

From deforestation to blossom – Large-scale restoration of montane heathland vegetation



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ABSTRACT

Land-use change and atmospheric nitrogen deposition have negatively affected heathlands with severe consequences for biodiversity. One possible way to counteract these negative impacts can be habitat restoration. The aim of this study was to evaluate the success of montane heathland restoration on former spruce forests using vascular plants as indicators. We compared the three following land-use types (i) grazed montane heathlands, (ii) grazed restoration sites on former spruce forests where seed transfer has been applied, and (iii) ungrazed clear-cuts of spruce forests.

Four to five years after restoration each land-use type was according to an indicator species analysis characterised by different indicator species. Despite the short time period since the implementation of the restoration measures and many similarities in plant species assemblages between restoration and clear-cut sites, *Calluna vulgaris* had vigorously established on restoration sites with a mean cover of nearly 20%, whereas it was largely absent at clear-cut sites. In addition, there was a clear trend that plant assemblages of restoration and clear-cut sites become more clearly separated. The cover of non-target species significantly increased at clear-cut sites and the cover of *C. vulgaris* remained extremely low.

The conducted restoration measures are able to initiate the establishment of typical montane heathland vegetation on former spruce forests. However, restoration of the complete plant assemblage would require additional sod transplantation as both *Vaccinium myrtillus* and *V. vitis-idaea* mainly depend on vegetative regeneration. Furthermore, topsoil removal of the most nutrient-rich parts would be necessary to counteract the encroachment of *Cytisus scoparius*.

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1. Introduction

Despite great conservation efforts during recent decades global biodiversity is still decreasing (Butchart et al., 2010). For terrestrial biomes, land-use change is recognised as the main threat to wild biota (Sala et al., 2000; Wessel et al., 2004). The transition from traditional to modern agriculture has caused a dramatic decline of semi-natural habitats, such as heathlands (Vitousek,

1994; Stoate et al., 2009). The loss of heathlands began in the middle of the 19th century (Keienburg and Prüter, 2004; Symes and Day, 2003). Lowland heathlands have been converted to farmland, whereas montane heathlands have become degraded by the abandonment of traditional management (e.g., sheep grazing, sod cutting or burning) (Hahn, 2007) and afforestation (Symes and Day, 2003; Walker et al., 2004, 2007). Recently, atmospheric nitrogen deposition has become a further threat to heathlands. Increased nitrogen availability reduces the regeneration of heather and favours the encroachment of nitrophilic grasses and mosses (Bobbink et al., 1992, 1998; Lindemann, 1993; Wessel et al., 2004).

Heathlands are characterised by many rare plant and animal species (Buchholz, 2010; Schirmel and Fartmann, 2014;

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Schirmel et al., 2011; Usher, 1992; Usher and Thompson, 1993), and some of these taxa are even restricted to heathlands (Symes and Day, 2003). Due to their high relevance for biodiversity conservation (Thompson and MacDonald, 1995; Usher, 1992), heathlands are protected under the EU Habitats Directive (Ssymank et al., 1998; Thompson and MacDonald, 1995). They are also known for their beauty and high cultural value (Haaland, 2003).

Montane heathlands are restricted to areas with a cold and wet mountain climate (Britton et al., 2005). Hence, their flora and fauna are particularly rich in arctic-alpine and boreal-montane species (Thompson and MacDonald, 1995). Besides *Calluna vulgaris*, two other Ericaceae dwarf shrubs, *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, often dominate these montane heathlands (Geringhoff and Daniëls, 2003). In Central Europe, the 'Rothaar' low mountain range is one of the last regions where large areas of montane heathlands have remained (Geringhoff and Daniëls, 2003). Due to their extent and biodiversity, these montane heathlands are of European relevance for nature conservation (Borchard and Fartmann, 2014; Frede, 1998).

Habitat restoration provides valuable and important opportunities for the protection of biodiversity (Dobson et al., 1997; Maron et al., 2012). Consequently, it is increasingly implemented throughout the world into conservation strategies (Clewett and Aronson, 2007). However, up to now montane heathlands did not attract much scientific attention (Borchard et al., 2013; Felton and Marsden, 1990), and studies on heathland restoration were clearly focused on lowland heathlands (Gimingham, 1992; Keienburg and Prüter, 2004; Symes and Day, 2003). Practices applied in lowland heathlands often have been transferred to montane heathlands (Hoffmann, 1998), irrespective of differences in climatic and edaphic conditions or community composition (Breder and Schubert, 1998).

The success of heathland restoration strongly depends on former land use and time in cultivation (Walker et al., 2004). In particular, seed limitation and high residual fertility (especially N and P) due to past fertilisation are among the most severe constraints (Härdtle et al., 2009; Walker et al., 2004). A possible seed limitation can be overcome by seed transfer from existing heathlands. However, high soil fertility, especially on former agricultural sites, remains a key constraint for heathland restoration. In contrast, soil eutrophication is mostly not a problem at sites of former coniferous forests, as forests are usually not fertilised. Nevertheless, forests are also affected by atmospheric nitrogen deposition with possibly adverse effects on the establishment of heathland vegetation.

The aim of this study was to evaluate the success of montane heathland restoration on former spruce forests in a Central European low mountain range using vascular plants as indicators. The potential of heathland restoration on coniferous plantations is generally poorly known (Walker et al., 2004). A special focus of this study was on the driving forces controlling the establishment of the typical plant species (cf. Münzbergová and Herben, 2005). We compared the three following land-use types (i) grazed montane heathlands, (ii) grazed restoration sites where seed transfer has been applied following spruce removal and (iii) clear-cuts of spruce forests as unprocessed and ungrazed clear-cut sites. Specifically, we addressed the following questions:

- (i) Do soil conditions limit the establishment of heathland vegetation at the restoration sites?
- (ii) Are the applied restoration measures suitable to create montane heathland vegetation with their characteristic plant species?
- (iii) How can the restoration measures be improved?

