Regeneration potential of a degraded alpine mountain bog: complex regeneration patterns after grazing cessation and partial rewetting

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SUMMARY

A typical degraded mountain bog in the Swiss Alps was restored by cessation of grazing and partial rewetting. We observed the development of the vegetation over 15 years, starting immediately after the grazing cessation (4 years before rewetting). Cessation of grazing stimulated the recolonisation of bare peat and the establishment of bryophytes. While many typical bog forest species benefited from grazing cessation, the relative abundance of Cyperaceae decreased. Rewetting (in our case: closing ditches with sheet piles and filling them with sawdust) as an additional restoration measure, had a stabilising effect on most environmental factors (e.g. water availability, soil aeration). Furthermore, rewetting had a stabilising effect on stress tolerators and promoted typical species of bog hummocks and hollows. The abundances of species of nearly all groups changed far less dynamically in the rewetted area than in the area that remained drained. It turned out that cessation of grazing as the only restoration measure was insufficient to maintain the vegetation of bogs, whereas the combination of grazing cessation and rewetting directed the site towards the desired development. However, even eleven years after rewetting and 15 years after cessation of grazing, the site had not yet reached a state that was close to an undisturbed alpine bog.

KEY WORDS: bog, growth form, indicator value, restoration, species composition

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INTRODUCTION

Across Europe and Central Asia, wetlands have been largely destroyed and their extent has declined by 87 % (Fischer *et al.* 2018), often because of urbanisation, over-exploitation or drainage for agricultural purposes. In Switzerland, a similar trend has been observed: 86 % of the wetlands have been lost since 1900 (Lachat *et al.* 2010). This massive decline resulted in wetlands being designated as the most threatened habitat type (Delarze *et al.* 2016) and also in many specialist wetland species being threatened, such as *Betula nana*, *Carex diandra*, *C. microglochin*, *Lycopodiella inundata* or *Rhynchospora fusca* (Cordillot & Klaus 2010, Kempel *et al.* 2020). In order to preserve valuable habitats and biodiversity, Switzerland has made large investments in environmental restoration in the past decades (Klaus *et al.* 2007, BAFU 2017a, BAFU 2018, BAFU 2020) and about 7000 biotopes of national importance have been designated since the beginning of the 1990s, including wetlands such as raised bogs and fens. However, reliable information not only on the state and trends of various habitat types, but also on population sizes and the distribution of many taxa, on threat factors and on the success of certain restoration measures is largely not available (Delarze *et al.* 2016, BAFU 2017b). As nature conservation policy and implementation are strongly dependent on such information, the establishment of well-designed long-term monitoring programmes with standardised sampling designs is essential for evaluating the success of restoration measures (e.g. Bergamini *et al.* 2019).

As bogs depend on a high degree of water saturation, drainage systems cause the largest problems for them: their peat shrinks, soil aeration increases and available nutrients increase due to mineralisation (Rydin & Jeglum 2006). Drainage systems create new hydrological conditions that lead to vegetation changes in bogs (Rydin & Jeglum 2006). Species characteristic of bogs decline, trees and shrubs start to invade, *Sphagnum* mosses vanish (Laine *et al.* 1995) and peat formation is reduced or even ceases completely. In Switzerland, nearly all bogs have been drained and in the Alpine region most of them are additionally pastured. Pasturing might counteract draining to a certain degree (Worrall *et al.* 2007) because trampling leads to peat compaction (Sjögren *et al.* 2007). However, the negative effects of trampling, e.g. destruction of the *Sphagnum* layer (Koning 2005, Sjögren *et al.* 2007), creation of bare peat and erosion (Martin *et al.* 2013), clearly outweigh the positive effects of reduced drainage.

The removal of cattle is therefore expected to be of great importance in bog restoration.

For degraded (drained and mown or pastured) peatlands, the primary conservation objective is to restore ecosystem functions by restoring hydrology, biogeochemical cycling and energy capture to enable autogenic plant succession (Gorham & Rochefort 2003). Rewetting of degraded peatlands by drainage removal and filling of ditches is a first essential step as restoration measure. Such restoration measures have been shown to successfully restore the environmental conditions towards wetter and nutrient poor conditions allowing peat formation. In addition, it has been shown that the vegetation composition can be restored and develop towards larger amounts of peatland specialist species, such as increased cover of peat mosses and stress tolerant species which has been shown in a wealth of studies (e.g. González *et al.* 2014, Maanavilja *et al.* 2015, Küchler *et al.* 2018, Bedolla *et al.* 2019). However, there is increasing evidence that rewetting might not be sufficient to fully restore the initial state of previously drained site with regard to ecohydrology and species composition (Kreyling *et al.* 2021).

To characterise site conditions, mean ecological indicator values are a commonly used tool. For nearly all Central European plant species ecological indicator values for, e.g. nutrients, moisture, temperature, etc. have been complied. Such indicator values describe the realised niche of a plant taxon on an ordinal scale (e.g. Ellenberg et al. 2001, Landolt *et al.* 2010). The simple or the abundance-weighted mean of all species of a given place is useful to characterise the edaphic and climatic site conditions and temporal changes of vegetation plots (Diekmann 2003, Tölgyesi *et al.* 2014). They are proposed to describe longer-term site conditions even better than exact point measurements do (Wamelink *et al.* 2002). As plant succession in restored peatlands mirrors environmental changes, mean ecological indicator values derived from relevés can be used to quantify and evaluate abiotic changes (e.g. Graf *et al.* 2010, Boch *et al.* 2019, Busch *et al.* 2019) beside plant strategies (Grime 1974) and life history traits (Strobl *et al.* 2018, Konings *et al.* 2019). In addition, recovery in terms of the number and the abundance of species characteristic to the original ecosystem can be used to characterise the development of an ecosystem (Haapalehto *et al.* 2017, Küchler *et al.* 2018). In rainwater-fed bogs this means, for instance, that the establishment of an increased cover of peat mosses (*Sphagnum* spp.) - many of which need permanently high water levels (Rydin & Jeglum 2006) - can be used as an indicator of restoration success because the hydrological conditions for peat mosses are often

unfavourable in degraded bogs, due to exceedingly high water-table fluctuations (Grootjans *et al.* 2012).

Here, we focus on a formerly drained and pastured peatland in the Swiss Alps where restoration measures were conducted in the mid-1990s. We used an exceptional time series of vegetation surveys: the first record was completed immediately after cattle exclosure from the site, and before a partial rewetting. The surveys were repeated 5 times over 15 years. In this study, we focused on a range of indicators derived from the vegetation surveys to study trends in the recovery of the vegetation. We addressed the following research questions:

- How does grazing cessation and partial rewetting affect the recolonisation of bare peat, mean ecological indicator values and vegetation composition?
- What are the main characteristics (e.g. plant strategies, life history traits, indicator values) of declining and increasing species?
- Are the restoration measures that were applied to this site suitable for shifting bog ecosystems towards pristine conditions (i.e., nutrient poor, acidic and permanent wet site conditions, a high abundance of specialised species and low abundance of trees and shrubs)?

METHODS

Study site
The bog "Gross Moos Schwändital" (47°06′30″ N, 8°49′40″ E) is located in the northern part of the Swiss Alps at about 1250 m a.s.l. The mean precipitation is about 1800 mm/y, the mean temperature of July is about 13°C. The area of the site is about 18 ha. The peat forming process started about 8000 ybp by sedimentation in a shallow lake and was interrupted several times by mineral deposits (Grünig & Steiner 1994). The valley was used as pasture since early medieval times (maybe since Bronze-Age, Grünig & Steiner 1994). However, whether the bog itself was also grazed remains unclear. In the early 1920s it was drained with a grid of ditches. Afterwards it was used as pasture for cattle and for litter harvesting (Grünig & Steiner 1994). Between 1992 and 1996 the cattle were removed in several steps by limiting their grazing area progressively. In 1996, the central part of the site still showed a heavily damaged surface because of former trampling. Over time the ditches became deeper and larger (in an extreme case up to 6 m wide and 2 m deep), caused by sagging of their margins and by trampling (Grünig & Steiner 1994). In 1999, one of the central ditches with an inclination of about 2–3 % was blocked by a

series of sheet piles every 20–50 cm of difference in elevation and filled with sawdust. This resulted in a rise of the mean water table from about 40–60 cm below ground to about (10–)20 cm below ground in the central area of the site (Steiner *et al.* 2001) The connected, horizontal lateral ditches remained open and became flooded. Two ditches to the west and to the east of this central area, without any connections to the flooded ones, limited the rewetted area (Figure 1).

Data

In 1995 and 1996 (immediately after complete grazing cessation), we conducted an exhaustive vegetation survey (1034 plots delineated previously on a coloured infrared-aerial picture). These areas appeared homogeneous in their colour, structure and texture (for details see Grünig *et al.* 2005). In 1995, the site was dominated by fragments of bog and bog forest, with some transition mire and small areas of poor fen, rich fen, *Nardus* meadows and other vegetation types. In 2001, 2003, 2006, 2008 and 2010, we continued the vegetation monitoring using a subsample of the plots studied in 1995/1996. To study effects of grazing cessation and rewetting, we compared trends in areas with grazing cessation plus rewetting (GCR-area) with trends in areas of grazing cessation only (GC-area). We analysed only vegetation records of areas classified as bog (or bog fragments) in the first survey, because this was the dominating entity within the GCR-area and constituted the target vegetation type. We excluded records from the construction site itself from the

analyses because the vegetation there was completely destroyed in 1999. Our subsample contained 43 plots in the GCR-area and 53 plots in the GC-area (Figure 1). These plots had an average area of 143 ± 126 m^2 (range: 10–733 m^2). The difference in area between the two area types was not significant (t-test, $p = 0.04$). On each survey occasion we conducted a vegetation relevé in all these plots. Each relevé consisted of a list of all vascular plants and bryophytes, together with their abundances. We estimated species abundances using a four-step logarithmic scale (< 0.1 %, 0.1–1 %, 1–10 %, 10–100 % cover). In addition, we computed the cumulative cover of the vegetation as the sum of the single species abundances in % (geometric mean of each abundance class). We further described the plot structure by estimating the percentage cover of bare peat and peat mosses, and from the second survey onwards also the percentage cover of litter and other bryophytes.

