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Effects of montane heathland rejuvenation on phytodiversity depend on management intensity and succession

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ABSTRACT

Heathlands are of high importance for biodiversity conservation, and most heathlands depend on management. While the effects of management on biodiversity are well-studied for lowland heathlands, studies on Central European montane heathlands are scarce. Therefore, we analysed the effects of heathland rejuvenation measures on soil characteristics and phytodiversity within Central European montane heathlands. We focused on four heathland types: sod-cut heathlands with (i) early-successional stages (SOD CUT-EARLY) and (ii) mid-successional stages (SOD CUT-MID), (iii) choppered heathlands with mid-successional stages (CHOP-MID) and (iv) late-successional heathland stages (CONTROL). For every heathland type, ten vegetation relevés were carried out. In every relevé, we analysed the cover of all vascular plant, bryophyte and terricolous lichen species. Additionally, soil characteristics were measured. Statistical analyses included generalised linear mixed-effects models and non-metric multidimensional scaling.

Our study revealed that rejuvenation of montane heathlands reduced soil nutrient levels, increased pH values and had positive effects on phytodiversity. The effects of rejuvenation were persistent. Even after around 20 years following the measures, SOD CUT-MID and CHOP-MID were characterised by lower nutrient levels and different plant assemblages compared to CONTROL.

Sod cutting and choppering promoted the rejuvenation of *Calluna vulgaris,* one target species of montane heathlands. However, the regeneration of *Vaccinium vitis-idaea* – another ericaceous target species – was clearly favoured by choppering in comparison to sod cutting. By contrast, overall vascular plant species diversity as well as the number of threatened vascular plant and target species were favoured by sod cutting in the long run while early-successional stages after sod cutting had positive effects on lichen diversity. Due to the contrary effects of the two rejuvenation measures, we recommend a spatial mix of high-intensity (sod cutting) and less intensive (choppering) rejuvenation methods in montane heathlands.

1. Introduction

Heathlands represent semi-natural habitats with high importance for biodiversity conservation. In Central Europe, most heathlands are man-made habitats that have developed through traditional land use such as low-intensity grazing, burning or sod cutting (Hüppe, 1993; Härdtle et al., 2009). Thus, they are dependent on regular management for long-term persistence (Gimingham, 1992). Heathlands are typically found on nutrient-poor, acidic soils and are characterised by the dominance of ericaceous dwarf shrubs such as *Calluna vulgaris*. They harbour many threatened and specialized plant and animal species (Usher, 1992; Härdtle et al., 2009; Borchard et al., 2017). Due to their high conservation value, heathland ecosystems are protected under the EU Habitats Directive (Ssymank et al., 1998). However, heathlands have declined extensively throughout Europe during the past two centuries as a consequence of land-use intensification or abandonment (Härdtle et al., 2009). Besides land-use change, atmospheric nitrogen deposition poses another severe threat for heathland biodiversity as it alters

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biogeochemical characteristics favouring the dominance of grasses (Bobbink et al., 2010; De Schrijver et al., 2011; Field et al., 2014).

For the maintenance of biodiversity in heathland ecosystems, a great variety of different management methods are applied (Gimingham, 1992; Härdtle et al., 2009; Fartmann et al., 2015). Besides low-intensity grazing or mowing, which are relevant for impeding succession, more intensive measures involving the complete removal of aboveground biomass and organic soil layers such as sod cutting and choppering are carried out in Central European heathlands for promoting phytodiversity, rejuvenating the dominant dwarf shrub species and/or compensating atmospheric nutrient deposition (Chytrý et al., 2001; Härdtle et al., 2006; Niemeyer et al., 2007; Fartmann et al., 2015). While sod cutting removes the total layer of organic material and parts of the A-horizon leading to the exposition of mineral soil, choppering only removes the largest part of the organic layer (Niemeyer et al., 2007). Typically, a thin layer of organic material remains after choppering. Intensity of choppering lies between sod cutting and mowing (Härdtle et al., 2009).

The effects of heathland management on biodiversity and biogeochemical properties have been intensively studied for lowland heathlands (e.g. De Graaf et al., 1998; Härdtle et al., 2006; Niemeyer et al., 2007; WallisDeVries et al., 2016; Vogels et al., 2020). By contrast, knowledge on the ecological effects of different management measures is still limited for montane heathland ecosystems in Central Europe. In comparison to Central European montane heathlands, there are numerous studies on the effects of management on biodiversity in UK upland heathlands (e.g. Pakeman et al., 2002; Britton et al., 2005; Davies and Legg, 2008). Montane heathlands are confined to mountainous regions with a cool and wet climate. Besides *C. vulgaris*, which is the dominant species within lowland heathlands in Central Europe, *Vaccinium myrtillus* and *Vaccinium vitis-idaea* are characteristic ericaceous species in Central European montane heathlands (Geringhoff and Daniëls, 2003). In addition, the occurrence of arctic-alpine and boreal-montane species is typical for this ecosystem (Thompson and MacDonald, 1995; Hahn, 2007).

In Central Europe, montane heathlands have declined extensively due to land-use abandonment and afforestation (Hahn, 2007; Schubert et al., 2008) and represent a highly threatened habitat (Finck et al., 2017). Therefore, there is an urgent need for effective conservation and restoration of this ecosystem. Fartmann et al. (2015) were the first to analyse the effects of choppering on species richness of vascular plants and arthropods within old-growth montane heathlands. In comparison to old-growth heathlands, choppered heathlands were characterised by an open vegetation structure and unique species assemblages, and they were favourable for vascular plant and grasshopper diversity (Fartmann et al., 2015). By contrast, knowledge on the impact of sod-cutting on montane heathland biodiversity is still limited. However, more detailed analyses of the effects of these two measures on biodiversity are also valuable from an economic viewpoint as choppering produces less waste material than sod cutting, making this method less costly (Koopmann and Mertens, 2004; Fartmann et al., 2015).