2. Materials and methods

2.1. Study area

The study was conducted in the Rothaar Mountains, a low mountain range (highest mountain peak: 843 m a.s.l.) at the border of the German Federal States of North Rhine-Westphalia and Hesse (51°28' N, 7°33' E). The study area comprises more than 1,000 km² of the highest parts of the Rothaar Mountains with elevations ranging from 540 to 830 m a.s.l. The Rothaar Mountains have a montane climate with a mean annual temperature of 5 °C, a mean annual precipitation of 1,450 mm (Borchard et al., 2013) and snow cover for 100 days per year (German Weather Service, pers. comm.), resulting in a relatively short growing season. The study area is dominated by non-native Norway spruce forests (*Picea abies*) that are interspersed by arable fields and grasslands. The montane heathlands which belong to the most representative in Central Europe (Borchard and Fartmann, 2014) are located on top of the mountain peaks.

2.2. Experimental design and restoration methods

In total, we established 19 permanent plots each with an area size of 500 m² (20 m × 25 m), and assigned to seven study sites. We analysed three different land-use types: (i) montane heathlands (CONTROL) (*N* = 7), (ii) restoration sites (RESSITE) (*N* = 7) and (iii) clear-cuts of spruce forests (CLEARCUT) (*N* = 5). At each of the seven study sites one CONTROL plot was randomly chosen within the existing montane heathland. RESSITE and CLEARCUT were restricted to three of the seven study sites. The elevation (mean ± SE = 705 ± 40 m a.s.l.) did not differ between the three land-use types (cf. Borchard et al., 2013).

All restoration and clear-cut sites were situated directly adjacent to still existing montane heathlands. At least until to the beginning of the 20th century they were also covered by heathland vegetation. However, due to the decline of traditional management they became abandoned and afforested with Norway spruce (*Picea abies*) and subsequently developed towards closed forest stands. Prior to the conduction of the restoration measures the age of the forests was at least 50 years, but most of them were much older (B. Gräfe, pers. comm.).

All restoration sites were part of the EU LIFE project "Medebacher Bucht – a building block for Natura 2000" which aimed to restore montane heathlands on former spruce forests in the Rothaar Mountains. The restoration measures were carried out in 2008/2009 and covered a total area of 40 ha. As described in Borchard et al. (2014), restoration was conducted in three steps: (i) deforestation of spruce forests, (ii) clearing of remaining branches and (iii) transfer of seed material (hydroseeding or application of chopper material) that was harvested on the largest montane heathland in the study area ('Neuer Hagen', 74 ha). At *Cytisus scoparius*-dominated restoration sites, *C. scoparius* shrubs were cut from 2010 onwards and removed.

The hydroseeding procedure is particularly known from revegetation of man-made steep slopes such as construction sites (Bochet and García-Fayos, 2004; Matesanz et al., 2006). The hydroseeding material is composed of the harvested seed material (threshed montane heathland species) from the donor site, water and erosion control agents. In order to evenly spread the seed material, the agents are mixed to a homogenous suspension in an all-terrain hydroseeder. The mixture was evenly sprayed on the restoration sites (Borchard and Fartmann, 2014).

The chopper material was harvested by a specifically designed machine that removes the complete biomass and organic layer down to the mineral soil (cf. Fartmann et al., 2015; Keienburg and Prüter, 2004). The material was collected in a tractor-drawn trailer

and transferred to the restoration sites. The application of the harvested chopper material on the restoration sites was then carried out using a manure wagon with a scatter roller (application rate of 1:1).

Harvesting took place during the period of fruiting of the three Ericaceae (*Vaccinium* species: August, *Calluna vulgaris*: January/February). CONTROL were generally grazed and RESSITE were grazed by sheep or goat after the application of the restoration measures (cf. Borchard et al., 2013). On CLEARCUT no further management measures were applied after the deforestation of spruce forests.

2.3. Field survey

Soil samples comprised the inorganic soil after removal of the humus layer and were taken with a soil corer (3 cm diameter) at a soil depth of 10 cm in September 2013 as mixed samples from three randomly chosen sub-samples per plot. Air-dried soil samples were sieved (2 mm mesh size) and analysed for calcium-acetate-lactate (CAL) soluble phosphorus (P) (spectrophotometer, Cadas 200, Düsseldorf, DE) and potassium (K) (flame photometer, Jenway PFP7, Burlington, US). After milling, the soil samples were analysed for percentage total nitrogen (N) and carbon (C) using an elemental auto-analyser (NA 1500, Carlo Erba, Milan, IT). The soil reaction was measured using CaCl₂ as detergent. All soil analyses were run twice accepting a maximum deviation of 10% between duplicates. We calculated mean values of duplicates for further analyses.

Vegetation sampling took place from 2011 to 2013 in August on three randomly established subplots (16 m², 4 m × 4 m) within each of the 19 permanent plots. In each year we estimated the cover of all Ericaceae, *Calluna vulgaris*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and further target species (hereafter referred to as 'target species', see below) and non-target species (see below) in 5% steps. In cases where the cover was above 95% or below 5%, 2.5% steps were used according to Behrens and Fartmann (2004). In addition, the cover of all vascular plant species was estimated in 2013. Plant species were identified according to Oberdorfer (2001) and Jäger and Werner (2001). The scientific nomenclature follows Wisskirchen and Haeupler (1998).