As a proxy for site factors, we used the abundance-weighted mean of ecological indicator values (Diekmann 2003, Landolt *et al.* 2010, Tölgyesi *et al.* 2014). We used recalibrated ecological indicator values of bryophytes and vascular plants based on the co-occurrence of species in 20300 vegetation records of Swiss mire monitoring (Klaus *et al.* 2007), because this data-driven adaptation has been shown to be more informative in mires (Feldmeyer-Christe *et al.* 2007). The values of the recalibrated indicator values sometimes went beyond the limits of the values of
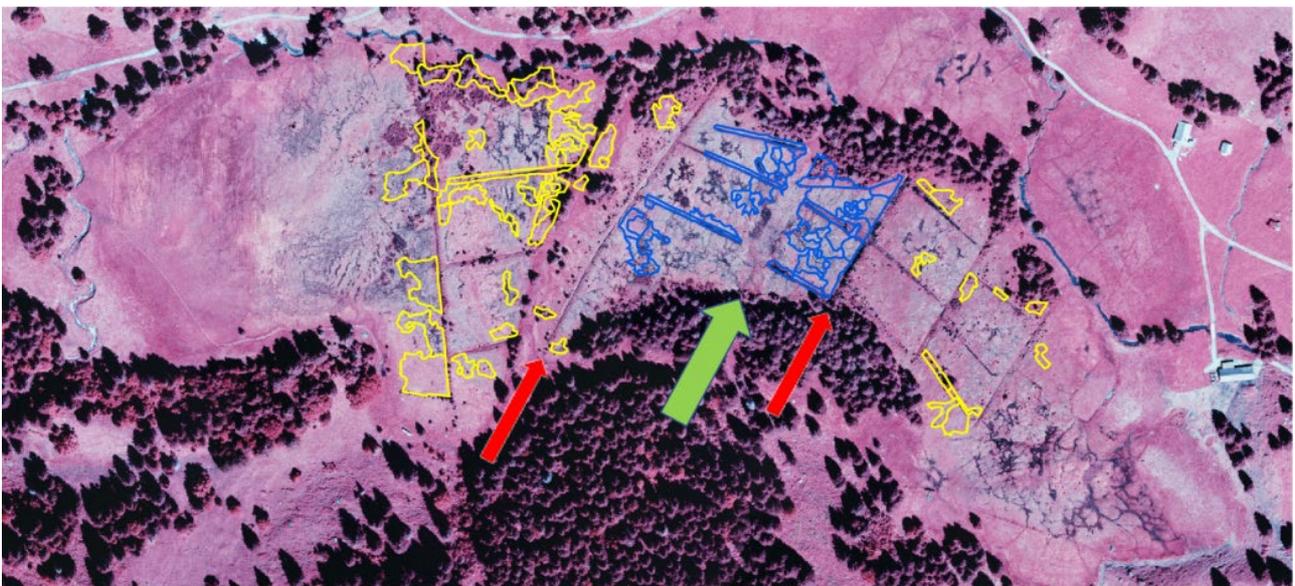

Figure 1. Coloured infrared photo of the site after the rewetting. The refilled ditch in the centre of the GCR-area (grazing cessation plus rewetting) is indicated by the green arrow. The GCR-area is defined by deep ditches to the west and to the east (red arrows). The locations of the plots are indicated in blue for the GCR-area and in yellow for the GC-area (grazing cessation).

Landolt *et al.* (2010), i.e. values were sometimes below 0 or above 5. In addition, we transformed the nominal measures of competition, ruderality and stress given in Landolt *et al.* (2010), which are based on Grime's C-S-R triangle (Grime 1974), into numerical values ranging from 0 to 3. For instance, we assigned a taxon with the strategy 'ccc', indicating highest competitive ability, a competition value of 3 and ruderality and stress values of 0, and we assigned a taxon with strategy 'css' a competition value of 1, a stress value of 2 and a ruderality value of 0. We further calculated relative species numbers and relative abundances of species groups. We did this for selected taxonomic groups (Cyperaceae, Ericaceae, Poaceae, Bryophytes), for some common growth forms (geophytes, long-living hemicyrptophytes, woody chamaepyhtes and phanerophytes, as defined in Landolt *et al.* 2010, see Appendix) and for species specialised to particular habitats (see Appendix).

For nomenclature, we followed Juillerat *et al.* (2017) for vascular plants and the Swissbryophytes Working Group (2019) for bryophytes.

Statistical analyses

We used linear mixed effects models to analyse and compare trends in the GCR- and GC-areas over the 15 years. We fitted an individual model in each area type to identify deviations from static development. We fitted an additional "common" model on the entire site to test for differences between the individual area trends. We used plot ID as a random factor to account for the non-independence of repeated observations. As fixed effects, we included a quadratic polynomial of time (i.e. year + year^2). The common model included an additional interaction term of time:area type. We used orthogonal coding of the polynomial of time to decompose the trend into a linear and a quadratic component, by means of the 'poly' function in the *stats* package of R (R Core Team 2020). The components were uncorrelated because the quadratic term in orthogonal coding only captures the unexplained part of the linear term. Thus, we obtained p-values for the trend components, which corresponded to p-values of a type I ANOVA. We used the 'lme' function of the R package *nlme* (Pinheiro 2020) to perform the mixed effects analysis. This package can account for structure in the random-effects covariance matrices (i.e. zero correlation, compound symmetry, no structure) and in the residuals (i.e. constant variance, group specific variance). We fitted each of the six combinations of variance type (2) and random-effects structure type (3) with either a random intercept alone (1|plotID) or both a random intercept and a random slope across

the years (year|plotID), ending up with 12 models per response variable. The model finally used was selected using the Akaike information criterion (AIC). To assure model assumptions of normally distributed residuals for the various types of indicators, we pre-transformed the response variables according to first aid rules (i.e. square root for species numbers, log for indicator values and abundance sums, arcsine for proportions; see Stahel 2002). Visual inspection of residual plots showed no obvious deviation from homoscedasticity and normality for the models presented in this paper. We standardised all response variables to a mean of 0 and standard deviation of 1 to obtain coefficients of comparable size for the trend components. To present individual trends in figures, we back-transformed the model predictions to the original scale of the response variable. This may result in curved lines for linear trends, but there were few such cases.

RESULTS

Trends in plot structure

The most striking trend over time in plot structure was a strong and steady decrease in bare peat to near disappearance in both GCR- and GC-plots (Table 1, Figure 2). Litter cover showed a peak in both areas around 2005 (i.e. six years after rewetting) and a slight overall increase in the GCR-area. In contrast, the cumulative cover of all plants had a temporary minimum 5–10 years after restoration measures were set in place in both areas and an overall increase in the GCR-area only. The cover of peat mosses showed a significant increase only in the GCR-area. Although trends in the cover of other bryophytes were not significant in the two areas when analysed separately, the two area types showed a significant trend difference in the full model, indicating a slight increase in the GC-area but not in the GCR-area (Table 1, Figure, 2).

Trends of mean ecological indicator values, life strategies and grazing tolerance

In the GC-area, the mean indicator value for moisture decreased, especially from 2005 onwards (i.e. ten years after cessation of grazing), with a similar but less pronounced pattern occurring for its variability, whereas the mean indicator value for aeration increased over this period (Table 2, Figure 3). In the GCR-area the trends of these mean indicator values were not significant (Table 2, Figure 3), but the trend differences between the two areas were so (Table 2).

The mean indicator values for reaction (i.e. soil acidity), nutrients and humus showed no significant

Table 1. Trends in the cover (%) of variables describing the plot structure in the two areas (GC and GCR) and the entire site. Results of separate regression models for the GC-area and GCR-area, as well as results from the combined model, are shown. Numbers are the effect sizes of the orthogonal polynomials of time and their interaction with area type. GC = grazing cessation; GCR = grazing cessation and rewetting; l = linear term; q = quadratic term; l:a = interaction linear term between time and area type; q:a = interaction quadratic term between time and area type; Significance levels: +: $p \leq 0.1$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

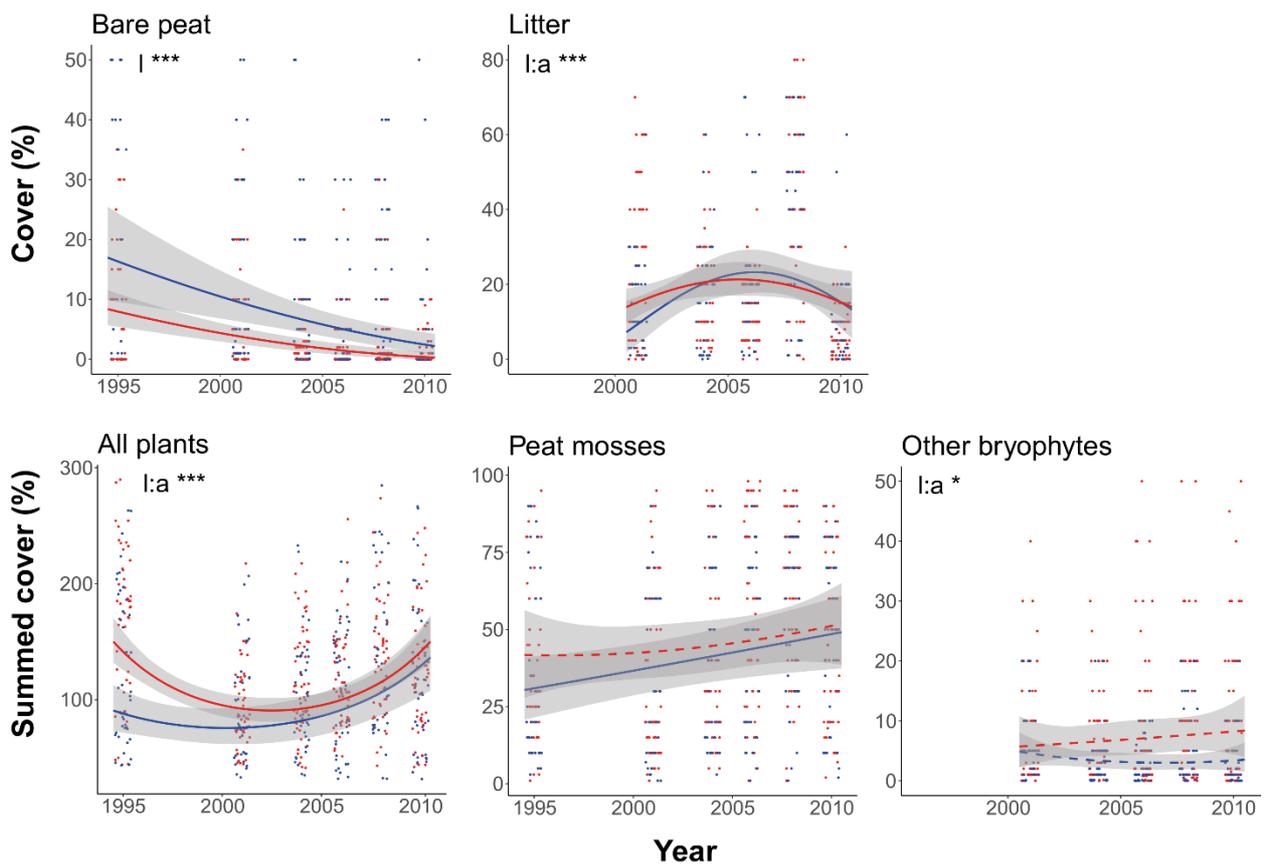|	GC Time		GCR Time		Entire site Time		Interaction	
	l	q	l	q	l	q	l:a	q:a
Cover of bare peat	-6.16***	1.08	-4.66***	-0.65	-6.69***	1.08	-1.02	-2.24+
Cover of litter	-1.47	-2.07*	1.76*	-3.35***	-1.40	-2.88*	4.44***	-2.31
Cover of all plants	-1.62+	5.29***	2.73***	2.90***	-1.50+	5.74***	5.04***	-0.46
Cover of peat mosses	1.49+	0.55	2.67**	0.94+	2.05+	0.75	1.83	0.61
Cover of other bryophytes	1.23+	0.02	-1.10	1.03	1.87+	0.03	-3.09*	1.12