Therefore, the aim of our study was to analyse the effects of different rejuvenation measures on biodiversity within montane heathlands. Besides vascular plants we focused on bryophytes and lichens, for which knowledge on the effects of heathland management is generally poor, as model groups and included four heathland types within our study: sod-cut heathlands with (i) early- and (ii) mid-successional stages, (iii) choppered heathlands with mid-successional stages and (iv) late successional heathland stages (old-growth heathlands) as a control. The study was carried out within a low-mountain range in Central Germany (Rothaar mountains) which is one of the most important strongholds for montane heathland conservation in Central Europe (Schubert et al., 2008; Borchard et al., 2013).

In particular, we addressed the following questions:

- How do the four heathland types differ in soil and habitat-structure characteristics as well as in vascular plant, bryophyte and lichen diversity?
- What management recommendations can be derived from the results of the study for the promotion of phytodiversity in montane heathlands?

2. Materials and methods

2.1. Study area

The study area is situated in the Rothaar Mountains, a low-mountain range at the border of the German Federal states of North Rhine-Westphalia and Hesse (51°28′N, 7°33′E). Elevation ranges from 540 to 830 m a.s.l. The study area is characterised by a montane climate with a mean annual temperature of 5 °C, an annual precipitation of around 1450 mm and a prolonged snow cover of 100 d/a (German Meteorological Service, pers. comm.). The dominating soils are nutrient-poor cambisols on acidic bedrock (Geologisches Landesamt NRW, 1998). Intensive forestry is typical of the study area, and non-native spruce (*Picea abies*) forests are the dominant habitat type. Remnants of montane heathlands are widespread within the study area. However, heathland area declined dramatically during the past century (Schubert et al., 2008).

To evaluate the effects of the two rejuvenation measures sod cutting and choppering on phytodiversity in montane heathlands, we focused on four different heathland types. Among heathlands where sod cutting had been applied, we distinguished between two seral stages: early-successional stages were represented by heathlands where sod cutting had been conducted 6 to 10 years ago (2008–2012; hereinafter termed SOD CUT-EARLY). Mid-successional stages included heathlands where sod cutting had been carried out 19 to 21 years ago (1997–1999; SOD CUT-MID). For sod cutting, parts of the mineral soil were removed. By contrast, above-ground vegetation and only parts of organic layer were removed by choppering, leaving the rootstocks, mycorrhiza and soil seed bank mainly undisturbed (Schubert et al., 2008; Fartmann et al., 2015). Choppering took place 19 to 20 years ago (1997–1998). Thus, choppered heathlands (CHOP-MID) represented mid-successional heathland stages. Size of the rejuvenated heathlands varied between 400 and 8000 m^2. Additionally, late-successional stages of montane heathlands where no rejuvenation measures had been applied during the last 30 years were included in the analysis as a control (CONTROL). Such stages dominate within the heathlands of the study area (Borchard et al., 2013). In total, we selected seven montane heathland patches for sampling. Patch size ranged between 4.6 and 74 ha. All patches were grazed by sheep.

2.2. Vegetation and soil sampling

For every heathland type, ten vegetation relevés (plots) were placed randomly within the seven study patches. Control samples were placed within all patches; rejuvenated heathlands were distributed among four patches. The plots had a size of 4 m × 4 m, and sampling was carried out in July/August 2018. Within every plot, all vascular plant species of all vegetation layers (herb and shrub layer) were identified using Oberdorfer (2001) and Jäger (2017). Nomenclature of vascular plants followed Metzing et al. (2018). Furthermore, all ground-dwelling bryophyte species and all species of terricolous lichens (species growing on soil or raw humus according to Bültmann, 2006) were identified by using Paton (1999) and Smith (2004) (bryophytes) and Ahti et al. (2013) and Wirth et al. (2013) (lichens). Nomenclature of bryophytes and lichens followed Caspari et al. (2018) and Wirth et al. (2011), respectively. For the estimation of the cover of all species, the Wilmanns scale was used (Wilmanns, 1998). For statistical analyses, the categories were translated into the following percentage-cover values: *r* = 0.1%, + = 0.5%, *1* = 1%, *2m* = 2.5%, *2a* = 10%, *2b* = 20.5%, *3* = 38%, *4* = 63% and *5* = 88%. In addition, the cover of each of the three Ericaceae species (*Calluna vulgaris*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*) was estimated in more detail (steps of 5% and with steps of 1% when the cover was below 5%). Furthermore, we analysed habitat structure by estimating the cover of the following layers: shrub layer (shrubs and woody species with heights >0.5 m), herb layer (including herbs, grasses, Ericaceae and woody species with heights <0.5 m), herbs, grasses, Ericaceaee, bryophytes, lichens, bare soil and stones/gravel. The parameters were estimated using the same steps as mentioned above for the three Ericaceae species. Additionally, mean herb-layer height was determined by measuring the maximum height at five randomly selected locations within the plot.

At three randomly selected spots within the plot, soil samples were taken to a depth of 10 cm after removal of the organic layer and mixed (resulting in one soil sample per plot, $N = 40$). After air-drying and sieving, the samples were analysed for soil reaction ($CaCl_2$; WTW Multi 3430, pH electrode SenTrix 940–3), mineralised nitrogen (water-soluble ammonium and nitrate; ion chromatography, Metrohm 761 Compact IC), calcium-acetate-lactate-soluble phosphate (spectrophotomer, Biochrom Libra S11) and potassium (flame photometer, BWB Technologies BWB XP), and total carbon (Elementar Vario EL III).