As target species we classified all species that are characteristic for heathlands according to Peppler (1992). In this study, the observed target species were *Carex leporina*, *Carex pilulifera*, *Danthonia decumbens*, *Galium saxatile*, *Genista germanica*, *Genista pilosa*, *Luzula campestris*, *Melampyrum pratense*, *Nardus stricta*, *Polygala serpyllifolia*, *Polygala vulgaris*, *Potentilla erecta* and *Veronica officinalis*. Shrubs and tall forbs typical of forest clearings (according to Oberdorfer, 1993) were classified as non-target species. These were *Cirsium vulgare*, *Cytisus scoparius*, *Digitalis purpurea*, *Epilobium angustifolium*, *Rubus idaeus*, *Rubus fruticosus* agg., *Salix caprea*, *Sambucus racemosa*, *Senecio ovatus* and *Senecio sylvaticus*.

2.4. Statistical analysis

The plots at which the two restoration procedures (hydroseeding, application of chopper material, cf. Section 2.2) were applied did not differ with regard to the soil chemical properties and the composition of plant species. Thus, we analysed data of both techniques together (cf. Borchard et al., 2013). Prior to statistical analyses we pooled the soil and vegetation data obtained from the subplots.

To investigate the land-use effects on soil chemical properties, vegetation parameters and vegetation dynamics over the course of the study period (= response variables), linear mixed-effects models (LMM) were fitted to the data using R 3.2.3 (R Core Team, 2015) and the function lme of the package nlme (version 3.1-122, Pinheiro et al., 2015). In each of the soil models the

categorical predictor variable was 'land-use type'. Each of the vegetation models contained two predictor variables 'land-use type', 'time' (metric), and the interaction between 'land-use type' and 'time'. First-order autoregressive covariance structures were employed in the vegetation models to account for the repeated measures in three successive years. The first year of the study period was represented by a value of zero of the predictor 'time', the second and third years by values of 1 and 2, respectively. 'Plot' and 'study site' were set up as random intercepts in all models, with plots nested in study sites. The slope of the predictor 'time' was allowed to vary across plots and study sites (random slope). The models were fitted using maximum-likelihood. The significance of the fixed effects was assessed using F-tests (function anova.lme) and Type III sums of squares. Differences between the levels of the categorical predictor 'land-use type' were analysed using conditional *t*-tests, in which RESSITE was set up as reference level (=baseline) and compared to CONTROL and CLEARCUT. McFadden's Pseudo-R², which indicates the ratio of the deviance explained by the model to the null deviance, was used as measure of model performance. Its calculation is based on the reduction in model deviance that was achieved owing to the explanatory power of the fixed effects only.

To assess the explanatory power of soil parameters on the establishment of the most abundant non-target species common broom (*Cytisus scoparius*) on RESSITE and CLEARCUT, we used a binomial generalised linear mixed-effects model (GLMM) with presence/absence of *C. scoparius* (package lme4; cf. Crawley, 2007). The variable 'study site' was set as a random factor, with 'plot' nested in 'study site'.

For ordination of plant species composition in 2013, a NMDS with the Bray-Curtis distance as distance measure, with a maximum number of 20 random starts in the search for stable solutions was used (VEGAN, Oksanen et al., 2016). Only vascular plant species that occurred in at least two plots were included in the analysis. The data were transformed by using autotransformation within the metaMDS function (cf. Oksanen et al., 2016). The environmental parameters were fitted onto the ordination afterwards. In cases of high intercorrelation (Pearson correlation coefficient [*r*] of $|r| > 0.6$) among variables, one of them was excluded from the analysis (Fielding and Haworth, 1995). Total carbon and potassium content as well as the cover of non-target species were excluded from the analysis as these were strongly intercorrelated with the following variables: potassium and carbon content ($r = 0.86$, $P \leq 0.001$), potassium and nitrogen content ($r = 0.86$, $P \leq 0.001$), carbon and nitrogen content ($r = 0.96$, $P \leq 0.001$), soil pH and carbon content ($r = -0.66$, $P \leq 0.01$) and cover of Ericaceae and non-target species ($r = -0.77$, $P \leq 0.001$).

For the three land-use types, indicator species were determined by indicator species analysis (ISA) (Dufrêne and Legendre, 1997). All analyses were done using R 3.2.3 (R Core Team, 2015) and PC-ORD 5.0 (MjM Software Design, Gleneden Beach, OR, US).

3. Results

3.1. Soil conditions

Analysed soil parameters did not show any significant difference between CONTROL, RESSITE and CLEARCUT (Table 1). Soils were generally acidic with a low concentration of carbon and macronutrients (N, P and K).

3.2. Establishment of montane heathland vegetation

Land-use type significantly influenced the cover of Ericaceae dwarf shrubs in general, *Vaccinium myrtillus*, *V. vitis-idaea* and non-target species (Table 2, Fig. 1). The cover of Ericaceae, *V. myrtillus* and *V. vitis-idaea* was lower in RESSITE than in CONTROL,

Table 1

Soil parameters (mean values $\pm$ SE) of montane heathlands (CONTROL), restoration sites (RESSITE) and clear-cut sites (CLEARCUT) as well as the results of the LMM of land-use type with the soil parameters in 2013. n.s. not significant. For details of the modelling procedure cf. Section 2.4.