Figure 2. Trends of variables describing the plot structure in percent cover for GC-areas (grazing cessation, red) and GCR-areas (grazing cessation plus rewetting, blue). Regression lines and confidence intervals from individual models are displayed. Solid lines show significant trend components. Dashed lines show the model fit of both trend components, if neither of them is significant. Labels denote significant overall trends or significant interactions between trends and the two areas derived from the common model. Dots indicate observed values on single plots. Outliers are not shown. l = linear time component; q = quadratic time component; a = area type; a colon indicates an interaction. Significance levels: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

Table 2. Trends of mean indicator values, life strategies and grazing tolerance in the two areas (GC and GCR) and the entire site. Results of separate regression models for the GC-area and GCR-area, as well as results from the combined model, are shown. Numbers are the effect sizes of the orthogonal polynomials of time and their interaction with area type. GC = grazing cessation; GCR = grazing cessation and rewetting; l = linear term; q = quadratic term; l:a = interaction linear term between time and area type. q:a = interaction quadratic term between time and area type. Significance levels: +: $p \leq 0.1$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

	GC Time		GCR Time		Entire site Time		Interaction	
	l	q	l	q	l	q	l:a	q:a
Mean indicator values								
Moisture	-2.37***	-1.12*	0.80	-0.30	-3.31***	-1.57*	4.45***	1.14
Moisture variability	-1.77*	-1.20*	0.45	0.44	-2.59**	-1.75*	3.18*	2.33*
Aeration	1.32*	1.39*	-0.89	0.63	1.93+	2.03*	-3.48**	-1.21
Reaction	-1.69*	0.41	-1.68*	2.43**	-2.31*	0.57	0.31	2.33+
Nutrients	-0.83	0.64	-2.11*	1.85*	-1.21	0.94	-0.14	1.33
Humus	1.63**	-1.34**	2.27*	-2.37**	1.27	-1.88*	0.40	0.14
Light	-2.92***	-0.03	-0.05	0.08	-4.30***	-0.04	4.23***	0.14
Life strategies / grazing tolerance								
Ruderality	-1.68**	1.44*	-2.28**	1.89*	-2.55**	2.18*	0.48	-0.52
Stress tolerance	-1.35*	-0.62	0.63	-0.98+	-2.08*	-0.95	2.70*	-0.01
Competition	2.73***	-0.02	-0.02	0.71	4.09***	0.11	-4.01***	0.63
Grazing tolerance	-2.54**	1.57*	-0.11	0.47	-3.38**	2.08*	3.24*	-1.45

differences in their trends over time between the two areas. The mean indicator value for reaction showed an overall decrease in both areas, with a small minimum around 2006 (i.e. seven years after rewetting) in the GCR-area only, the mean value for nutrients decreased in the GCR-area only and flattened in about 2004 (i.e. five years after rewetting), and the mean value for humus increased in both areas at first but flattened in about 2005 (i.e. six years after rewetting, see Table 2, Figure 3). The mean indicator value for light decreased in the GC-area only. The difference between the trends in the two areas was highly significant (Table 2, Figure 3).

Mean ruderality decreased across the whole site, especially during the first five years, and then stabilised (Table 2, Figure 4). The mean values of the other two strategies, stress tolerance and competition, showed opposite trends in the GC-area (i.e. stress-tolerance decreased, competition increased), but no significant trends in the GCR-area. The difference between trends in the two areas was significant and pronounced for competition (Table 2, Figure 4).

Mean grazing tolerance remained unchanged in the GCR-area but decreased in the GC-area, stabilising in later years. The difference between trends in the two areas was significant for this mean indicator value (Table 2, Figure 4).

Trends of habitat specialists

The species of the rather dry communities (bog forests, heaths and other forests; Table A1 in the Appendix) increased in relative abundance and in relative species number in the GC-area, whereas they showed no significant trends in the GCR-area. The trend differences were significant for all these groups, with the exception of the relative number of heath species (Tables 3, 4, Figures 5, 6).

The species of the rather wet communities (bogs, bog hollows and poor fens) showed more complex patterns: species of bogs showed a slight temporary maximum in relative abundance in the GCR-area only (Table 3, Figure 5) and an increase in relative species number in the GC-area but not in the GCR-area (Table 4, Figure 6). Species of hollows decreased in relative abundance and relative species number in the GC-area, approaching the stable and lower values of the GCR-area. For relative abundance, the difference between the areas was significant for bog hollow specialists (Tables 3, 4, Figures 5, 6). Species of poor fens declined strongly in relative abundance and relative species number in the GC-area (Tables 3, 4, Figures 5, 6). While abundance seemed to stabilise at very low values, there was no indication of a stabilisation for relative species richness of poor-fen species. The trend
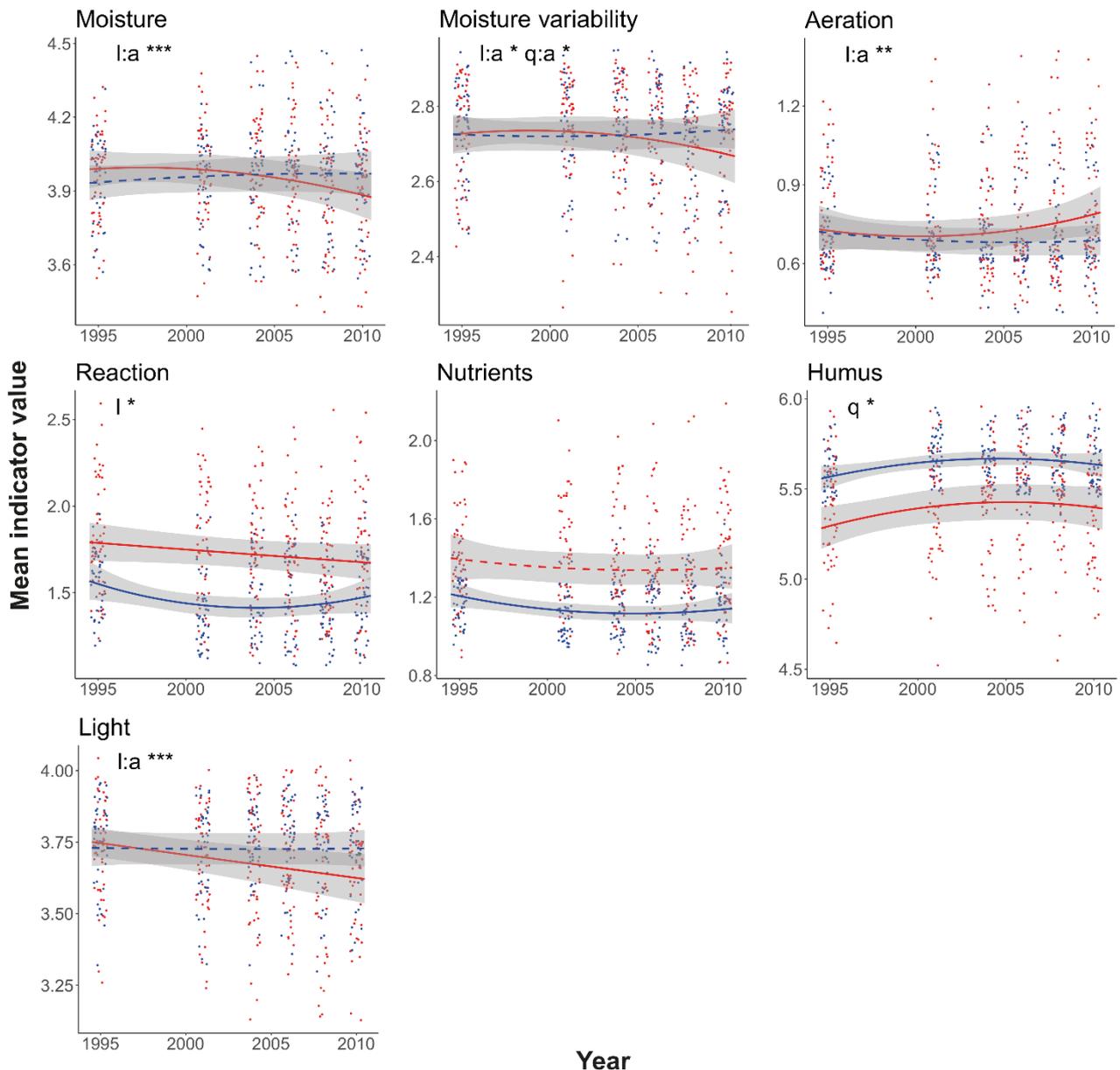
Figure 3. Trends of mean indicator values for GC-areas (grazing cessation, red) and GCR-areas (grazing cessation plus rewetting, blue). Regression lines and confidence intervals from individual models are displayed. Solid lines show significant trend components. Dashed lines show the model fit of both trend components, if neither of them is significant. Labels denote significant trend differences or significant overall trends derived from the common model. Dots indicate observed values on single plots. Outliers are not shown. l = linear time component; q = quadratic time component; a = area type; a colon indicates an interaction. Significance levels: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

differences between the areas were significant for both of these variables in poor fens (Tables 3, 4).