2.3. Statistical analysis

For the characterisation of phytodiversity, we analysed the number (all and threatened species separately) of vascular plant, bryophyte and terricolous lichen species per plot. As threatened species we defined all species which were classified as 'critically endangered', 'endangered', 'vulnerable' and 'near threatened' (red-list categories: 1, 2, 3 and V) on at least one of the red lists of endangered species of Hesse, North Rhine-Westphalia and Germany, respectively (vascular plants: HMULV, 2008; Raabe et al., 2011; Metzing et al., 2018; bryophytes: HMUELV, 2013; Schmidt, 2011; Caspari et al., 2018; lichens: Schöller, 1996; Bültmann et al., 2011; Wirth et al., 2011). Additionally, the number of target species was analysed for every plot. Target species were defined as all character species of the phytosociological class Nardo-Callunetea (heathlands and acidic grasslands) and its lower units according to Peppler (1992), Peppler-Lisbach and Petersen (2001) and Oberdorfer (2001) (Appendix A).

To detect significant differences among the four different heathland types, (generalised) linear mixed-effects models (GLMM; LMM) were calculated (R packages lme4, Bates et al., 2020) using patch as a random factor. Within the models, heathland type was used as the nominal fixed factor and the analysed parameters were inserted as dependent variables. Depending on the variables, binomial (percentage data), Poisson or Gaussian (for normally distributed or square-root- or log-transformed variables with normal distribution) models were applied with the respective standard link functions. Observation-level random effects were added within overdispersed models (Harrison, 2014, 2015). The effect of heathland type on the dependent variables was analysed with likelihood-ratio tests (comparison of full model and model without fixed factor). Significant differences between the different heathland types were detected by Tukey contrasts (glht function, R package multcomp, Hothorn et al., 2020).

For detecting significant indicator species for the different heathland types, an indicator-species analysis (ISA, Dufrêne and Legendre, 1997) was carried out. Additionally, non-metric multidimensional scaling was applied for analysing differences in vegetation composition (NMDS; R package vegan, metaMDS function; Oksanen et al., 2019). The Bray-Curtis distance was used as a distance measure, and a maximum number of 100 random starts was defined for the search for a stable solution. Vascular plant, bryophyte and lichen data were included within the NMDS. Species occurring less than three times within the data set were excluded from the analysis. For overlay (envfit function, R Package vegan; Oksanen et al., 2019), we only used environmental variables (soil parameters and habitat-structure characteristics) for which a significant effect of heathland type was detected and which were non-intercorrelated among each other (Spearman correlation coefficient r_s; $|r_s| < 0.6$; see Appendix B). Analyses were carried out with R 3.4.2 (LMM; GLMM; NMDS) (R Core Team, 2020) and PCORD 5 (ISA).

3. Results

3.1. Soil conditions

Soil acidity as well as phosphate and potassium contents were significantly lowest in the sod-cut plots (SOD CUT-EARLY and -MID), intermediate in CHOP-MID and highest in CONTROL (Table 1). Furthermore, the two sod-cut heathland types were characterised by significantly lower carbon concentrations compared to CHOP-MID and CONTROL (Table 1). The concentration of mineral nitrogen increased significantly in the order SOD CUT-EARLY, CHOP-MID and CONTROL; in SOD CUT-MID, nitrogen concentration was only significantly lower compared to CONTROL (Table 1).

3.2. Habitat structure

Except for the cover of the shrub layer, which was generally low, and grasses, heathland type had a significant effect on habitat-structure (Table 1). Especially SOD CUT-EARLY differed significantly in habitat structure from the three other types. SOD CUT-EARLY had the shortest swards, the lowest cover of the herb layer and of Ericaceae and bryophytes but the highest cover of lichens, bare soil and stones/gravel. By contrast, the cover of herbs was highest in SOD CUT-MID, differing

Table 1
Mean values (± SE) of soil and habitat-structure characteristics in the four different heathland types. $N = 10$ per group. Comparison between groups was done by Tukey contrasts, see materials and methods for details. Heathland types without consistent letters indicate significant differences ($P < 0.05$). $^{**}P < 0.01$, $^{***}P < 0.001$, n.s. = not significant.

Parameter	SOD CUT-EARLY	SOD CUT-MID	CHOP-MID	CONTROL	*P*
Soil characteristics					
pH ($CaCl_2$)	3.6 ± 0.3^a	3.6 ± 0.0^a	3.2 ± 0.0^b	3.0 ± 0.1^c	***
C (%)	5.5 ± 0.6^a	7.1 ± 0.5^a	13.4 ± 1.1^b	20.9 ± 2.1^b	***
N_{min} (mg/100 g)	0.3 ± 0.04^a	0.4 ± 0.04^{ab}	0.5 ± 0.03^b	1.1 ± 0.1^c	***
PO_4^{3-} (mg/100 g)	0.1 ± 0.0^a	0.1 ± 0.0^a	0.3 ± 0.1^b	0.6 ± 0.1^c	***
K (mg/100 g)	6.8 ± 1.0^a	6.5 ± 0.7^a	12.3 ± 1.7^b	21.5 ± 2.8^c	***
Habitat structure					
Cover [%]					
Shrub layer	0.0 ± 0.0	1.1 ± 0.7	1.0 ± 0.7	2.0 ± 2.0	n.s.
Herb layer	63 ± 6.3^a	88.5 ± 3.1^b	94.9 ± 1.8^b	89.8 ± 1.7^b	***
Grasses	8.6 ± 2.4	20.2 ± 4.5	25.5 ± 9.8	6.2 ± 1.5	n.s.
Herbs	3.7 ± 0.9^a	11.5 ± 2.1^b	5.1 ± 1.8^a	3.1 ± 0.9^a	**
Ericaceae	58.0 ± 6.5^a	72.5 ± 6.5^b	79.5 ± 7.7^b	87.0 ± 2.1^b	**
Bryophytes	32.9 ± 9.0^a	64.0 ± 4.5^b	67.0 ± 3.0^b	68.0 ± 3.3^b	***
Lichens	14.3 ± 4.5^a	1.9 ± 0.7^b	0.3 ± 0.1^b	0.2 ± 0.1^b	***
Bare soil	4.9 ± 2.5^a	0.0 ± 0.0^b	0.0 ± 0.0^b	0.0 ± 0.0^b	**
Stones/gravel	10.8 ± 4.0^a	0.0 ± 0.0^b	0.0 ± 0.0^b	0.0 ± 0.0^b	***
Height herb layer [cm]	15.1 ± 1.7^a	26.1 ± 1.2^b	32.7 ± 2.6^b	31.7 ± 2.5^b	***