Soil parameters	CONTROL N = 7	RESSITE N = 7	CLEARCUT N = 5	P
pH	3.6 $\pm$ 0.1	3.9 $\pm$ 0.0	3.8 $\pm$ 0.1	n.s.
Carbon (%)	6.1 $\pm$ 1.5	3.1 $\pm$ 0.6	4.2 $\pm$ 0.6	n.s.
Nitrogen (%)	0.4 $\pm$ 0.1	0.2 $\pm$ 0.04	0.3 $\pm$ 0.04	n.s.
P ₂ O ₅ (mg/100 g)	2.6 $\pm$ 1.1	1.0 $\pm$ 0.5	0.7 $\pm$ 0.2	n.s.
K ₂ O (mg/100 g)	2.1 $\pm$ 1.0	0.7 $\pm$ 0.2	1.0 $\pm$ 0.4	n.s.

but did not differ between RESSITE and CLEARCUT. The cover of non-target species increased in the order CONTROL, RESSITE and CLEARCUT; however, the pairwise comparisons with RESSITE as a baseline did not reveal a significant difference. In contrast, the

cover of *Calluna vulgaris* and of target species did not differ among the land-use types.

Time significantly affected the cover of Ericaceae, *Calluna vulgaris* and target species. While the cover of Ericaceae in general and *C. vulgaris* increased during the study period from 2011 to 2013, the cover of target species decreased.

Significant interactions between land-use type and time were observed for non-target species and *Calluna vulgaris*. At CLEARCUT, the cover of non-target species increased with time, whereas it remained almost constant at CONTROL and RESSITE. The cover of *C. vulgaris* increased with time in RESSITE while it remained roughly constant at CONTROL and CLEARCUT.

3.3. Plant species composition and soil conditions

Four to five years after the restoration measures, NMDS ordination showed a clear separation of vascular plant species into two

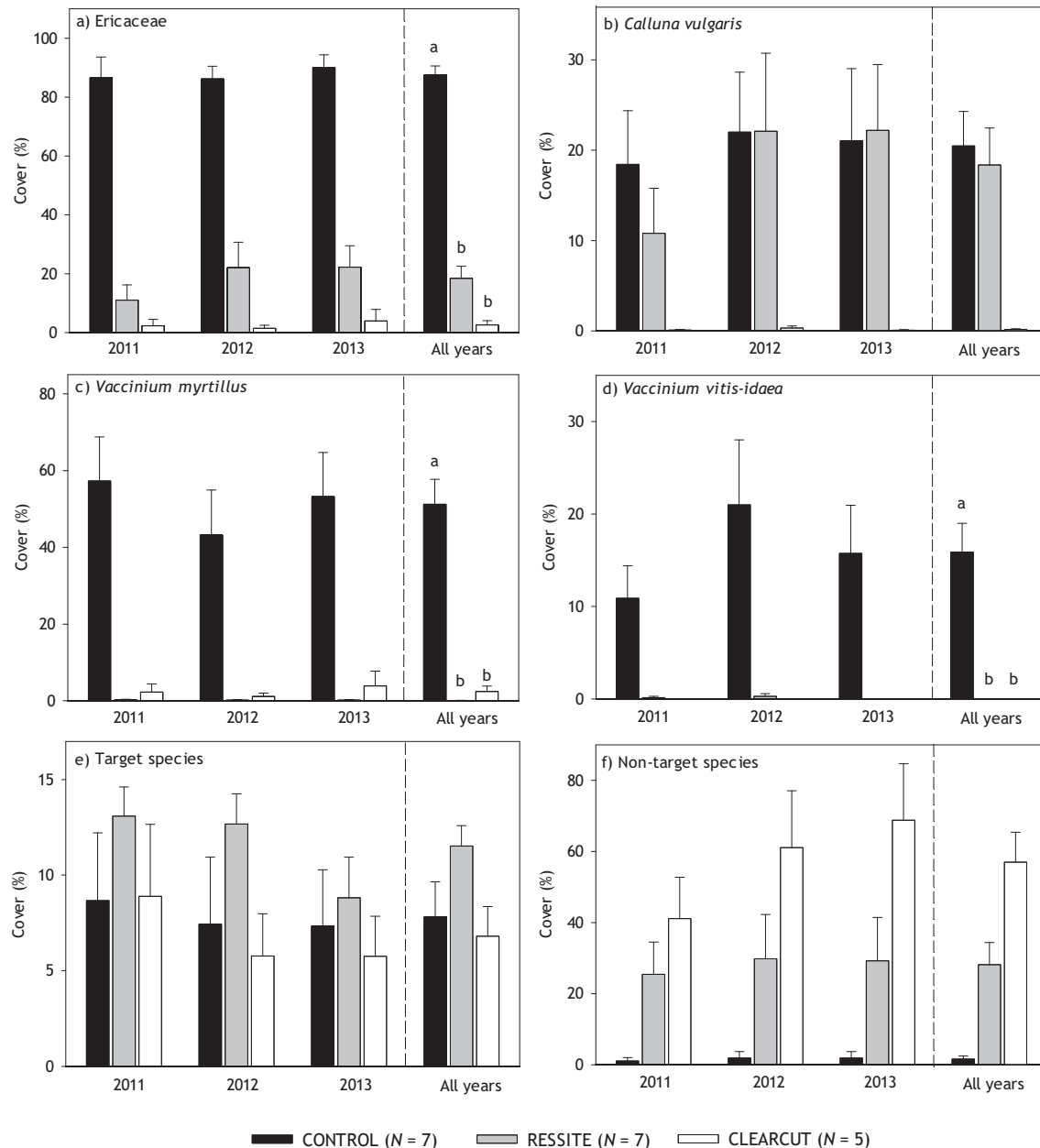


Fig. 1. Cover of (a) Ericaceae, (b) *Calluna vulgaris*, (c) *Vaccinium myrtillus*, (d) *Vaccinium vitis-idaea*, (e) target species and (f) non-target species in all study years. For the classification of target and non-target species see Section 2.3. Different symbols indicate significant differences between land-use types ($P < 0.05$). For further statistics see Table 2.