Trends of taxonomic groups
Cyperaceae showed a marked decrease in relative abundance in the GC-area, but not in the GCR-area. Relative abundance of Ericaceae increased mainly from 2005 (i.e. ten years after cessation of grazing)

onwards in the GC-area and remained stable in the GCR-area, whereas the relative abundance of Poaceae showed a temporary decline in the latter area. Concerning the relative abundance of bryophytes, we observed a flattening increase in the GC-area and a temporary maximum around the years 2000–2005 (i.e. ten years after cessation of grazing) in the GCR-area (Table 3, Figure 7).
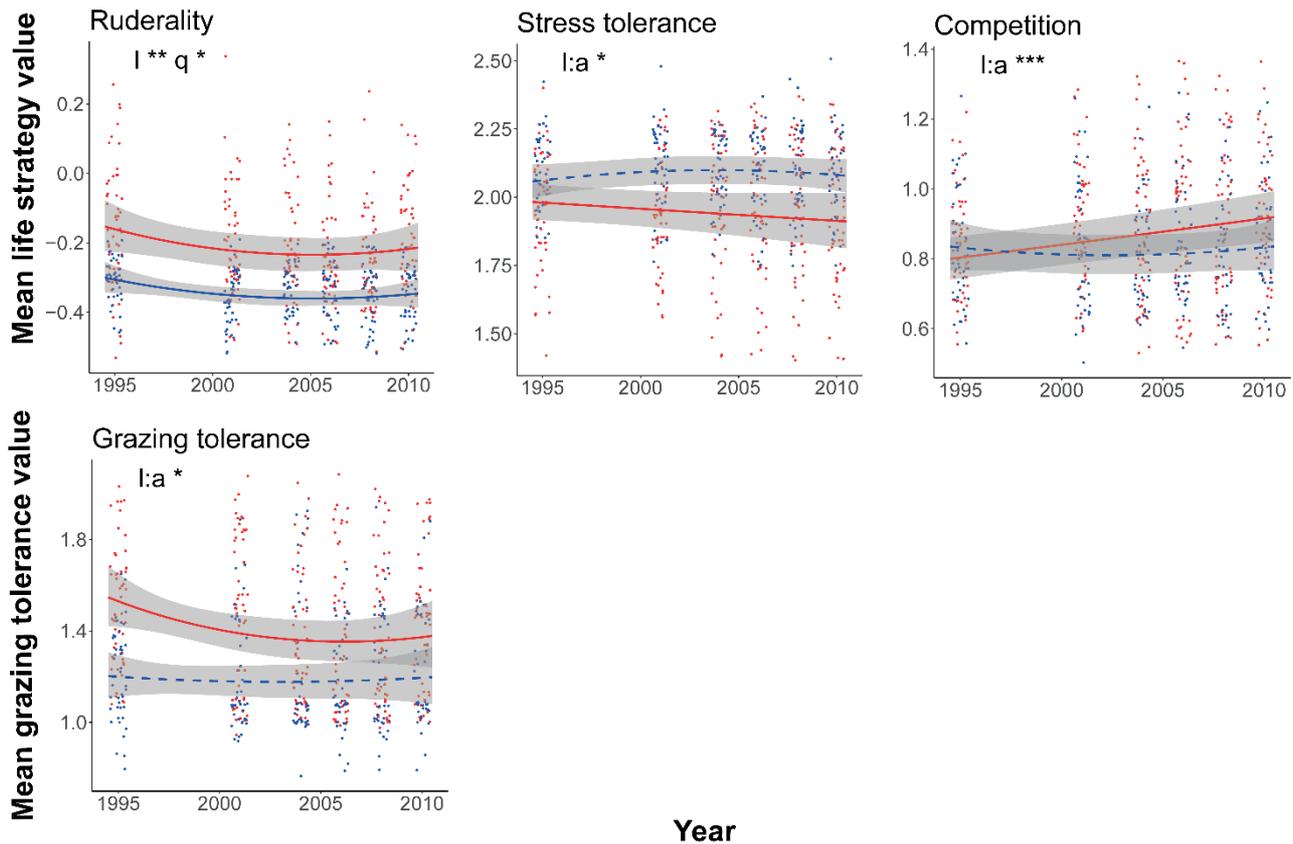
Figure 4. Trends of mean life strategy values and mean grazing tolerance for GC-areas (grazing cessation, red) and GCR-areas (grazing cessation plus rewetting, blue). Regression lines and confidence intervals from individual models are displayed. Solid lines show significant trend components. Dashed lines show the model fit of both trend components, if neither of them is significant. Labels denote significant trend differences or significant overall trends derived from the common model. Dots indicate observed values on single plots. Outliers are not shown. l = linear time component; q = quadratic time component; a = area type; a colon indicates an interaction. Significance levels: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

Trends of growth forms

Geophytes strongly declined in relative abundance in the GC-area but not in the GCR-area. The relative abundance of long-living hemicryptophytes declined in both areas, but in the GCR-area the trend was partly reversed towards the end of the observation period. In contrast, woody species (woody chamaephytes and phanerophytes) gained in relative abundance in the GC-area. In the GCR-area, we found a temporary minimum in the relative abundance of phanerophytes around 2005 (i.e. six years after rewetting, see Table 3, Figure 8).

Trends of single species

We observed a large difference in the abundance dynamics of single species between the two areas. Whereas 19 species significantly declined and 5 increased in the GC-area, we found only 7 significant declines and 7 increases in the GCR-area (Table A2).

Species which performed better in the GCR-area usually did not increase there, but rather showed a smaller or no decline (e.g. *Carex canescens, C. echinata, C. nigra, Eriophorum angustifolium, E. vaginatum, Homogyne alpina, Polytrichum commune*; see Table A2). Exceptions were *Aulacomnium palustre* which declined in the GC-area and increased in the GCR-area, and *Vaccinium oxycoccos* which increased in the GCR-area with marginal significance. There were only a few species that performed better in the GC-area. Among them, *Vaccinium myrtillus* increased in an accelerating manner there but remained unchanged in the GCR-area, *Huperzia selago* remained unchanged in the GC-area but declined in the GCR-area, and *Hylocomium splendens* showed no significant trends in either area type. All these species had a significant negative interaction between time and area type (Table A2).

Table 3. Trends of the cumulative relative cover of species belonging to various habitats, taxonomic groups and growth forms (only vascular plants) in the two areas (GC and GCR) and the entire site. Results of separate regression models for the GC-area and GCR-area, as well as results from the combined model, are shown. Numbers are the effect sizes of the orthogonal polynomials of time and their interaction with area type. GC = grazing cessation; GCR = grazing cessation and rewetting; l:a = interaction linear term between time and area type; q:a = interaction quadratic term between time and area type. Significance levels: +: $p \leq 0.1$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

	GC Time		GCR Time		Entire site Time		Interaction	
	l	q	l	q	l	q	l:a	q:a
Habitat specialists								
Bogs	1.18+	-0.69	-1.31	-1.29*	1.41	-0.83	-3.22*	-0.95
Bog forests	3.67***	-0.17	0.89	-0.46	4.99***	-0.23	-3.70**	-0.44
Bog hollows	-4.41***	1.02	-0.08	0.58	-5.70***	1.65*	5.52***	-0.63
Poor fens	-8.38***	4.13***	-2.54*	1.37*	-12.41***	6.12***	10.38***	-5.03***
Heaths	2.51***	1.66**	-0.86	0.84	3.15***	2.09**	-4.51***	-0.76
Other forests	2.81***	-0.13	-0.65	0.92+	4.25***	-0.19	-5.03***	1.29
Taxonomic groups								
Cyperaceae	-3.97***	0.33	-0.78	0.18	-5.01***	0.42	3.79**	-0.14
Ericaceae	2.72***	2.15***	-0.89	0.79	3.39***	2.68***	-4.78***	-1.45
Poaceae	-1.50	1.28	-0.96	2.67***	-2.11	1.81	0.85n	1.72
Bryophytes	3.84***	-2.00*	0.20	-1.93**	5.20***	-2.71*	-3.06+	0.10
Growth forms								
Geophytes	-5.30***	0.28	0.61	-0.52	-5.99***	0.31	7.06***	-1.21
Long-living hemicryptophytes	-2.54***	1.06	-2.39***	1.77**	-3.25***	1.36	-0.50	1.43
Woody chamaephytes	2.84***	0.83+	-0.28	0.48	4.22***	1.94*	-4.63***	-1.23
Phanerophytes	2.59***	-0.9+	0.15	2.24***	3.965***	-1.4+	-3.78**	4.01***

DISCUSSION

Habitat structure

In our study area, bare peat was largely recolonised by vegetation and almost completely disappeared by 15 years after restoration measures began in both the GC-area and the GCR-area. This observation is in line with other studies showing that after a reduction or cessation of grazing, erosion scars can be nearly completely recolonised within 5–10 years (Anderson & Radford 1994, Evans 2005).

We found a peak in litter 7–10 years after grazing cessation, followed by a strong expansion of cover of all kinds of plants (Figure 2). It seems that in our case the accumulated litter did not hamper bryophytes in the long run, as observed in various studies on fens and calcareous grasslands (e.g. Bard 1965, Bobbink & Willems 1993, Vanderpoorten *et al.* 2004, Peintinger & Bergamini 2006, Jasmin *et al.* 2008). Maybe a maximal amount of only 25 % cover was not enough to shade out bryophytes, as observed by Peintinger &

Bergamini (2006), so that enough light and open space always remained and therefore bryophytes were not affected by the litter accumulation, as it was also observed by Guêné-Nanchen (2017), even though in their study the litter accumulation did not exceed a cover of 8 %. Similar observations were made by Feldmeyer-Christe *et al.* (2011): in their study mosses were colonising mainly open parts after a bog burst and were not influenced by the sedges.

The increase of peat mosses was significant in the GCR-area only, but the difference between the area types was not significant in this regard. Peat mosses are highly sensitive to trampling (Studlar 1980, Studlar 1983, Arnesen 1999). We thus expected that they would profit from the cessation of grazing, but they did not increase in a significant way. As most of the peat mosses need high to very high water levels (Rydin & Jeglum 2006), they only increased in cover when water levels were also increased. An expansion of peat mosses in newly rewetted bogs has been observed in many studies (e.g. González *et al.* 2014,
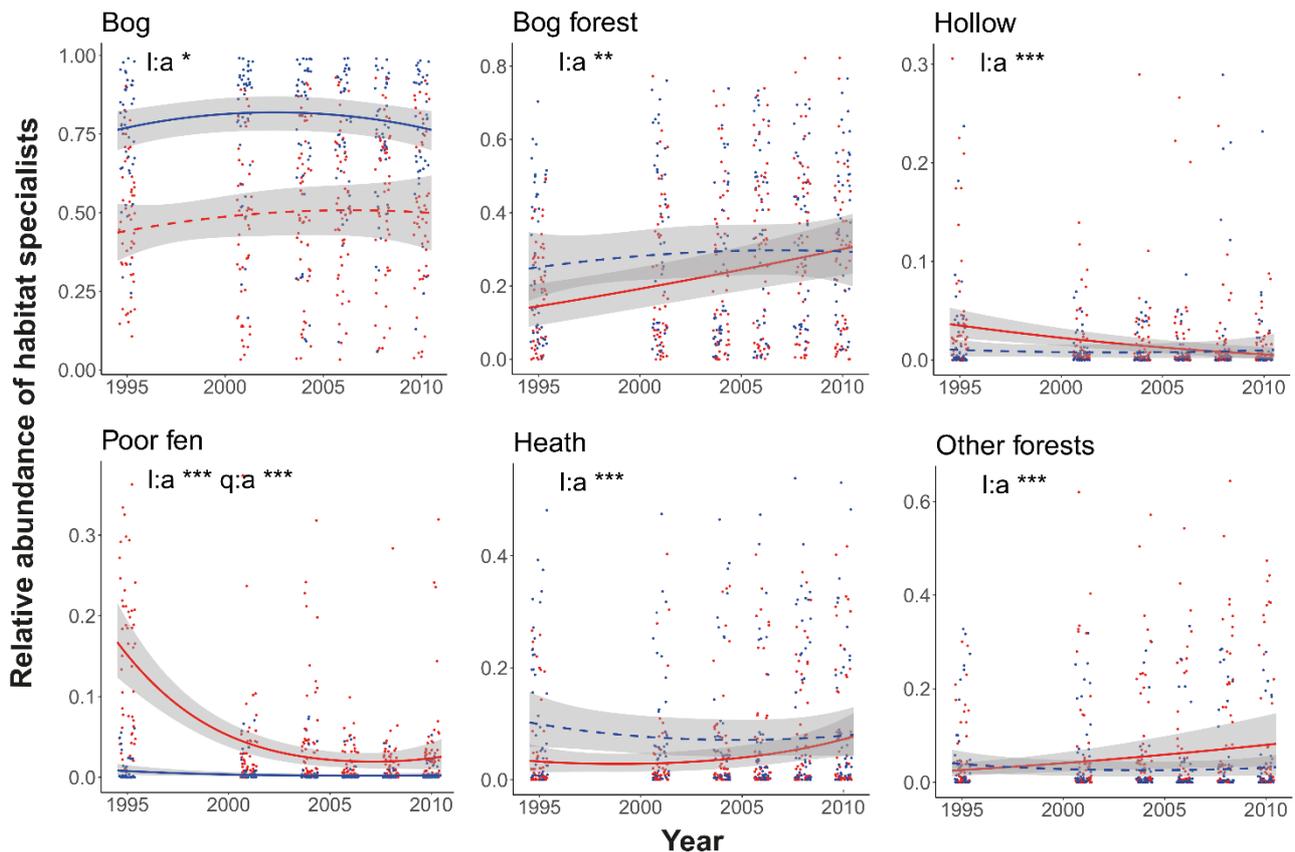
Figure 5. Trends of relative abundance of habitat specialists for GC-areas (grazing cessation, red) and GCR-areas (grazing cessation plus rewetting, blue). Regression lines and confidence intervals from individual models are displayed. Solid lines show significant trend components. Dashed lines show the model fit of both trend components, if neither of them is significant. Labels denote significant trend differences or significant overall trends derived from the common model. Dots indicate observed values on single plots. Outliers are not shown. l = linear time component; q = quadratic time component; a = area type; a colon indicates an interaction. Significance levels: *: $p \le 0.05$; **: $p \le 0.01$; ***: $p \le 0.001$.