significantly from the three other heathland types.

3.3. Phytodiversity and community composition

In total, we observed 45 vascular plant, 38 bryophyte and 14 lichen species on the 40 plots. In contrast to species richness of bryophytes, the diversity of vascular plants and terricolous lichens was significantly influenced by the rejuvenation measures (Fig. 1). The diversity of vascular plant species decreased in the order SOD CUT-MID, SOD CUT-EARLY/CHOP-MID and CONTROL. The number of threatened vascular plant species also peaked in SOD CUT-MID, differing from the three other heathland types. Both the number of all and threatened terricolous lichen species were significantly higher in SOD CUT-EARLY compared to CHOP-MID and CONTROL; SOD CUT-MID had an intermediate position.

By contrast, the number of target species was highest in SOD CUT-MID, differing significantly from SOD CUT-EARLY and CONTROL (Fig. 2). In CHOP-MID, the number of target species was intermediate. The cover of the three Ericaceae species differed significantly between the heathland types, however, the patterns varied for each of the species (Fig. 3). *Calluna vulgaris* had the highest cover in the three rejuvenated heathlands (SOD CUT-EARLY and -MID, CHOP-MID), differing from CONTROL. Opposite to this, *Vaccinium myrtillus* had the lowest cover in

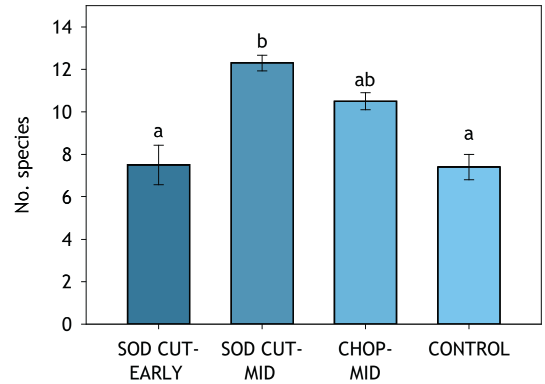

Fig. 2. Mean (± SE) number of target species in the four different heathland types. $N = 10$ per group. Comparison between groups was done by Tukey contrasts, see materials and methods for details. Heathland types without consistent letters indicate significant differences. $*P < 0.05$.