Table 2

Results of the LMM of the main effects (land-use type, time) and the respective interaction terms with different response variables (a–f). In all models, the significance of the predictors was assessed using F-tests. Differences between the three levels of the categorical predictor 'land-use type' were analysed using conditional t-tests in which restoration sites (RESSITE) were set up as reference level (= baseline) and compared to montane heathlands (CONTROL) and clear-cut sites (CLEARCUT). R^2_{MF} = McFadden's Pseudo- R^2 . Sample size: CONTROL = 7 plots, RESSITE = 7 and CLEARCUT = 5. n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. For further explanations cf. Section 2.4.

Parameter	Estimate	SE	F/t	P	R ² _{MF}
a) Cover of Ericaceae					
Intercept	7.484	6.380	1.538	n.s.	0.13
Land-use type			131.911	***	
CONTROL	78.294	5.910	13.249	***	
CLEARCUT	2.802	6.955	0.403	n.s.	
Time	5.593	1.501	15.514	***	
Land-use type × Time			2.936	n.s.	
CONTROL × Time	−3.879	2.123	−1.827	n.s.	
CLEARCUT × Time	−4.803	2.326	−2.065	*	
b) Cover of <i>Calluna vulgaris</i>					
Intercept	12.528	5.858	5.113	*	0.04
Land-use type			2.455	n.s.	
CONTROL	6.595	8.284	0.796	n.s.	
CLEARCUT	−12.358	9.075	−1.362	n.s.	
Time	5.690	1.647	13.350	***	
Land-use type × Time			3.315	*	
CONTROL × Time	−4.381	2.329	−1.881	n.s.	
CLEARCUT × Time	−5.700	2.551	−2.235	*	
c) Cover of <i>Vaccinium myrtillus</i>					
Intercept	−4.538	9.274	0.268	n.s.	0.06
Land-use type			33.063	***	
CONTROL	56.156	7.607	7.382	***	
CLEARCUT	19.659	9.042	2.174	n.s.	
Time	−0.098	0.893	0.013	n.s.	
Land-use type × Time			2.579	n.s.	
CONTROL × Time	−1.926	1.262	−1.526	n.s.	
CLEARCUT × Time	0.898	1.383	0.649	n.s.	
d) Cover of <i>Vaccinium vitis-idaea</i>					
Intercept	−0.023	3.913	0.000	n.s.	0.05
Land-use type			11.905	**	
CONTROL	14.334	4.239	3.381	**	
CLEARCUT	−4.667	4.947	−0.944	n.s.	
Time	0.000	1.024	0.000	n.s.	
Land-use type × Time			1.987	n.s.	
CONTROL × Time	2.429	1.448	1.678	n.s.	
CLEARCUT × Time	0.000	1.586	0.000	n.s.	
e) Cover of target species					
Intercept	14.962	2.988	26.730	***	0.04
Land-use type			1.969	n.s.	
CONTROL	6.406	3.260	−1.965	n.s.	
CLEARCUT	−6.490	3.800	−1.708	n.s.	
Time	−2.135	0.823	9.242	**	
Land-use type × Time				n.s.	
CONTROL × Time	1.349	1.164	1.159	n.s.	
CLEARCUT × Time	0.565	1.276	0.443	n.s.	
f) Cover of non-target species					
Intercept	25.847	8.873	9.484	**	0.05
Land-use type			5.222	*	
CONTROL	−24.727	12.548	−1.971	n.s.	
CLEARCUT	16.222	13.746	1.180	n.s.	
Time	1.876	3.601	0.303	n.s.	
Land-use type × Time			3.699	*	
CONTROL × Time	−1.448	5.092	−0.284	n.s.	
CLEARCUT × Time	11.967	5.578	2.145	*	

clusters, representing CONTROL and RESSITE/CLEARCUT (Fig. 2). Altogether, three out of the five environmental variables correlated significantly with the NMDS scores (Fig. 2, Table 3). The segregation of CONTROL and RESSITE/CLEARCUT along the first axis reflects a gradient of Ericaceae cover and is mainly the result of the land-use types themselves and not of soil conditions. CONTROL is characterised by a high cover of Ericaceae dwarf shrubs, while their cover is low at RESSITE and CLEARCUT. The second axis represents a gradient in soil conditions. Nitrogen content increases, while pH values decrease along this axis. CONTROL and RESSITE were found along

