitberger et al., 2021a). Such conditions are known to facilitate warming close to the ground much better than dense vegetation (Stoutjesdijk & Barkman, 1992). The differences in shading preference of ground beetle communities between EARLY/RESTORED and LATE/WIND confirm these conclusions. Overall, the carabid beetle assemblages of the two latest successional stages consisted mainly of non-threatened habitat generalists and were poorly characterised by indicator species.

Recent studies have shown that heterogeneous habitats with a high phytodiversity foster overall species richness of ground beetles and abundance of large carabid beetles (Wang et al., 2021; Zou et al., 2019). Additionally, warm ambient temperatures are known to favour reproduction and survival of ectotherms, such as carabid beetles, and, hence, increase their abundance (Speight et al., 2008). These findings are consistent with our study. Overall species richness and carabid beetle biomass were highest in RESTORED, the most heterogeneous and also relatively warm successional stage; for species richness, however, the difference was not significant. In contrast, WIND, exhibiting a dense vegetation, had the lowest beetle biomass. In addition to providing a cool microclimate, dense vegetation is known to act as a spatial barrier, thus impairing carabid mobility and resulting in lower catch numbers (cf. Ekschmitt et al., 1997; Thiele, 1977).

The number of macropterous species peaked in earlier successional stages (RESTORED), whereas the number of brachypterous species was highest in later seral stages (LATE). These results are in line with previous work showing that dynamic habitats with sparse vegetation are mainly colonised by mobile carabid beetle species capable of flight (Kotze & O'Hara, 2003; Ng et al., 2018). In contrast, in stable habitats having a dense vegetation, flightless, brachypterous species are more characteristic.

In conclusion, rejuvenation and restoration measures fostered specialised and threatened carabid beetle species of montane heathland ecosystems. Vegetation structure and the interrelated microclimate were the key drivers of assemblage composition. Threatened and heathland species were dependent on early-successional stages, in particular EARLY but also RESTORED, exhibiting a warm microclimate. A high beetle biomass, however, was enhanced by heterogeneous and warm microhabitats, which was particularly true for RESTORED. Carabid beetle assemblages of the two later, dense successional stages, LATE and WIND, however, consisted mainly of non-threatened habitat generalists. Streitberger et al. (2021a) made similar observations for phytodiversity in montane heathlands of the study area. According to their study, the early- and mid-successional stages also played a vital role for the conservation of rare bryophytes, lichens and vascular plants.

IMPLICATIONS FOR CONSERVATION

As shown by our study, the conducted rejuvenation and restoration measures are an indispensable tool to maintain montane heathlands with their specialised carabid beetle assemblages in the long run. Montane heathlands rejuvenated by sod cutting provide warm and bare-ground-rich microhabitats – suitable for threatened carabid beetles typical of heathlands – for at least 10–20 years. These conditions are also attained on ski pistes through the regular disturbance by skiing in winter and mulching in late summer.

Choppering is another, albeit less intensive, way to rejuvenate heathlands (Fartmann et al., 2015; Streitberger et al., 2021a). It involves the removal of biomass and the organic layer but not of the mineral soil. Hence, in contrast to sod cutting, choppering is less effective in favouring early-successional plant and arthropod species (Fartmann et al., 2015; Streitberger et al., 2021a). However, in choppered montane heathlands, *Calluna vulgaris* rapidly re-establishes from the seed bank and the two *Vaccinium* species can re-sprout from the rhizomes with their ericoid mycorrhizas.

Restored heathlands, about 10 years after the transfer of autochthonous seed material (e.g. by the application of chopper material and hydroseeding), were still characterised by a high beetle biomass and represented an important habitat for threatened and heathland carabid beetles. However, both *Vaccinium* species had hardly established (Streitberger et al., 2021a), since they poorly regenerate from seeds (Borchard et al., 2017; Streitberger et al., 2021b).

As a result, we recommend continuing the enlargement of existing montane heathlands (Fartmann et al., 2015) through the restoration measures applied in this study. Despite the poor establishment of the two *Vaccinium* species, we do not suggest further measures that may foster the colonisation of restored heathlands by these species (Streitberger et al., 2021a). On the one hand, such methods are often expensive (e.g. the translocation of sods) (Pywell et al., 2011), and on the other hand, both dwarf-shrub species are still widespread and are often dominant within the heathlands of the study area (Streitberger et al., 2021a).

Concerning heathland rejuvenation, sod cutting is clearly the most effective way to foster the threatened assemblages of early-successional heathlands (see also Streitberger et al., 2021a, 2021b). However, it produces a lot of waste material resulting in high costs for its disposal (Streitberger et al., 2021a). Consequently, choppering should also be applied for heathland regeneration (Fartmann et al., 2015). A positive side effect of choppering would be the rejuvenation of the *Vaccinium* species. Both rejuvenation measures should be carried out within species-poor late-seral stages of heathland succession in a mosaic-like manner (Streitberger et al., 2021a). Management intervals in the grazed heathlands can clearly exceed more than two decades. Besides typical heathland ground beetles (this study) and plants (Streitberger et al., 2021a, 2021b), our management recommendations are likely to benefit other taxa, such as the woodlark (*Lullula arborea*) (Borchard et al., 2013; Fartmann et al., 2018), butterflies (cf. Maes et al., 2004; Schirmel & Fartmann, 2014), grasshoppers (Borchard et al., 2013; Fartmann et al., 2015; Schirmel et al., 2011) and spiders (Schirmel & Buchholz, 2011).