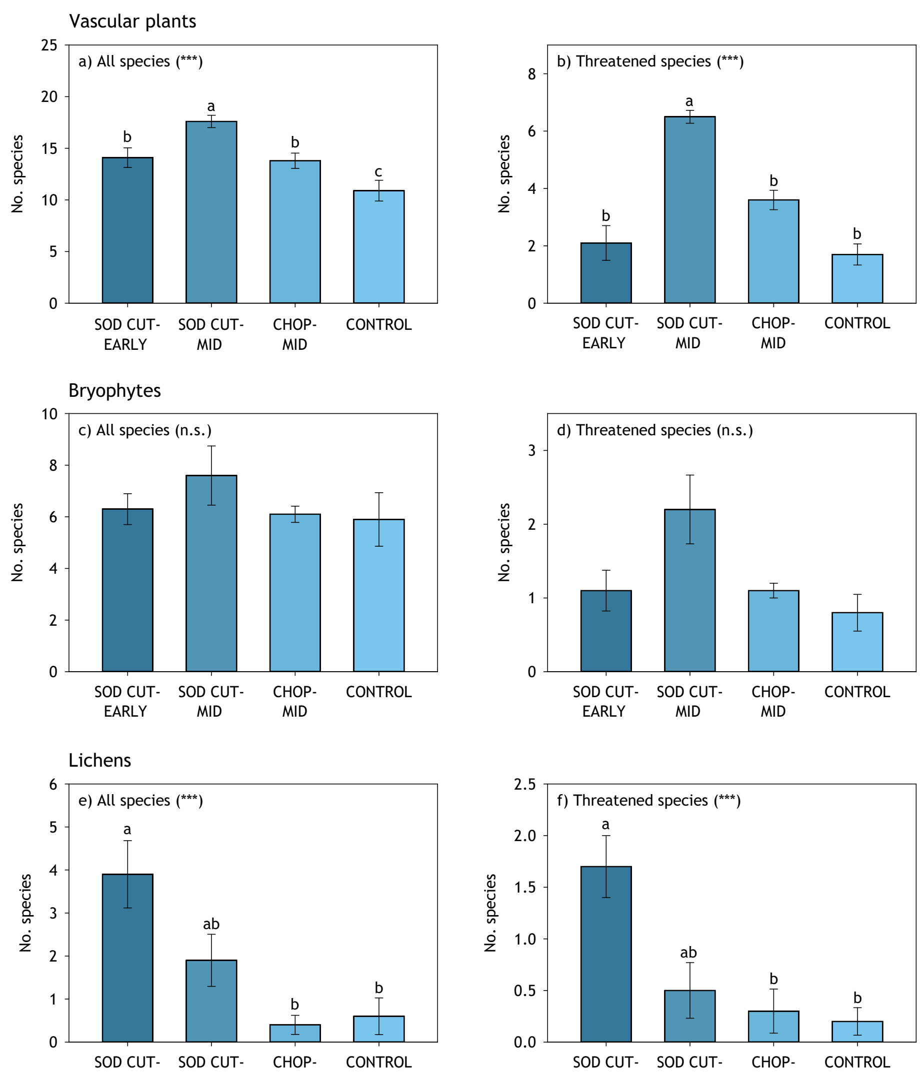

Fig. 1. Mean (± SE) species richness of vascular plants, bryophytes and lichens in the four different heathland types. $N = 10$ per group. Comparison between groups was done by Tukey contrasts, see materials and methods for details. Heathland types without consistent letters indicate significant differences ($P < 0.05$). $***P < 0.001$, n.s. = not significant.

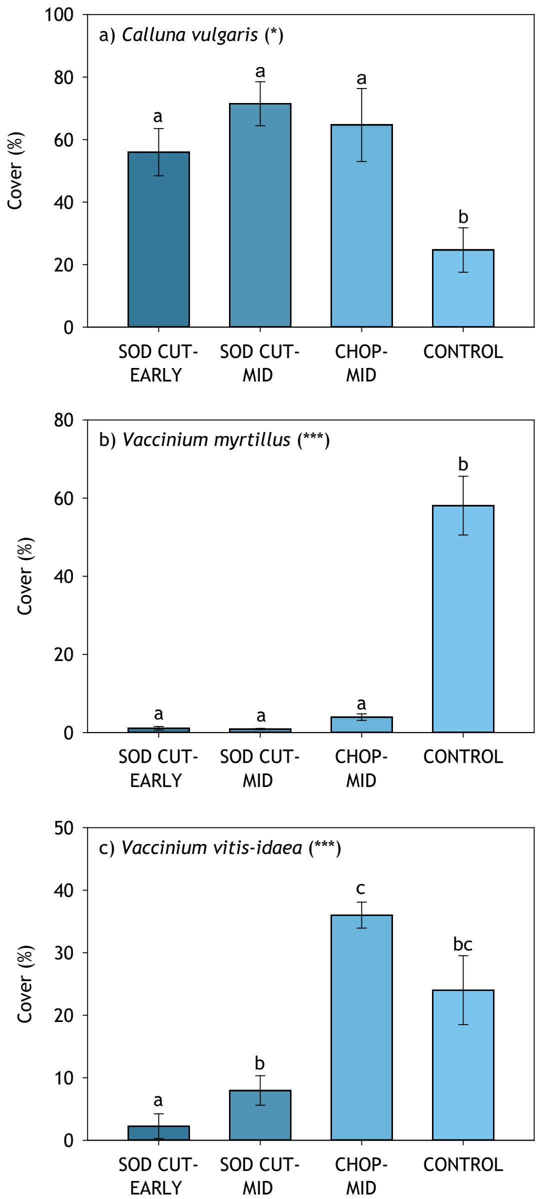

Fig. 3. Mean (± SE) cover of *Calluna vulgaris*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea* in the four different heathland types. $N = 10$ per group. Comparison between groups was done by Tukey contrasts, see materials and methods for details. Heathland types without consistent letters indicate significant differences ($P < 0.05$). $*P < 0.05$, $***P < 0.001$.

the three rejuvenated heathlands but the highest cover in CONTROL. The cover of *Vaccinium vitis-idaea* decreased significantly from CHOP-MID over SOD CUT-MID to SOD CUT-EARLY. In CONTROL, the cover was intermediate between the choppered and sod cut heathlands but differed significantly only from SOD CUT-EARLY.

Although every heathland type was characterised by certain indicator species, especially the two types of sod-cut heathlands were rich in typical species (Table 2). For SOD CUT-EARLY, altogether 13 species (four species each of vascular plants and lichens, and five bryophyte species) were identified as indicator species. Among vascular plants, nearly all indicator species were woody species (pioneer trees) such as *Pinus sylvestris*. Two species of each the bryophyte and lichen indicator species were threatened (*Ditrichum heteromallum*, *Polytrichum juniperinum* vs. *Cladonia macilenta* ssp. *floerkeana*, *Dibaeis baeomyces*). For SOD CUT-MID, altogether 12 indicator species were identified. Among them were seven vascular plants, which was the highest number for this plant group within one heathland type. Five of them were threatened species (*Huperzia selago*, *Juniperus communis*, *Lycopodium clavatum*, *Polygala serpyllifolia*, *Potentilla erecta*). Among the four bryophyte indicator species were two threatened ones (*Isopaches bicrenatus*, *Polytrichum commune* var. *perigoniale*). CHOP-MID and CONTROL were characterised by only four indicator species. One of the indicator species of CHOP-MID was considered threatened (*Vaccinium vitis-idaea*).

NMDS revealed clear differences in species communities between the different heathland types (Fig. 4). The first axis represented a successional gradient from SOD CUT-EARLY over SOD CUT-MID/CHOP-MID to CONTROL. SOD CUT-EARLY was separated from the later successional stages (SOD CUT-MID, CHOP-MID, CONTROL) by a higher proportion of bare soil and lichens, lower cover of bryophytes and Ericaceae as well as a lower content of mineralised nitrogen. SOD CUT-MID and CHOP-MID were separated from CONTROL and SOD CUT-EARLY along the second axis by a higher cover of herbs.