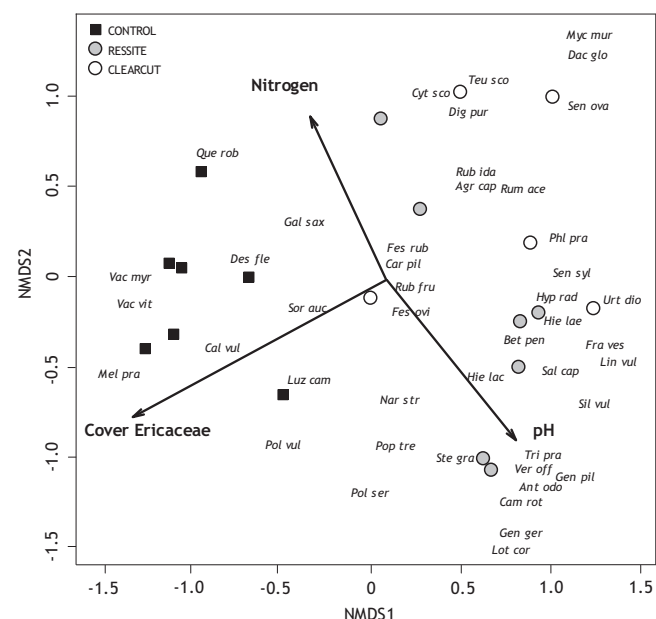


Fig. 2. Results of NMDS ordination (stress: 5.8, three dimensions, Bray-Curtis distance) based on the most frequent vascular plant species and environmental parameters in 2013. Only significant environmental parameters (arrows) are shown (at $P < 0.05$, based on 1000 permutations). For statistics see Table 3. Abbreviations of species names: Agr cap = *Agrostis capillaris*, Ant odo = *Anthoxanthum odoratum*, Bet pen = *Betula pendula*, Cal vul = *Calluna vulgaris*, Cam rot = *Campanula rotundifolia*, Car pil = *Carex pilulifera*, Cyt sco = *Cytisus scoparius*, Dac glo = *Dactylis glomerata*, Des ces = *Deschampsia cespitosa*, Des fle = *Deschampsia flexuosa*, Dig pur = *Digitalis purpurea*, Fes ovi = *Festuca ovina* agg., Fes rub = *Festuca rubra* agg., Fra ves = *Fragaria vesca*, Gal sax = *Galium saxatile*, Gen ger = *Genista germanica*, Gen pil = *Genista pilosa*, Hie lac = *Hieracium lachenalii*, Hie lae = *Hieracium laevigatum*, Hyp rad = *Hypochaeris radicata*, Lin vul = *Linaria vulgaris*, Lot cor = *Lotus corniculatus*, Luz cam = *Luzula campestris*, Mel pra = *Melampyrum pratense*, Myc mur = *Mycelis muralis*, Nar str = *Nardus stricta*, Phl pra = *Phleum pratense*, Pol ser = *Polygala serpyllifolia*, Pol vul = *Polygala vulgaris*, Pop tre = *Populus tremula*, Que rob = *Quercus robur*, Rub ida = *Rubus idaeus*, Rub fru = *Rubus fruticosus* agg., Rum ace = *Rumex acetosella*, Sal cap = *Salix caprea*, Sen ova = *Senecio ovatus*, Sen syl = *Senecio sylvaticus*, Sil vul = *Silene vulgaris*, Sor auc = *Sorbus aucuparia*, Ste gra = *Stellaria graminea*, Teu sco = *Teucrium scorodonia*, Tri pra = *Trifolium pratense*, Urt dio = *Urtica dioica*, Vac myr = *Vaccinium myrtillus*, Vac vit = *Vaccinium vitis-idaea*, Ver off = *Veronica officinalis*.

Table 3

Summary of NMDS: Correlation of environmental variables with ordination. P-values are based on 1000 permutations (only significant variables are shown).

Parameter	Axis 1	Axis 2	R^2	P
pH	0.64	−0.77	0.54	**
Nitrogen content	−0.40	0.92	0.34	**
Cover of Ericaceae	−0.88	−0.50	0.90	***

a wide range of nitrogen and pH conditions. In contrast, CLEARCUT was associated with more nitrogen-rich sites.

The ISA supports the findings of the NMDS and identified the two Ericaceae dwarf shrub species *Vaccinium myrtillus* and *Vaccinium vitis-idaea* as indicator species for MONTHEATH (Table 4, Fig. 2). Indicator species of RESSITE were the four grass species *Festuca rubra* agg., *Festuca ovina* agg., *Agrostis capillaris* and *Carex pilulifera*. All four indicator species of CLEARCUT, *Digitalis purpurea*, *Cytisus scoparius*, *Rubus idaeus* and *Senecio ovatus* belong to the group of non-target species that is associated with forest clearings.

Establishment of the non-target species common broom (*Cytisus scoparius*) on RESSITE and CLEARCUT was clearly affected by soil conditions. Plots with presence of the species had significantly higher contents of carbon and nitrogen (Fig. 3). All the other soil parameters did not differ between presence and absence plots.

Table 4

Results of ISA (Dufrêne & Legendre, 1997) for montane heathlands (CONTROL), restoration sites (RESSITE) and clear-cut sites (CLEARCUT). Species are sorted by 'IV' for the considered land-use type. Only significant species are shown. IV = indicator value, ab = relative abundance comparing all types, fr = percentage frequency. Grey shaded values: species are indicator species for this land-use type.

Species	CONTROL N = 7			RESSITE N = 7			CLEARCUT N = 5			P
	IV	ra	rf	IV	ra	rf	IV	ra	rf	
<i>Vaccinium myrtillus</i>	93	93	100	–	0	14	–	7	20	***
<i>Vaccinium vitis-idaea</i>	86	100	86	–	0	0	–	0	0	***
<i>Festuca rubra</i> agg.	–	6	29	81	94	86	–	0	0	**
<i>Festuca ovina</i> agg.	–	3	14	70	97	71	–	0	0	**
<i>Agrostis capillaris</i>	–	0	0	68	68	100	–	32	100	**
<i>Carex pilulifera</i>	–	17	29	66	66	100	–	18	60	*
<i>Digitalis purpurea</i>	–	0	0	–	18	71	82	82	100	**
<i>Cytisus scoparius</i>	–	3	14	–	30	29	67	67	100	**
<i>Rubus idaeus</i>	–	0	14	–	37	71	62	62	100	*
<i>Senecio ovatus</i>	–	0	0	–	0	0	60	100	60	**