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available on request from the authors.

ORCID

Thomas Fartmann 🄳 https://orcid.org/0000-0002-2050-9221

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APPENDIX

TABLE A1 List of collected carabid species and the number of caught individuals in the four different successional stages (Hannig & Kaiser, 2011)

Species	HS	Threat	EARLY	RESTO	LATE	WIND	Total
Abax ovalis (Duftschmid, 1812)			1			12	13
Abax parallelepipedus (Piller & Mitterpacher, 1783)			4	69	123	9	205
Amara aenea (De Geer, 1774)			9	12			21
Amara communis (Panzer, 1797)				15	1	18	34
Amara convexior (Stephens, 1828)			3	11	7	44	65
Amara curta (Dejean, 1828)		VU		6			6
Amara equestris (Duftschmid, 1812)	x	NT	17	8			25
Amara lunicollis (Schlödte, 1837)			1	15	2	3	21
Amara nitida (Sturm, 1825)		VU				1	1
Amara ovata (Fabricius, 1792)				3			3
Badister bullatus (Schrank, 1798)				2			2
Bembidion lampros (Herbst, 1784)			13	10		6	29
Bembidion mannerheimii (C.R. Sahlberg, 1827)				3		1	4
Bradycellus caucasicus (Chaudoir, 1846)	x		1				1
Bradycellus harpalinus (Audinet-Serville, 1821)	x	EN		1	1	1	3
Calathus fuscipes (Goeze, 1777)			162	2	1		165
Carabus arvensis (Herbst, 1784)		VU	12	11	30		53
Carabus auratus (Linnaeus, 1761)				16	5		21
Carabus auronitens (Fabricius, 1792)					14	9	23
Carabus glabratus (Paykull, 1790)		VU			6	5	11
Carabus nemoralis (O.F. Müller, 1764)			1	3	2		6
Carabus problematicus (Herbst, 1786)			174	95	82	102	453
Carabus violaceus (Linnaeus, 1758)				62	12	2	76
Cicindela campestris (Linnaeus, 1758)	x	NT	84	10			94
Clivina fossor (Linnaeus, 1758)						1	1
Dyschirius globosus (Herbst, 1784)			3			1	4
Epaphius secalis (Paykull, 1790)			2			6	8
Harpalus honestus (Duftschmid, 1812)		NT	1				1
Harpalus laevipes (Zetterstedt, 1820)						8	8
Harpalus latus (Linnaeus, 1758)			2	22	3	2	29
Harpalus rufipalpis (Sturm, 1818)	x		2	5	2		9
Harpalus rufipes (De Geer, 1774)			1	1	2		4
Harpalus solitaris (Dejean, 1829)		CR	16				16
Leistus ferrugineus (Linnaeus, 1758)					1		1
Leistus terminatus (Hellwig in Panzer, 1793)						1	1
Microlestes minutulus (Goeze, 1777)				3			3
Molops piceus (Panzer, 1793)			1	4	1		6
Nebria brevicollis (Fabricius, 1792)			1				1
Notiophilus aestuans (Dejean, 1826)					1		1
Notiophilus aquaticus (Linnaeus, 1758)	x		37		1		38
Notiophilus palustris (Duftschmid, 1812)				1	6	8	15
Olisthopus rotundatus (Paykull, 1790)	x	VU	4				4
Poecilus versicolor (Sturm, 1824)			443	540	89	42	1114

(Continues)

TABLE A1 (Continued)

Species	HS	Threat	EARLY	RESTO	LATE	WIND	Total
Pterostichus aethiops (Panzer, 1796)				2	18	2	22
Pterostichus burmeisteri (Heer, 1838)			14	5	208	208	435
Pterostichus diligens (Sturm, 1824)					1		1
Pterostichus madidus (Fabricius, 1775)			6	53	35		94
Pterostichus melanarius (Illiger, 1798)				1			1
Pterostichus niger (Schaller, 1783)			1	6	4	8	19
Pterostichus oblopunctatus (Fabricius, 1787)			2		19	27	48
Pterostichus pumilio (Dejean, 1828)			4		1		5
Pterostichus strenuus (Panzer, 1796)				3		4	7
Pterostichus vernalis (Panzer, 1796)				2			2
Syntomus truncatellus (Linnaeus, 1761)				4			4
Synuchus vivalis (Illiger, 1798)				1			1
Trechus obtusus (Erichson, 1837)			2	7	6	5	20
Trichotichnus laevicollis (Duftschmid, 1812)			1			22	23
Trichotichnus nitens (Heer, 1837)				1		1	2
No. individuals	174	214	1025	1015	684	559	3283
No. species	7	10	32	37	30	29	58

Abbreviations: CR, critically endangered; EN, endangered; HS, heathland species; NT, near threatened; Threat, threat status; VU, vulnerable.