Maanavilja *et al*. 2015, Küchler *et al.* 2018, Bedolla *et al*. 2019).

Mean indicator values and life strategies
We interpret the stable mean soil moisture indicator value of about 4 (which is suitable for most *Sphagnum* species growing on hummocks, see Landolt *et al.* 2010) and the stable mean aeration value of about 0.7 as a positive effect of the ditch blocking in the GCR-area, given the ongoing drying and the increasing mean aeration without this restoration measure in the GC-area. The enhanced aeration in the GC-area could be due to several factors. According to Lloyd (2006), soil respiration is mainly dependent on the depth of the water table. Pengthamkeerati *et al*. (2005) state that gas fluxes are correlated with the amount of macropores in the soil, but negatively correlated with its amount of micropores. According to them the compaction of the soil reduces the macropores, the water content and

the aeration of clayey soils. Simulated trampling resulted in increased bulk density of peat, reduced respiration and enhanced photosynthesis. This enhanced the net exchange during autumn but reduced it in winter (Clay & Worrall 2013). Cessation of simulated trampling resulted in a two-month peak of net ecosystem exchange, then the values turned back to the levels of trampled cores (Clay & Worrall 2013). One possible explanation according to Clay & Worrall (2013) is the recovery of the soil fauna which was deteriorated by trampling. However, the success of rewetting seems to be limited in our study area, as the mean value of moisture variability in the GCR-area after 10 years was still on a level (ca. 2.7) which indicates a possible drying to moderately moist conditions (i.e. a fluctuation of the moisture which corresponds values between 5 and 3 and which is suitable only for one third of all *Sphagnum* species of Switzerland, see Landolt *et al*. 2010). This was confirmed by water

Table 4. Trends of the relative species number (np) of species belonging to various habitats in the two areas (GC and GCR) and the entire site. Results of separate regression models for the GC-area and GCR-area, as well as results from the combined model, are shown. Numbers are the effect sizes of the orthogonal polynomials of time and their interaction with area type. GC = grazing cessation; GCR= grazing cessation and rewetting; l:a = interaction linear term between time and area type; q:a = interaction quadratic term between time and area type. Significance levels: +: $p \le 0.1$; *: $p \le 0.05$; **: $p \le 0.01$; ***: $p \le 0.001$.

| | GC | | GCR | | Entire site | | | |
| | Time | | Time | | Time | | Interaction | |
	l	q	l	q	l	q	l:a	q:a
Bogs	1.40**	0.53	0.62	0.55	1.55**	0.59	-0.77	0.10
Bog forests	3.28***	-0.38	0.55	-0.54	4.39***	-0.5	-3.66***	-0.21
Hollows	-1.35**	-0.16	-0.18	0.76	-1.87*	-0.22	1.61	1.31
Poor fens	-5.94***	0.65	-0.92	0.75	-4.94***	0.54	3.50*	0.64
Heaths	1.19*	0.71	-0.67	0.21	1.58+	0.94	-2.52+	-0.64
Other forests	1.98**	-0.23	0.02	-0.43	2.80**	-0.33	-2.76*	-0.27

table measurements in 2001: piezometers and walrags in the rewetted area indicated that after about a week without rainfall the water table may sink 20 to 30 cm below ground (Steiner *et al.* 2001). We suspect that seven decades of drainage and trampling damaged the structure of the peat and reduced its capacity to store water, leading to the drying of the uppermost layer of the peat during periods of dry weather. This might also be responsible for the ongoing reduction of the mean indicator value for moisture in the GC-area. This ongoing reduction is linked with the decline of numerous species demanding high soil moisture, such as *Eriophorum vaginatum*, *Juncus filiformis* and *Trichophorum cespitosum*, and the increase of *Vaccinium myrtillus* and *Picea abies* (Table A2).

We observed a slight, flattening decrease in the mean nutrient indicator value in the GCR-area only. The vegetation did not indicate an initial pulse of nutrients after rewetting, as observed in many other studies (e.g. Vasander *et al.* 2003, Sallantaus & Koskinen 2012, Haapalehto *et al.* 2014, Menberu *et al.* 2017, Lundin *et al.* 2017, Koskinen *et al.* 2017, Shah & Nisbet 2019, Howson *et al.* 2021). Most of these studies were conducted in previously afforested bogs. The initial nutrient increase was explained by decomposed forest residues, by the disturbance of the soil during the clearcutting, and by previous fertilisation for forestry purposes (Vasander *et al.* 2003, Howson *et al.* 2021). A subsequent decrease has been observed in several cases too (Haapaletto *et al.* 2014, Menberu *et al.* 2017, Shah & Nisbet 2019), so that nutrient levels comparable to pristine sites could be reached after 10 (Haapalehto *et al.* 2011) to 17 years (Howson *et al.* 2021). Similar patterns to those observed in our study have been found in a

Canadian restoration study (Andersen *et al.* 2006, 2013).

In accordance with Lundin *et al.* (2017), who observed a reduced soil pH after the rewetting of a cutover nutrient-poor mire, we found a consistent decline in the mean reaction indicator value in both area types to even more acidic conditions. It was linked to the sum of often non-significant declines in species of only moderately acidic to neutral conditions in both areas (e.g. *Aulacomnium palustre*, *Briza media*, *Juniperus communis*, *Linum catharticum*, *Menyanthes trifoliata* and others, with *Nardus stricta* having the greatest importance amongst them) and the increase of *Vaccinium myrtillus* in the GC-area only (Table A2).

We observed an increase in the mean humus indicator value in both areas, but this trend flattened over time. But as Urbanova *et al.* (2018) detected changes in microbial characteristics in rewetted peat, bringing the quality of its soil organic matter closer to pristine conditions, a restoration of peat formation seems possible. As we did not find any difference between the two area types, we assume that in our case the increase in the mean soil-humus value was mainly due to the cessation of grazing and likely the very strong decrease of *Nardus stricta* in both areas (Table A2). This grass species is known to grow in a wide range of site conditions (W.G. Smith 1918), but has a humus value of 3 (Landolt *et al.* 2010) which is far below the mean values of our observations (about 5).

The models suggest a clear influence of rewetting on light availability. There was a decrease in the mean light indicator value in the GC-area, while it was stable in the GCR-area. The trend in the GC-area is in line with expectations for cattle removal and subsequent recovery of the vegetation layer due to the absence of disturbance. The decreasing trend of the
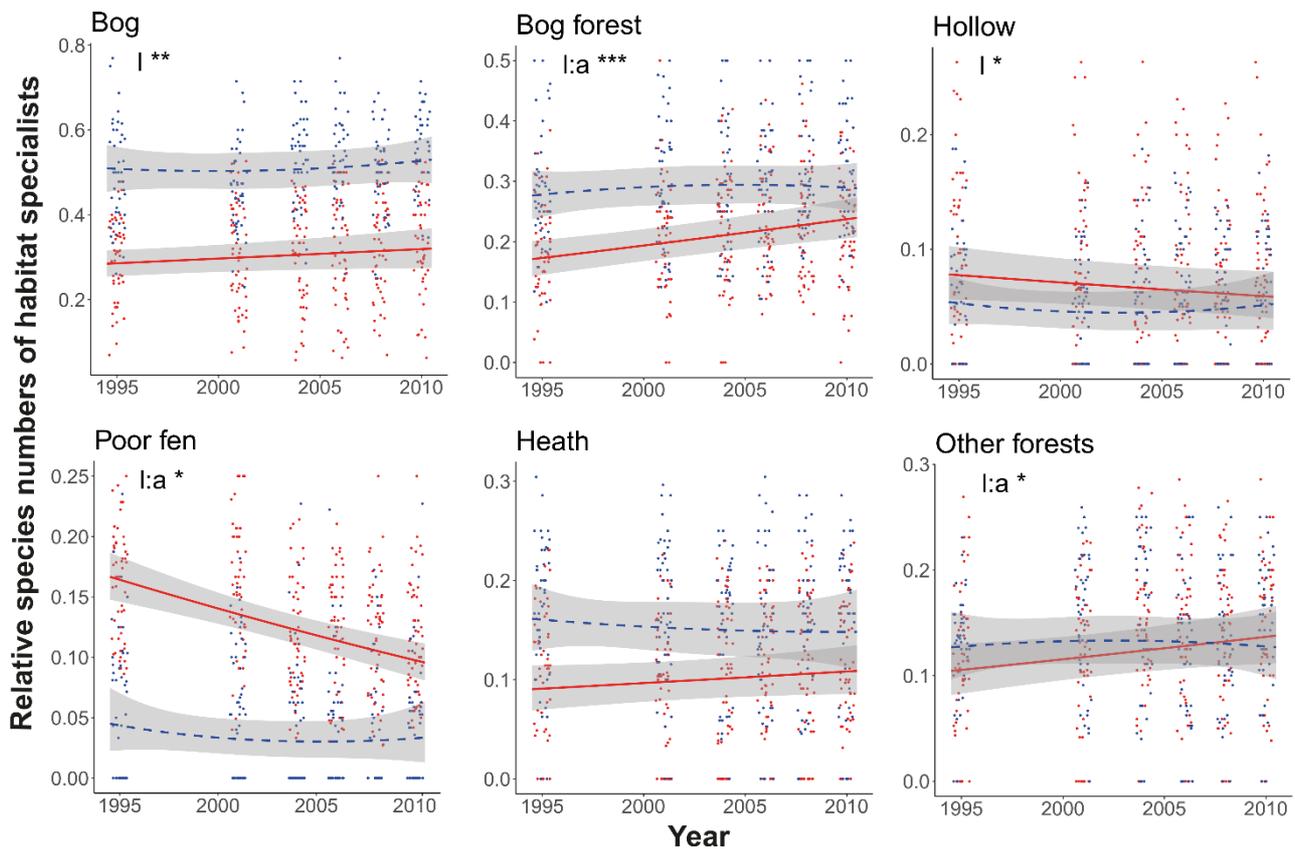
Figure 6. Trends of relative species numbers of habitat specialists for GC-areas (grazing cessation, red) and GCR-areas (grazing cessation plus rewetting, blue). Regression lines and confidence intervals from individual models are displayed. Solid lines show significant trend components. Dashed lines show the model fit of both trend components, if neither of them is significant. Labels denote significant trend differences or significant overall trends derived from the common model. Dots indicate observed values on single plots. Outliers are not shown. l = linear time component; q = quadratic time component; a = area type; a colon indicates an interaction. Significance levels: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