4. Discussion

Our study clearly revealed that rejuvenation of montane heathlands reduced soil nutrient levels, increased pH values, favoured an open vegetation structure and promoted species richness of vascular plants and lichens, including threatened species. In general, the effects of rejuvenation were persistent. Even after around 20 years following the measures, SOD CUT-MID and CHOP-MID were characterised by lower nutrient levels and different plant assemblages compared to CONTROL.

However, the effects of heathland rejuvenation were dependent on management intensity and succession. Sod cutting, as the most intensive rejuvenation measure, clearly had a stronger impact on nutrient depletion than choppering with only superficial removal of the organic layer—with respect to carbon, phosphate and potassium concentration. Soil characteristics of SOD CUT-MID even more resembled those of SOD CUT-EARLY than those of CHOP-MID. By contrast, nitrogen levels were similar at the sod-cut and choppered plots after about 20 years after rejuvenation. Within our study area, atmospheric nitrogen deposition lies within the range of critical loads for dry heathlands of 10–20 kg ha^{-1} y^{-1} (Bobbink and Hettelingh, 2011) (cf. UBA, 2018). In heathland ecosystems, nitrogen deposition results in acidification and increased ammonium concentrations and, therefore, leads to a loss of species sensitive to acidification and/or high ammonium concentrations (Bobbink et al., 1998; van den Berg et al., 2005; Kleijn et al., 2008; De Graaf et al., 2009). Grass species that are competitive under increased nitrogen availability, such as *Deschampsia flexuosa*, are promoted. Negative effects of nitrogen deposition have not only been observed for species richness of vascular plants but also for cryptogam diversity (Field et al., 2014). Therefore, the removal of excessive nitrogen is of vital importance for the conservation of species diversity in heathlands. However, as shown for lowland heathlands in the Netherlands, intensive management techniques such as sod cutting are often of limited success for restoring species diversity (Vogels et al., 2020). High soil acidity and increased ammonium concentrations due to reduced nitrification may inhibit the establishment of target species sensitive to acidification and/or high NH_4^+/NO_3^- ratios after sod cutting (Dorland et al., 2004; Vogels et al., 2020). Additionally, sod cutting might favour the shift from a nitrogen- to a phosphorus-limited ecosystem, with negative consequences for plant species diversity (Vogels et al., 2020). Therefore, sod cutting is often only recommended for small-scale application together with measures for restoring buffer capacity of the soils such as liming and P addition (Vogels et al., 2020). In our study, we found the highest pH values in sod-cut plots while they were intermediate in CHOP-MID and lowest in CONTROL. The low phosphate concentrations at the sod-cut heathlands might suggest a P limitation. However, the high species richness at SOD CUT-MID indicates that biogeochemical factors do not constrain the recovery of species diversity after sod cutting within the montane heathlands of our study area—at least in the long run. By contrast, the lower pH value might be one reason for the lower species

Table 2
Results of ISA (Dufrêne and Legendre, 1997) for the four heathland types. $N = 10$ per type. TaS = target species, ThS = threatened species. The maximum indicator values for significant indicator species are shown. Grey-shaded values: species are indicator species for this heathland type. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Species	TaS	ThS	Heathland type				*P*
			SOD CUT-EARLY	SOD CUT-LATE	CHOPPER	CONTROL	
Vascular plants							
Pinus sylvestris	.	.	61.8	.	.	.	***
Hypochaeris radicata	.	.	50.0	.	.	.	**
Salix caprea	.	.	50.0	.	.	.	**
Betula pendula	.	.	47.8	.	.	.	**
Lycopodium clavatum	x	x	.	71.6	.	.	**
Polygala serpyllifolia	x	x	.	62.9	.	.	***
Juniperus communis	.	x	.	59.5	.	.	***
Festuca ovina agg.	.	.	.	56.9	.	.	**
Huperzia selago	.	x	.	56.8	.	.	**
Potentilla erecta	x	x	.	45.5	.	.	*
Carex pilulifera	x	.	.	42.9	.	.	**
Vaccinium vitis-idaea	x	x	.	.	50.3	.	***
Luzula pilosa	.	.	.	.	36.6	.	*
Vaccinium myrtillus	x	.	.	.	.	85.7	***
Festuca rubra agg.	.	.	.	.	.	53.5	**
Deschampsia flexuosa	.	.	.	.	.	42.2	*
Rumex acetosa	.	.	.	.	.	30.0	*
Bryophytes							
Dicranella heteromalla	.	.	67.6	.	.	.	***
Cephaloziella spec.	.	.	62.9	.	.	.	***
Ditrichum heteromallum	.	x	40.7	.	.	.	*
Polytrichum piliferum	.	.	40.0	.	.	.	**
Polytrichum juniperinum	.	x	30.0	.	.	.	*
Polytrichum commune var. *perigoniale*	.	x	.	51.3	.	.	**
Cephalozia bicuspidata	.	.	.	30.0	.	.	*
Isopaches bicrenatus	.	x	.	30.0	.	.	*
Scapania nemorea	.	.	.	30.0	.	.	*
Hypnum cupressiforme s.l	x	.	.	.	48.7	.	**
Lophocolea bidentata	.	.	.	.	46.5	.	*
Lichens							
Dibaeis baeomyces	.	x	87.6	.	.	.	***
Placynthiella icmalea	.	.	60.0	.	.	.	***
Baeomyces rufus	.	.	46.6	.	.	.	*
Cladonia macilenta ssp. *floerkeana*	.	x	38.6	.	.	.	*
Cladonia chlorophaea agg.*	.	.	.	35.2	.	.	*

*Includes *C. grayi* and *C. pyxidata* ssp. *chlorophaea*.

diversity at CHOP-MID and CONTROL as it hampers the establishment of acid-sensitive species (cf. van den Berg et al., 2005; Kleijn et al., 2008).