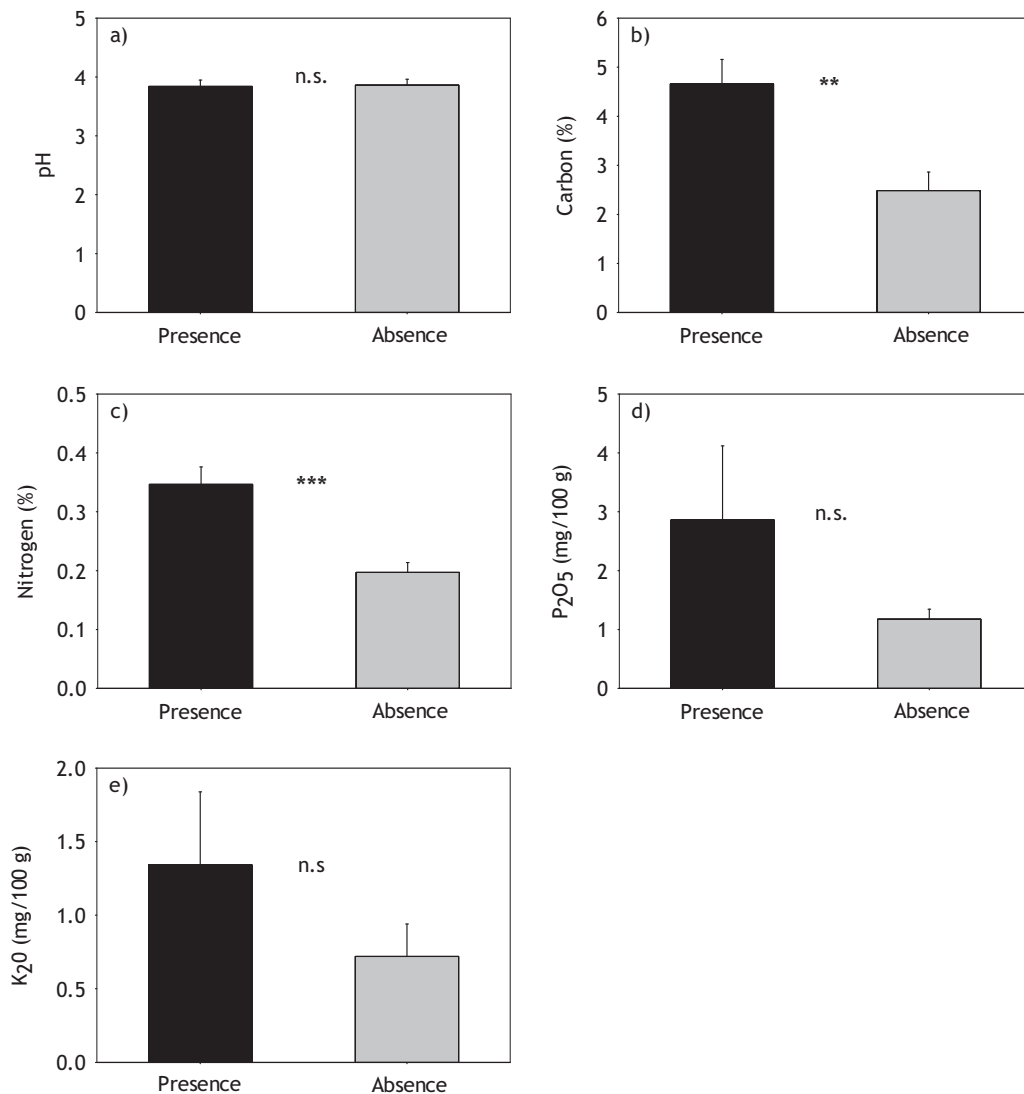


Fig. 3. Effects of soil parameters (mean values $\pm$ SE) on the establishment of the non-target species common broom (*Cytisus scoparius*) on RESSITE and CLEARCUT (N = 12). Differences between plots with presence (N = 6) and absence (N = 6) of the species were tested using GLMM with 'study site' as a random factor. n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

4. Discussion

Four to five years after restoration each land-use type was characterised by different indicator species. Despite the short time period since the implementation of the restoration measures and

many similarities in plant species assemblages between RESSITE and CLEARCUT, *Calluna vulgaris* had vigorously established on RESSITE with a mean cover of nearly 20%, whereas it was largely absent at CLEARCUT. In addition, there was a clear trend that plant assemblages of RESSITE and CLEARCUT become more clearly

separated. At CLEARCUT the cover of non-target species significantly increased and the cover of *C. vulgaris* remained extremely low during the three years of the study. Altogether, this shows that the restoration measures were effective at modifying the plant community composition. Hence, the measures may facilitate succession towards heathland instead of typical clear-cut vegetation.

Abiotic environmental factors can be of crucial importance for the success of restoration projects because they determine germination, survival and growth of target plant species (Eriksson and Fröberg, 1996; Fleischer et al., 2013; Hill and Vander Kloet, 2005; Walker et al., 2004, 2007). Among the key abiotic factors that constrain restoration results are soil properties. According to Grime et al. (2007) most heathland plants are confined to acidic (pH 3–5) and nutrient-poor soils. All RESSITE fulfilled these requirements. In line with this, soil conditions (pH, content of C, N, P and K) did not differ significantly from those of the existing montane heathlands. Hence, it is unlikely that these soil properties limited the restoration success.

Seed and dispersal limitation (sensu Münzbergová and Herben, 2005) are important constraints for successful restoration in our highly modified and fragmented landscapes (Bakker and Berendse, 1999; Baur, 2014; Bossuyt and Hermy, 2003). According to Eycott et al. (2006) soil seed banks are potentially major sources of propagules that can have significant impacts on community structure following disturbance. In particular, *Calluna vulgaris* is known to produce a large amount of long-lived seeds (up to over 40 years, possibly even up to 80 years; Bossuyt and Honnay, 2008; Pakeman and Hay, 1996; Pywell et al., 2002), whereas *Vaccinium* species have a very poor representation in soil seed banks (up to 15–17 years, Hill and Stevens, 1981; Hill and Vander Kloet, 2005). *Calluna vulgaris* successfully colonized RESSITE and occurred there in high abundance. In contrast, the two *Vaccinium* species nearly completely failed to establish. Due to a forest cover of at least 50 years, but mostly a much longer time period prior to tree cutting, it is very unlikely that the soil seed bank played any role for the establishment of the three Ericaceae species. This assumption is supported by the observation that we found a high cover of *C. vulgaris* only on RESSITE (where transfer of seed material took place), but not on CLEARCUT.