mean light value was likely due to a decrease in species demanding much light rather than to an increase in shade plants, with the exception of *Sphagnum capillifolium*, *Picea abies* and *Vaccinium myrtillus*, three species of medium or low light demand which increased in the GC-area. The stable mean light indicator value in the GCR-area might be explained by an equilibrium of increasing light-demanding species (e.g. *Sphagnum magellanicum* aggr., *Betula pubescens*, *Dactylorhiza maculata* and *Carex limosa*) and decreasing ones (e.g. *Carex nigra*, *C. pauciflora* and *Nardus stricta*).

If wetlands are subjected to fluctuating water levels or grazing, one might expect an enhancement of ruderals and gap colonisers, and an enhancement of clonal dominant species due to increased disturbance (Boutin & Keddy 1993). In line with this, we observed a decline in ruderality in both areas that flattened over time. As the three strategy types (ruderals, competitors, stress tolerators) are not

independent from each other (for each species their sum is always 3), a decline in one value causes an increase in at least one of the other two. In fact, we observed that the elimination of a stress factor ("grazing") resulted in an additional reduction of the stress tolerance in the GC-area. A bog is a habitat of extreme site conditions in terms of moisture, soil reaction and nutrients and therefore harbours many stress tolerators. Successful restoration in theory should drive a deteriorated bog back to these extreme conditions, or as in our case at least stabilises them. We observed in the GCR-area a compensation of the effect described above, as indicated by the stabilisation of stress tolerators in the GCR-area at the expense of competitors. In our study, the mean grazing tolerance decreased strongly in the GC-area towards the lower and stable values in the GCR-area. R.S. Smith *et al.* (2003) explained differences in the development of vegetation after cessation of grazing with varying intensities of prior pasturing. The initial
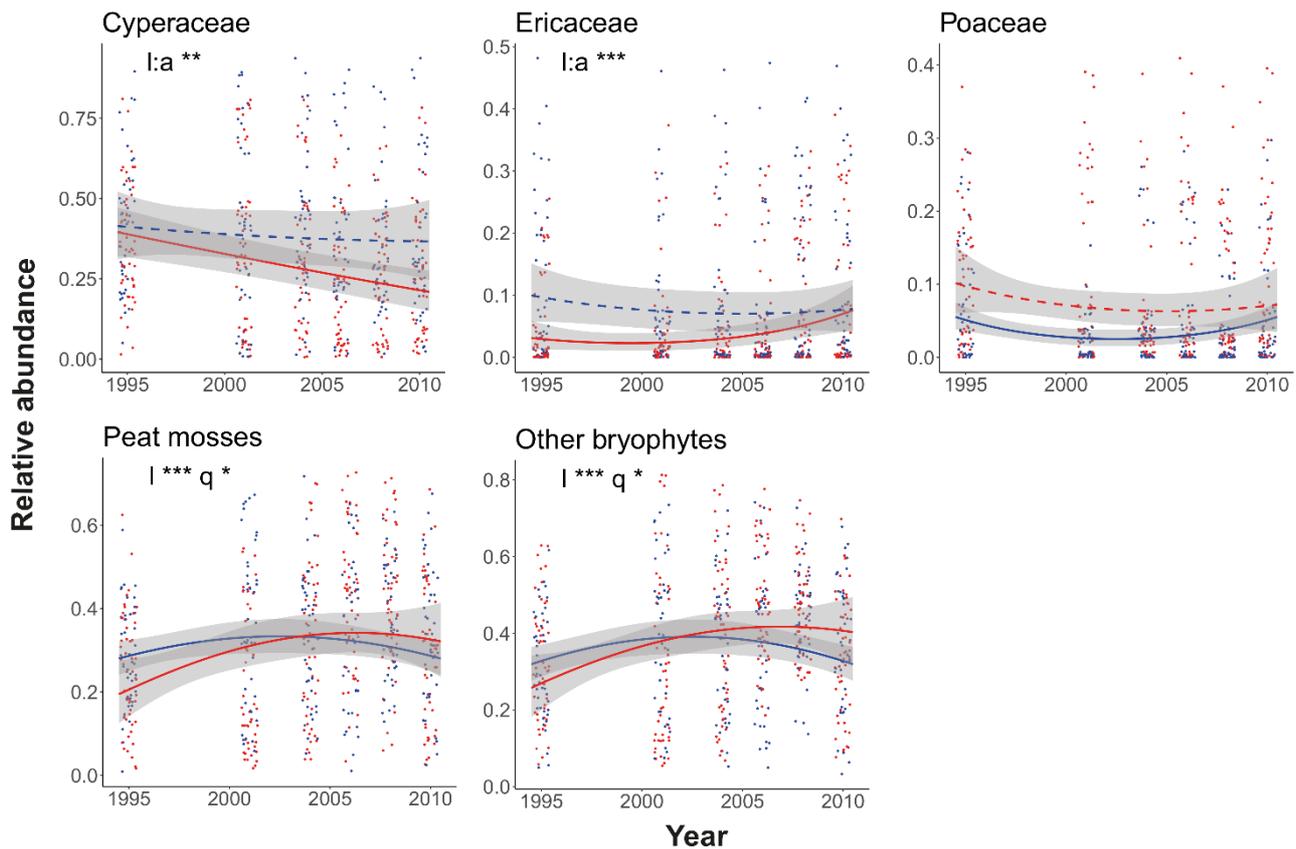
Figure 7. Trends of the relative abundance of taxonomic groups for GC-areas (grazing cessation, red) and GCR-areas (grazing cessation plus rewetting, blue). Regression lines and confidence intervals from individual models are displayed. Solid lines show significant trend components. Dashed lines show the model fit of both trend components, if neither of them is significant. Labels denote significant trend differences or significant overall trends derived from the common model. Dots indicate observed values on single plots. Outliers are not shown. l = linear time component; q = quadratic time component; a = area type; a colon indicates an interaction. Significance levels: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

values of mean grazing tolerance suggest similar differences for our site. In fact, the GCR-area was separated from the rest of the site by two deep ditches and was thus most likely less accessible for cattle.

Habitat specialists

A significant succession towards target communities after rewetting could be seen in a Finish peatland (Haapalehto *et al*. 2017) where in addition tree stands were partially removed, as well as in Canadian peatlands (González *et al*., 2014). Whereas Haapalehto *et al*. (2017) found a success within only about 10 years, González et al. (2014) found no effect of time between 4 and 17 years after rewetting in restoration success. Czech bogs did not reach the characteristics of their pristine stages, but their vegetation composition was tending towards them (Urbanova *et al*. 2018). The target communities of a restoration can be assessed by their status in the Red List of communities (Delarze *et al*. 2016) and by the

question, whether they were present on the site in its pristine state. Bog, hollow and bog forest communities are rated as EN, whereas heath communities are rated as NT (Delarze *et a*l. 2016). The information of the past vegetation in Gross Moos is weak (one core with pollen analyses, see Grünig & Steiner 1994), we only can speculate about the present communities in its pristine state. Species of hollows (*Scheuchzeria palustris*), bogs (*Sphagnum* spp., *Drosera* spp.) and bog forests (*Betula* spec.) are present since at least 6000 years (or longer) and species of heath (*Calluna vulgaris* and other *Ericaceae*) were present since at least 2500 years. This may be interpreted as the presence of these communities in the pristine state of the site. To our opinion the communities of bog, hollows and bog forests should be enhanced with first priority.