SOD CUT-EARLY was clearly distinguished from the other heathland types by an open vegetation structure. However, after about twenty years, the effects of rejuvenation on habitat structure were negligible. Habitat-structure characteristics in SOD CUT-MID and CHOP-MID were similar to CONTROL. Nonetheless, SOD CUT-MID had a higher cover of herbs compared to the other three heathland types.

In contrast to habitat structure, every heathland type was characterised by a distinct species community. Characteristic for the heathlands where rejuvenation measures had been applied was a higher cover of *Calluna vulgaris* compared to CONTROL. *Calluna vulgaris* reproduces mainly by seeds (Gimingham, 1960) and builds up large and persistent soil seed banks (Pakeman and Hay, 1996; Pywell et al., 2002; Bossuyt and Honnay, 2008). Seedling establishment is especially successful on mineral soils (Watt, 1955), and this species is highly competitive under acidic conditions with low concentrations of inorganic N and P due to its ericoid mycorrhizal symbiosis enabling the use of organic sources of N and P (cf. Vogels et al., 2020). Therefore, *C. vulgaris* typically dominates within early stages of montane heathland succession (Borchard et al., 2017; Fartmann et al., 2015). By contrast, *Vaccinium vitis-idaea* and *Vaccinium myrtillus* dominated in CHOP-MID and CONTROL, respectively. These two species reproduce poorly by seed (Ranwala and Naylor, 2004; Borchard et al., 2017) and are favoured in late-successional heathland stages due to their clonal growth (cf. Ritchie, 1955, 1956). While the cover of *V. myrtillus* was low after sod cutting and choppering, even after about 20 years, choppering clearly favoured the rejuvenation of *V. vitis-idaea*. In contrast to *V. myrtillus*, this species seems to recover rapidly after choppering by vegetative growth from the remaining rootstocks.

In general, the rejuvenation measures favoured the diversity of vascular plant and terricolous lichen species. However, species richness differed according to management intensity and timing. In line with the high cover of herbs, SOD CUT-MID was characterised by the highest diversity of all and threatened vascular plant species. By contrast, vascular plant species diversity was intermediate in SOD CUT-EARLY and CHOP-MID and lowest in CONTROL. The higher species richness of SOD CUT-MID compared to CHOP-MID is very likely explained by i.) the higher pH values that stem from sod cutting's removal of acidic top soil and humus and ii.) the high proportion of bare ground as another effect of sod cutting. Though there were no structural differences in vegetation between SOD CUT-MID and CHOP-MID 20 years after rejuvenation, our study showed that sod cutting promoted an open vegetation structure. Even six to ten years after sod cutting, the proportion of bare ground and stones/gravel was still comparably high in SOD CUT-EARLY. We do not have data on vegetation structure on the earliest successional stages on choppered plots. However, it is very likely that the herb layer closes more quickly after choppering as the establishment of clonally growing species such as *V. vitis-idaea* is favoured by this method. A rapid spread of such clonal species should constrain the long-term establishment of low-competitive plant species. This assumption is underlined by the establishment of several threatened species on SOD CUT-MID, such as *Lycopodium clavatum* or *Juniperus communis*, which were identified as indicator species for this heathland type and are dependent on bare ground for germination (Schröder, 1984; Bennert, 1999; De Frenne et al., 2020). However, development of species-rich heathland communities seems to be a slow process. SOD CUT-EARLY had a lower overall species diversity and a lower number of target species in contrast to SOD CUT-MID. The removal of seeds, spores of mycorrhizal fungi and rootstocks with their mycorrhiza in the upper soil layers are constraints for vegetation development after sod cutting (Vergeer et al., 2006; Fartmann et al., 2015). Additionally, the surface of the sod-cut heathlands is possibly too dry during the first years of succession due to a high proportion of stones/gravel and an only slowly growing humus layer which inhibits the establishment of species that are dependent on moist soil conditions such as *Huperzia selago* or *Polygala serpyllifolia (*cf. Ellenberg et al., 2001) and were indicator species for SOD CUT-MID.

Our study highlights the importance of rejuvenation not only for the promotion of vascular plant species diversity but also for favouring cryptogam diversity in montane heathland ecosystems. Even though the number of bryophyte species did not differ between the heathland types, there was a tendency for a higher number of threatened bryophyte species in SOD CUT-MID (Fig. 1), and several bryophyte species were detected as indicator species for the sod-cut plots. Among them were the threatened species *Ditrichum heteromallum*, *Isopachus bicrenatus*, *Polytrichum commune* var. *perigoniale* and *Polytrichum juniperinum*. For lichen species diversity, especially the early phase of succession after sod cutting plays a vital role due to the open vegetation structure. SOD CUT-EARLY was characterised by higher overall lichen diversity and a higher number of threatened lichen species compared to CHOP-MID/CONTROL. The importance of vegetation disturbance and early- to mid-successional stages for promoting cryptogam diversity, especially lichens, was also demonstrated for lowland heathlands in northern Germany (Schellenberg and Bergmeier, 2020).