In contrast to *Calluna vulgaris*, transfer of *Vaccinium* seeds did not result in the colonisation of RESSITE by the species. Our knowledge on seed regeneration of both *Vaccinium* species is poor (Grime et al., 2007). According to Eriksson and Fröberg (1996) their seedling establishment depends on very specific microsites with a high moisture and organic content of the soil. Consequently, most authors state that both species reproduce mainly by vegetative regeneration (Fartmann et al., 2015; Geringhoff and Daniëls, 2003; Grime et al., 2007; Schwabe-Braun, 1980).

The most severe biotic constraint of montane heathland restoration was the fast establishment of the non-target shrub *Cytisus scoparius* that can rapidly form dense thickets. However, it was only found on nitrogen-rich restoration sites. The high competitive power of *C. scoparius* severely affects the light demanding seedlings of *Calluna vulgaris* and other heathland target species by shading (Britton et al., 2000; Iason and Hester, 1993; Gimingham, 1992). Additionally, as a legume it is a nitrogen fixer substantially altering the fertility of the soils and threatening plant species adapted to nutrient-poor conditions (Fogarty and Facelli, 1999) such as heathland species. *Cytisus scoparius* produces large numbers of seeds already after three years of age (Schwabe-Braun, 1980; Smith and Harlen, 1991) and thus rapidly replenishes the seed bank (cf. Peterson and Prasad, 1998), which leads to a further decline of target species. In addition, *C. scoparius* is ranked among the most unpalatable central European woody plants (Borchard et al., 2011). Hence, grazing alone was not suitable to reduce

the vitality of the species on RESSITE and shrubs had to be cut additionally (cf. Section 2.2).

Seed dispersal in *C. scoparius* usually takes place along distances of a few meters by autochory and myrmecochory (Odom et al., 2003). Consequently, it is very unlikely that the rapid and large-scale colonization after clear-felling occurred by seed dispersal from adjacent areas. Germination from seeds in the seed bank seems to be a more reasonable explanation. *Cytisus scoparius* builds a long-term persistent seed bank (Smith and Harlen, 1991). Seeds remain viable for more than 80 years in soils under coniferous forests (Fickeler, 1958; cf. also Turner, 1933). Based on the results of our study a large number of *C. scoparius* seeds seems to be able to germinate after at least more than 50 years (= minimum age of the spruce forests), but probably much longer.

5. Implications for conservation

We conclude that the transfer of seed material is a feasible and successful method to initiate establishment of typical montane heathland vegetation on former spruce forests. Specifically, the transfer of chopper material is a common practice that has already been successfully applied to restore lowland heathlands (cf. Smith et al., 1991; Anderson, 1995). The seed material used can cheaply be collected as part of routine heathland management (Fartmann et al., 2015) and is adequate to reinstate a heathland plant community (Pywell et al., 1996). Compared to other restoration measures it is highly sustainable, because it preserves existing heathlands in the long term (Pywell et al., 1996). In our study, we used autochthonous seed material to ensure that the seeds were best adapted to the local environmental conditions.

However, the two *Vaccinium* species that are characteristic of montane heathlands and mainly reproduce by vegetative regeneration failed to establish by seeds. To secure establishment of both dwarf shrubs we recommend sod transplanting from existing heathlands. First experiments with sods having a size of 1 m × 1 m provided promising results. Plants in the centre of the sods successfully established on RESSITE (own observation).

Our study showed that in the first years following restoration a subsequent management is required on nitrogen-rich sites to eradicate *Cytisus scoparius* and to achieve long-term success of the restoration measures conducted. However, these measures are associated with high costs and will possibly require long time periods as *C. scoparius* vigorously re-sprouts after cutting. As *C. scoparius* is very sensitive to deep frost (Oberdorfer, 1993), global warming with warmer winters might additionally enhance its vitality in future. A sustainable increase in the restoration success on more nutrient-rich sites might only be achieved by topsoil removal, which would reduce the seed bank of *C. scoparius* and other non-target plants of the clear-felling flora (cf. Allison and Ausden, 2006; Pywell et al., 2002). Furthermore, this practice could help to reduce the amount of nitrogen in the upper soil layer (Niemeyer et al., 2007), which is also known to hamper regeneration of heather and favours the encroachment of grasses and mosses (Bobbink et al., 1998; Lindemann, 1993; Wessel et al., 2004). Topsoil removal would also be beneficial to counteract atmospheric nitrogen deposition. Current deposition rates of 15–20 kg ha⁻¹ y⁻¹ in the study area (Wichink Kruit et al., 2014) are already at the level of the critical loads for heathlands (10–20 kg ha⁻¹ y⁻¹, Achermann and Bobbink, 2003). However, in contrast to former agricultural land (Walker et al., 2004) topsoil removal on former coniferous forests is only necessary at the most nutrient-rich parts of the sites.

Restoration of complete montane heathland ecosystems with their typical flora and fauna is a time-consuming process (Borchard et al., 2013) that takes much longer than the time covered by this study. Montane heathland ecosystems are particularly sensitive

to climate change including extreme events (cf. Schellenberg and Bergmeier, 2014; Streitberger et al., 2016). Consequently, for future restoration we recommend to choose sites with a high variety of aspects and heterogeneous relief to compensate for example for dry summers or late spring frosts that might otherwise negatively impact restoration results.

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