In the GC-area, we found a relative increase (abundance and number) of characteristic species of *bog forests, other forests and heaths (mainly Betula*
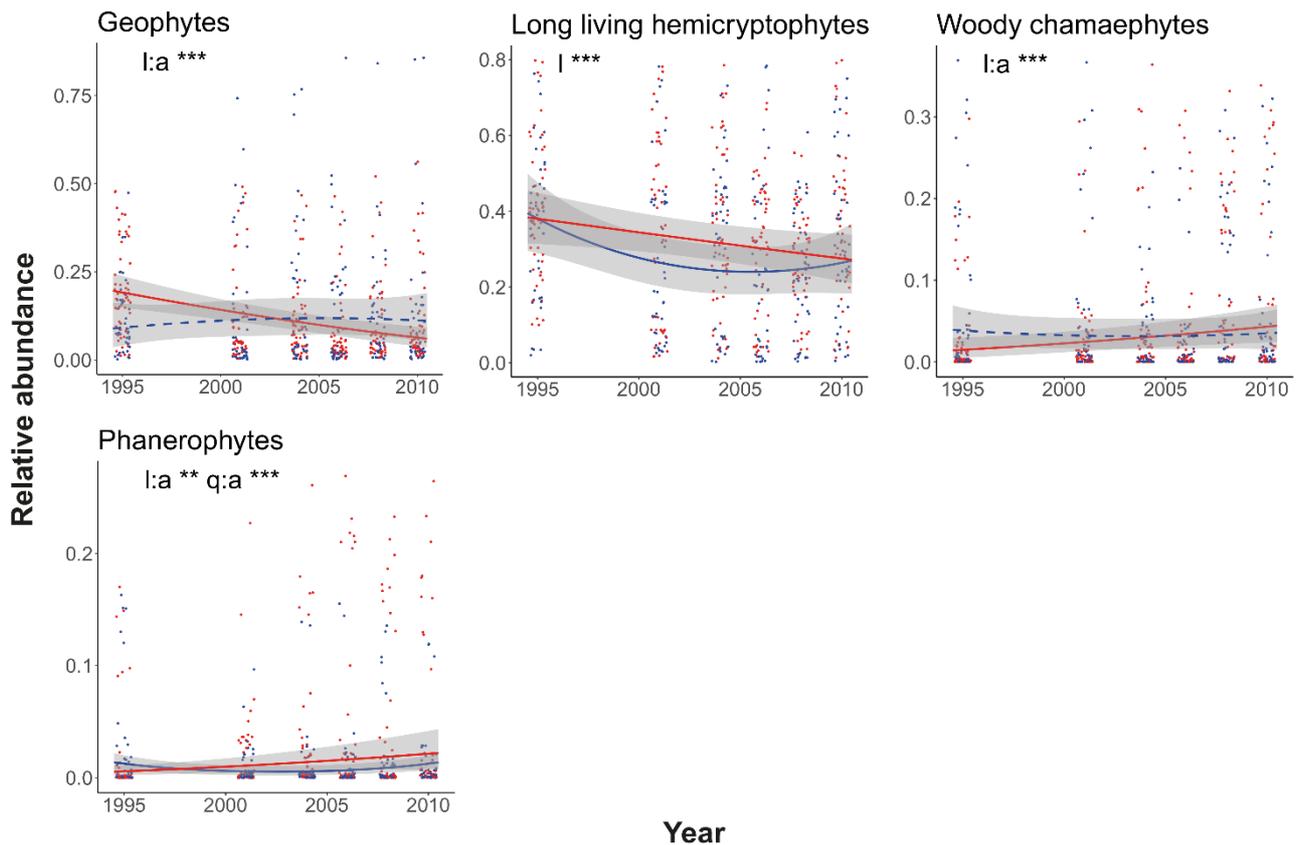
Figure 8. Trends of the relative abundance of growth forms for GC-areas (grazing cessation, red) and GCR-areas (grazing cessation plus rewetting, blue). Regression lines and confidence intervals from individual models are displayed. Solid lines show significant trend components. Dashed lines show the model fit of both trend components, if neither of them is significant. Labels denote significant trend differences or significant overall trends derived from the common model. Dots indicate observed values on single plots. Outliers are not shown. l = linear time component; q = quadratic time component; a = area type; a colon indicates an interaction. Significance levels: *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

pubescens, *Sphagnum capillifolium*, *Picea abies* and *Vaccinium myrtillus*; Table A2). This corresponds to the findings of other studies (Rawes & Hobbs 1979, Welch 1998, Medina-Roldán *et al.* 2012), where an increase in dwarf shrubs was observed after cessation of grazing, sometimes at the expense of *Eriophorum vaginatum* (Rawes & Hobbs 1979), as we observed as well. Furthermore, we observed an increase in the relative number of species in the GC-area, but not of the relative abundance of species characteristic of bogs. In the GC-area, we found a marked decrease in the relative abundance and the relative number of species characteristic of hollows (*Menyanthes trifoliata* and *Scheuchzeria palustris*) and an even stronger decrease in species of poor fens (*Aulacomnium palustre*, *Carex canescens*, *C. echinata*, *C. flava* aggr., *C. nigra*, *Eriophorum angustifolium*, *Nardus stricta*, *Juncus filiformis* and *Viola palustris*; Table A2). The species trends in the GC-area were ambiguous, as the decline in poor-fen

species supports the restoration goals but the trend for bog species was not distinctive and the relevance to nature conservation of the increases in bog forest and heath species is not clear.

In the GCR-area, we did not find any adverse shifts in the species composition but a temporary gain in the relative abundance of bog species (mainly due to the not significant trends of *Sphagnum compactum* and *S. russowii*, Table A2) and a desired decrease in the relative abundance of poor-fen species (mainly of *Carex nigra* and *Nardus stricta*). The lack of persistent gains for the target species contrasts the findings of Urbanova *et al.* (2018) and partially of Haapalehto *et al.* (2017), who did not find increasing species numbers either but an increase of their abundance. However, the target species in the GCR-area succeeded in retaining their dominant position and thus appeared to be competitive in the colonisation process of bare peat and to cope well with the intermediate litter increase.

Taxonomic groups

The increase in bryophyte cover in the GC-area was mainly due to the development of *Sphagnum capillifolium* aggr. and *S. magellanicum* aggr. (Table A2). This goes along with other studies where an increase in bryophytes was observed after grazing cessation and reduced trampling (Studlar 1980, Studlar 1983, Hill *et al.* 1992, Arnesen 1999). The observed decline in Cyperaceae was mainly because of a reduction of abundant species. The observed increase in Ericaceae was only due to a change in *Vaccinium myrtillus* cover (Table A2), while all other members of this family remained unchanged. Similar observations were made in other studies: Welch (1998) stated that *V. myrtillus* is highly sensitive to grazing (which is more or less in line with Landolt *et al.* 2010), and Rawes & Hobbs (1979) found a decrease in *Eriophorum vaginatum* in favour of *Calluna vulgaris* after cessation of grazing. Other studies (e.g. Medina-Roldán *et al.* 2012, Milligan *et al.* 2016) indicated that grazing exclusion increased the relative abundance of dwarf shrubs and reduced that of Poaceae. We therefore expected Poaceae species to decrease after the removal of cattle in our study, but they showed no reaction to this measure and only a small temporary decrease in response to the additional restoration measure of rewetting. This family was dominated by *Molinia caerulea*, which is quite sensitive to grazing (Marrs *et al.* 2004) and declined only temporarily in both areas (Table A2).

Bryophytes showed only a temporary increase in relative abundance in the GCR-area, which was caused by some opposing trends at the species level (increasing *Aulacomnium palustre*, *Pleurozium schreberi*, *Sphagnum capillifolium* and *S. magellanicum*, decreasing *Polytrichum formosum*) and the sum of many non-significant trends (Table A2). It seems that bryophytes were in competition with *Calluna vulgaris*, *Molinia caerulea* and *Trichophorum cespitosum* because these species showed the strongest opposite trend to the bryophytes as a group. We found a clear influence of rewetting, which hampered *Vaccinium myrtillus* and stabilised many Cyperaceae (*Carex canescens*, *C. echinata*, *C. flava* aggr., *C. nigra*, *C. pallescens*, *C. rostrata*, *Eriophorum angustifolium* and *E. vaginatum*; Table 3, Figure 7, Table A2), which maintained stable or less decreasing abundances in the GCR-area.

Growth forms

Vinther & Hald (2000) stated that continued grazing is hampering the regrowth of phanerophytes and chamaephytes whose perennial buds are in the canopy, and that geophytes and hemicryptophytes, which have their perennial buds at ground level, can cope better with grazing. Grazing creates gaps and removes biomass and promotes the establishment of species this way (Vinther & Hald 2000). In our case long-living hemicryptophytes decreased in both areas. This trend was mainly due to the decline of *Trichophorum cespitosum* (Table A2) which might have been promoted by removing of biomass and created gaps when grazed, and maybe was shaded out to a certain extent after grazing was stopped. This goes along with our observation of declining open peat and increased litter in the first period after grazing cessation. Geophytes decreased in the GC-area but remained stable in the GCR-area. This was caused by the decline of *Carex nigra*, *C. rostrata* and *Eriophorum vaginatum* in the GC-area (Table A2), which, as *T. cespitosum*, could have been promoted by biomass removal and created gaps when grazed. As species of very wet places *C. rostrata* and *E. vaginatum* profited from the rewetting and compensated the effect of grazing cessation. Woody chamaephytes were represented only by Ericaceae. Their development is discussed in the section above. Phanerophytes were mainly represented by *Acer pseudoplatanus*, *Betula pubescens*, *Picea abies* and *Pinus mugo*. Whereas *Acer pseudoplatanus* and *Pinus mugo* showed no trends, *Betula pubescens* and *Picea abies* were promoted by the cessation of grazing but *Picea abies* was hampered by rewetting.

CONCLUSIONS

We observed the vegetation in a degraded alpine bog over a period of 15 years after the cessation of grazing and of 11 years after the additional restoration measure of partial rewetting. Both measures had their desired restoration effects: cessation of grazing enhanced the recolonisation of bare peat. The mean indicator values of soil reaction and humus content developed towards very acidic and nearly mineral free conditions as it was described as ideal in Frei *et al.* (2021). As the peat was very acidic before the restoration and contained very little mineral components, there was little room for improvement in these aspects. Cessation of grazing enhanced the abundance of peat mosses as the dominant group of bryophytes, but it led to drier conditions and promoted the species of drier communities (heaths, forests). Rewetting had a desired stabilising effect on many parameters: the abundances of habitat specialists, the mean indicator value for moisture and its variation, aeration and light availability, stress and grazing tolerance, and competition.

Concerning shifts in species composition, the rewetting was only a partial success and the grazing

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cessation, when applied as the only restoration measure, turned out to be insufficient in our case. This partly confirms the results of Kreyling *et al.* (2021) who compared rewetted and near-natural fen peatlands across Europe and found that rewetting does not fully restore the initial species composition in previously drained sites.

According to Haapalehto *et al.* (2017) there is a risk of drawing premature conclusions on the efficiency of ecological restoration with the current practice of short-term monitoring. For a Canadian cutover bog, Lucchese et al. (2010) estimated that a period of at least 17 years after restoration would be needed to accumulate a 19 cm thick moss layer for half of the site, which would be able to act as new acrotelm and could stabilise the water table near the surface of the mire. Maybe it will take even longer, as McCarter & Price (2015) found for the same place that 15 years after restoration, the peat was not able to store moisture to the same amount as natural peat. Our study ended only 11 years after the rewetting, so we assume, in line with Urbanova (2018), that the site had not yet reached its final state. Indeed, there are some indications that a return of the peat-forming process and a re-establishment of natural vegetation can be expected in the coming decades. We recommend further observation of the vegetation trends in this alpine bog.

AUTHOR CONTRIBUTIONS

UHG initiated the study, made baseline analyses of the data and wrote the manuscript. MK designed the sampling. KE did the statistical modelling and created most of the Figures and Tables. The data were collected by AnBe, UHG, MK, HK, together with many other people. All authors contributed to the interpretation of the results and to the writing of the final manuscript.

ACKNOWLEDGEMENTS

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Appendix

Definition of life forms, according to Landolt *et al.* (2010)

Geophyte: Plant with resting buds below the ground (e.g. with rhizomes, tubers, bulbs, below-ground runners).

Hemicryptophyte (long-lived): Plant with resting buds on or directly below the ground (rosettes, tussocks) and flowering and fructification for several to many years (pollacanthic species).

Woody chamaephyte: Dwarf shrub with resting buds above the ground, and woody parts usually smaller than 0.4 m.