4.1. Management recommendations

In our study, we identified sod cutting and choppering as suitable methods for the rejuvenation of *Calluna vulgaris* and both methods, especially sod cutting, were favourable for other target species. However, after sod cutting, regeneration of the two *Vaccinium* species was low, while *V. vitis-idaea* was clearly promoted by choppering. By contrast, species diversity of all and threatened vascular plant species was clearly favoured by sod cutting in the long run. Due to the contrary effects of the two rejuvenation measures on community composition, we recommend a spatial mix of high-intensity (sod cutting) and less intensive (choppering) rejuvenation methods for creating habitat diversity and supporting species diversity in montane heathlands (cf. Härdtle et al., 2006). Furthermore, different successional heathland stages should be promoted by different timing of rejuvenation management. Our study showed that sod cutting is a suitable tool for increasing diversity of terricolous lichens and bryophytes in montane heathlands. Especially early stages of heathland succession with a high proportion of bare soil play an important role for lichen diversity in montane heathlands. In contrast, mid-successional stages after sod cutting provided the most favourable conditions for vascular plant species diversity. Thus, rejuvenation measures should only be carried out within species-poor late-successional stages of heathland succession, and according to our results, management intervals should exceed far more than 20 years—at least when the heathlands are regularly grazed.

Nonetheless, management of waste material is a constraint in heathland rejuvenation as its disposal is extremely expensive. When removal of excessive nitrogen is the main goal of heathland management, choppering is recommended over sod cutting from an economic viewpoint as it produces less waste material. It only removes the above ground vegetation and the organic layer but not parts of the A-horizon which is carried out by sod-cutting. Due to the higher content of nitrogen within the organic layer compared to the A-horizon, choppering removes a higher amount of nitrogen per volume unit compared to sod cutting (Niemeyer et al., 2007). Choppering is proved to compensate 61 years of nitrogen input in lowland heathlands. However, more nutrients are removed by sod cutting in total due to the partial removal of the A-horizon.

Credit author statement

T.F. conceived the idea. T.F., L.H. and M.S. designed the study. L.H. and M.S. coordinated data collection. M.S. carried out analyses with inputs from T.F. H.B. determined lichens. C.S. determined bryophytes. M.S. and T.F. led writing of the manuscript. All co-authors carefully

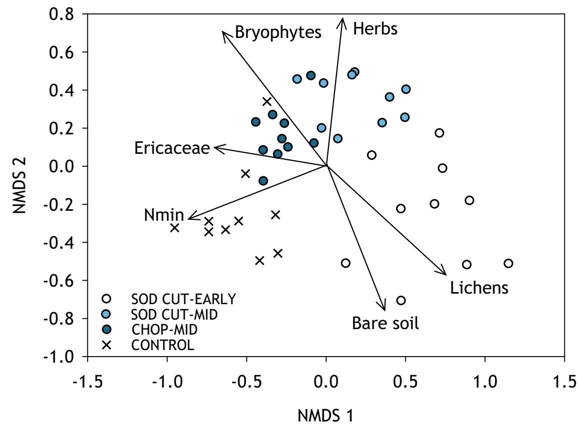

Fig. 4. NMDS ordination with vegetation relevés of the four heathland types ($N = 40$) and environmental variables as overlay ($P < 0.05$). Four dimensions, stress: 8.5.

revised the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

List of target species that occurred within the data set (according to Peppler, 1992; Peppler-Lisbach and Petersen, 2001; Oberdorfer, 2001): *Arnica montana*, *Calluna vulgaris*, *Carex pilulifera*, *Danthonia decumbens*, *Galium saxatile*, *Hieracium lachenalii*, *Hypnum cupressiforme* s.l., *Luzula campestris*, *Lycopodium clavatum*, *Nardus stricta*, *Pleurozium schreberi*, *Polygala serpyllifolia*, *Potentilla erecta*, *Ptilidium ciliare*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Veronica officinalis*

Appendix B

Overview of Spearmann correlation coefficients (r_s) among environmental data. All correlations with $|r_s| > 0.6$ are significant ($P < 0.001$). Bold variables were included in NMDS.

Parameter	pH	C	N_{min}	PO_4^{3-}	K	Shrub layer	Herb layer	Grasses	Herbs	Ericaceae	Bryophytes	Lichens	Bare soil	Stones/ gravel
C	−0.96	/	.	.	.	.	.	.	.	.	.	.	.	.
N_{min}	−0.66	0.70	/	.	.	.	.	.	.	.	.	.	.	.
PO_4^{3-}	−0.91	0.87	0.67	/	.	.	.	.	.	.	.	.	.	.
K	−0.89	0.86	0.65	0.87	/	.	.	.	.	.	.	.	.	.
Shrub layer	−0.06	0.10	0.05	−0.06	−0.02	/	.	.	.	.	.	.	.	.
Herb layer	−0.39	0.45	0.09	0.26	0.32	0.08	/	.	.	.	.	.	.	.
Grasses	0.31	−0.24	−0.11	−0.36	−0.37	0.07	0.02	/	.	.	.	.	.	.
Herbs	0.33	−0.27	−0.19	−0.42	−0.42	0.07	0.11	0.45	/	.	.	.	.	.
Ericaceae	−0.53	0.58	0.15	0.46	0.52	0.15	0.66	−0.50	−0.20	/	.	.	.	.
Bryophytes	−0.34	0.45	0.47	0.37	0.39	0.21	0.24	−0.03	0.03	0.36	/	.	.	.
Lichens	0.59	−0.64	−0.58	−0.50	−0.58	−0.07	−0.50	−0.05	0.01	−0.34	−0.37	/	.	.
Bare soil	0.43	−0.54	−0.34	−0.29	−0.30	−0.18	−0.61	−0.15	−0.18	−0.50	−0.58	0.50	/	.
Stones/gravel	0.51	−0.61	−0.52	−0.35	−0.37	−0.22	−0.58	−0.16	−0.31	−0.44	−0.58	0.69	0.82	/
Herb-layer height	−0.62	0.66	0.48	0.51	0.50	0.17	0.56	−0.30	−0.09	0.70	0.41	−0.56	−0.57	−0.70

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