Phanerophyte: Woody plant growing as a shrub or tree, taller than 4 m.

Definition of habitat specialists

The plots were assigned to the Pantke (2008) association they were most similar to (Van-der-Maarel's Index), and subsequently grouped into the entities of Delarze habitats (Delarze *et al.* 2015). The local habitat specialist species were derived by calculating an INDVAL (Dufrêne & Legendre 1997) for each species j per habitat i:

$$INDVALij = \frac{cij}{\sum_{i=1}^{n} cij} * cij,$$

where c_{ij} is the constancy of the species j within the habitat i. We tested various limits of the INDVAL for designating species as characteristic of a habitat. It turned out that a quantile of 66.66 % led to a long species list for each habitat with only a small habitat overlap.

Table A1. Habitat specialists for selected habitats in Schwaendital. The INDVAL is given for a species if it is within the upper third of all INDVALs for the relevant habitat.

	Bog	Bog forest	Bog hollow	Poor fen	Heath	Other forest
Carex pauciflora	0.636					
Eriophorum vaginatum	0.379	0.179				
Sphagnum recurvum aggr.	0.323					
Andromeda polifolia	0.301					
Trichophorum cespitosum	0.282					
Vaccinium oxycoccos	0.267					
Aulacomnium palustre	0.222			0.067		
Calluna vulgaris	0.203				0.062	
Drosera rotundifolia	0.190		0.159			
Polytrichum juniperinum aggr.	0.174					
Sphagnum compactum	0.091					
Sphagnum fuscum	0.091					
Sphagnum russowii	0.091					
Betula pubescens		0.603				

	Bog	Bog forest	Bog hollow	Poor fen	Heath	Other forest
Sphagnum capillifolium aggr.	0.122	0.409				
Polytrichum commune		0.360				
Sphagnum girgensohnii		0.333				
Sphagnum magellanicum	0.216	0.262				
Dryopteris dilatata aggr.		0.173				
Vaccinium vitis-idaea		0.175			0.048	
Dicranodontium denudatum		0.155				
Rhytidiadelphus triquetrus		0.323				0.054
Hylocomium splendens		0.320				0.039
Sorbus aucuparia		0.315				0.063
Polytrichum formosum		0.315				0.018
Picea abies		0.158				0.068
Dicranum scoparium aggr.		0.215			0.054	0.052
Pleurozium schreberi		0.286			0.058	0.025
Vaccinium myrtillus		0.157			0.088	0.030
Hieracium murorum aggr.						0.229
Acer pseudoplatanus						0.120
Maianthemum bifolium						0.058
Atrichum undulatum aggr.						0.051
Athyrium filix-femina						0.050
Carex flacca						0.026
Rubus idaeus						0.024
Solidago virgaurea aggr.					0.057	0.150
Carex pilulifera					0.079	
Campanula rotundifolia					0.072	0.017
Huperzia selago					0.068	
Homogyne alpina					0.062	
Lycopodium clavatum					0.045	
Carex limosa			0.477			
Trichophorum alpinum			0.290			
Equisetum fluviatile			0.232			
Menyanthes trifoliata			0.223			
Lycopodiella inundata			0.222			
Scheuchzeria palustris			0.222			
Eriophorum angustifolium			0.118	0.096		
Viola palustris				0.624		
Carex echinata				0.361		
Juncus filiformis				0.319		
Carex canescens				0.314		
Carex nigra				0.201		
Straminergon stramineum				0.138		
Nardus stricta				0.131		
Luzula sudetica				0.095		
Carex flava aggr.				0.067		

Table A2. Abundance trends in the individual area types (GC and GCR) and the entire site for species occurring in at least 10 plots. Species that were not precisely identified ("sp." or "cf.") were not considered. Results of separate regression models for the GC-area and GCR-area, as well as results from the combined model, are shown. Numbers are the effect sizes of the orthogonal polynomials of time and their interaction with area type. GC = grazing cessation; GCR = grazing cessation and rewetting; n = number of plots in which the species was observed at least once; l = linear term; q = quadratic term; l:a = interaction linear term between time and area type; q:a = interaction quadratic term between time and area type. Significance levels: +: $p \leq 0.1$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

| | GC-area | | | GCR-area | | | Entire site | | | | |
| | | Time | | | Time | | | Time | | Interaction | |
	n	l	q	n	l	q	n	l	q	l:a	q:a
Vascular plants											
Andromeda polifolia	33	0.74	1.53*	40	0.73	1.36	73	1.22	2.54*	-0.57	-1.32
Anthoxanthum odoratum	30	-3.15*	1.74**	0							
Arnica montana	20	-0.43	0.39	5	0.21	1.62*	25	-2.55+	2.37+	2.62+	-1.85
Betula pubescens	19	1.59**	-0.15	27	2.83***	1.43+	46	3.03*	0.25	0.30	1.92
Calluna vulgaris	43	-1.45	3.17***	45	-0.49	2.01**	88	-1.38	3.03***	0.53	0.45
Carex canescens	28	-3.51***	0.50	10	1.21	-0.38	38	-5.94**	0.85	6.82**	-1.13
Carex echinata	46	-4.86***	4.58***	31	-0.65	0.87	77	-8.14***	7.67***	7.77***	-7.18***
Carex flacca	11	-1.09	1.94**	0							
Carex flava aggr.	19	-3.10*	2.99***	3	0.13	-1.06	22	-5.44***	5.24***	5.49***	-5.63***
Carex limosa	14	-0.01	-0.88	7	0.06*	-0.01	21	-0.01	-1.02	0.12	1.01
Carex nigra	50	-4.34***	2.17**	30	-2.06*	1.27	80	-7.18***	3.58*	6.07***	-2.90*
Carex pallescens	17	-2.35*	1.03	7	-2.90**	0.24	24	-5.12**	1.70	4.35*	-1.64
Carex panicea	13	0.35	2.14**	0							
Carex pauciflora	43	-2.84***	1.40+	43	-2.22**	1.20	86	-3.65**	1.80	0.18	0.07
Carex rostrata	49	-2.20**	0.16	39	-0.10	0.62	88	-2.92**	0.21	3.13*	1.03
Dactylorhiza maculata	22	1.56+	0.53	4	1.86*	0.18	26	2.73	0.92	-2.32	-0.88
Eriophorum angustifolium	38	-5.76***	4.57***	19	-2.71+	1.42*	57	-9.34***	7.42***	7.10**	-6.25***
Eriophorum vaginatum	49	-2.36*	2.05*	45	1.01	0.60	94	-2.54*	2.20*	4.29*	-1.17
Festuca rubra aggr.	14	-1.26	-1.65*	1							
Homogyne alpina	33	-2.57+	2.03**	10	0.48	0.46	43	-4.46**	3.53*	4.57**	-3.43*
Huperzia selago	12	-1.45	1.24	20	-4.34**	2.12***	32	-0.69	0.59	-8.46***	3.89**
Juncus articulatus	12	-2.08+	0.75	2	-0.64	-1.15	14	-4.80**	2.66	4.49**	-3.22+

| | GC-area | | | GCR-area | | | Entire site | | | | |
| | Time | | | Time | | | Time | | | Interaction | |
	n	l	q	n	l	q	n	l	q	l:a	q:a
Juncus filiformis	29	-6.06***	2.45***	7	-1.55	1.16*	36	-10.34***	4.18***	9.29**	-3.40***
Luzula multiflora	12	-3.37*	2.80***	1	0.41	-0.61	13	-6.03***	5.01**	6.13***	-5.17**
Menyanthes trifoliata	23	-2.85*	1.54*	1	-1.82+	1.21	24	-4.97**	2.69	4.44*	-2.33
Molinia caerulea	51	-1.11	2.66***	45	-0.04	3.23***	96	-1.53	3.67***	1.47	0.83
Nardus stricta	29	-6.86***	4.11***	20	-5.91***	3.33***	49	-11.98***	7.18***	9.40***	-5.72***
Picea abies	50	2.17**	0.22	45	0.54	2.58***	95	3.15***	0.32	-2.44+	3.11**
Prunella vulgaris	11	-2.20	2.50**	0							
Scheuchzeria palustris	14	-2.96***	1.13	6	0.06	-1.02	20	-4.98***	1.91	5.02***	-2.64+
Sorbus aucuparia	40	0.86	-0.63	15	1.10	-0.34	55	3.95***	-1.99+	-2.56+	1.56
Succisa pratensis	20	-0.81	2.00**	4	-1.55*	-0.24	24	-1.43	3.55*	1.10	-3.60*
Trichophorum cespitosum	47	-2.31**	1.51*	45	-1.24+	3.03***	92	-3.21**	2.11*	1.48	2.13
Vaccinium myrtillus	48	2.35**	1.08+	40	-0.29	0.87+	88	3.18***	1.45+	-3.62**	-0.16
Vaccinium oxycoccos	15	-1.14	2.27**	21	1.70+	0.68	36	-1.80	3.60**	3.65*	-2.85+
Vaccinium uliginosum aggr.	35	1.51+	1.65*	38	0.08	1.16*	73	1.35*	1.47*	-0.80	1.53
Veratrum album aggr.	16	1.53+	-0.23	1	0.41	-0.61	17	2.76**	-0.41	-2.73+	0.38
Viola palustris	23	-3.56**	1.48*	1	0.37	-0.67	24	-6.36***	2.64+	6.39***	-2.70+
Bryophytes											
Aulacomnium palustre	38	-3.02*	1.71*	11	2.22*	1.64+	49	-5.18***	2.92+	6.25***	-2.13
Hylocomium splendens	32	1.45+	-0.08	7	0.26	-0.29	39	2.19+	-0.19	-2.70*	-0.19
Pleurozium schreberi	42	1.63	1.65*	31	2.44**	-0.09	73	2.26*	2.28*	1.25	-2.42
Polytrichum commune	41	-1.89*	1.17*	18	0.57	-0.60	59	-3.37**	2.05+	3.78**	-2.48*
Polytrichum formosum	22	-2.38+	0.54	23	-5.75***	2.62**	45	-3.81*	0.87	-2.22	1.89
Sphagnum capillifolium aggr.	44	2.14**	0.18	45	3.13***	1.42+	89	2.47**	0.21	2.48+	2.04
Sphagnum compactum	44	0.20	0.47	40	0.34	-0.62	84	-0.99	2.65**	1.53	-3.65**
Sphagnum magellanicum	50	1.43*	0.28	45	1.42*	1.49*	95	1.93*	0.38	0.16	1.81
Sphagnum recurvum aggr.	40	0.57	-1.58*	25	-0.87	2.31**	65	0.92	-2.56*	-1.49	4.07**
Sphagnum russowii	36	-1.33	1.18+	26	1.44	-1.45	62	-1.78	2.09	3.04+	-3.36*
Sphagnum subsecundum	31	-0.78	0.39	19	1.12	1.36	50	-2.85*	1.87	3.37*	-1.25