Thirty years later: How successful was the restoration of a raised bog in the Swiss Plateau?

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SUMMARY

Raised bogs as huge carbon stocks are of worldwide importance, but they have been severely decreased and degraded globally. To stop this development, restoration measures are being carried out in many countries. The recovery of raised bogs is, however, slow and the success of restoration projects is uncertain. Long-term monitoring is thus needed. The Hagenmoos raised bog in the Swiss Plateau was restored by logging within former peat-cutting pits and by blocking drainage pathways. The vegetation in the bog was recorded 3 times within 72 permanent plots: immediately before, 10 years after and 30 years after restoration. Based on these vegetation surveys, changes in habitat conditions (ecological indicator values) and in species richness and single species were analysed. Overall, the restoration measures proved to be successful. Mean indicator values for light and moisture both increased over time. The increase of these indicators was strongest during the first 10 years after restoration and weakened afterwards. Within former peat-cutting pits, both indicator values reached values from a reference dataset composed of 21 plots from Swiss raised bogs representing typical bog communities. However, 30 years after restoration, mean light and moisture indicator values were still significantly lower outside former peat-cutting pits than within them, indicating a need for further restoration measures.

KEY WORDS: bryophyte, conservation, ecological indicator value, long-term monitoring, vegetation

INTRODUCTION

Raised bogs are characterised by constantly high water tables. As they are mostly disconnected from groundwater, precipitation needs to exceed evapotranspiration. Raised bogs are nutrient-poor and acidic ecosystems, and only specialist plant species can thrive in intact raised bogs (Vitt 2006). Although raised-bogs are generally species-poor ecosystems (Rydin & Jeglum 2013), they are habitat for many rare and protected plant species. Furthermore, many of these species are almost exclusively found in raised bogs or transitional bogs – development stages between fen and raised bog – and are therefore strongly bound to these habitat types (Küchler 2018). Raised bogs belong to the largest long-term carbon stores of the world and are thus of great importance for climate regulation (Joosten *et al.* 2016).

Peatlands, areas with a peat layer, have experienced a severe decrease and degradation globally. With 44 % of its peatlands affected, Europe has the largest decrease in peatland area of all continents. In parts of Europe, the decrease of peatland area is even larger (Joosten 2016). Causes for the decrease and degradation of peatlands are mainly drainage, peat extraction, infrastructure development and urbanisation (Joosten *et al.* 2016). To prevent further decrease of peatlands, restoration measures are being carried out in many countries (Andersen *et al.* 2017). However, the long-term effectiveness of restoration measures is not well studied.

Ecological restoration measures have the aim of “returning an ecosystem to a close approximation of its condition prior to disturbance” (National Research Council 1992). The goals of restoration projects can be diverse, but they generally involve returning an ecosystem to a more natural and self-sustaining stage that enables the growth and reproduction of species typical for the ecosystem (Laine *et al.* 2006). In the case of raised bogs, a main motivation for restoration measures is to restore ecosystem services such as carbon storage (Bonn *et al.* 2016). As many raised bogs suffer from desiccation due to drainage systems, restoration measures often focus on restoring bog hydrology by raising the water table (Andersen *et al.* 2017). However, the success of restoration is not guaranteed, and conservation measures should therefore be accompanied by monitoring to enable evidence-based adaptive management in the case of any negative developments (Wheeler & Shaw 1995).

Short-term (< 5 years) and mid-term (< 15 years) effects of restoration measures on water table depth and on vegetation in bogs have been studied extensively (e.g. Andersen *et al.* 2010, Haapalehto *et al.* 2014, Gaffney *et al.* 2018, Bedolla *et al.* 2019). Many of these studies showed that a rise in the water table leads to a positive development towards typical bog vegetation. However, some studies indicated that full recovery was not yet observed during the monitoring period (Seabloom & van der Valk 2003, Howie *et al.* 2009, Haapalehto *et al.* 2011, Lundin *et al.* 2017). Unfortunately, only few studies have been conducted to assess the long-term (> 15 years) impacts of restoration measures on water chemistry (Poschlod *et al.* 2007, Gaffney *et al.* 2018), on plant traits (Konings *et al.* 2019) or on vegetation (Poschlod *et al.* 2007).

Although monitoring is a well-established part of many restoration projects, there are thus hardly any long-term monitoring projects which assess the effects of the restoration measures taken. Furthermore, many monitoring projects lack clear goals or appropriate reference sites, which are necessary to assess the effects of restoration (Andersen *et al.* 2017). As bog recovery is slow (Seabloom & van der Valk 2003, Haapalehto *et al.* 2011), long-term monitoring conducted over decades and with clear goals is needed to assess the performance and the success of restoration measures.

In Switzerland, the area of bogs and fens has decreased by approximately 90 % since 1850 (Stuber & Bürgi 2018). Since the legal protection of bogs and fens in Switzerland in 1987, their decrease in area has almost stopped (Klaus 2007). Nevertheless, the condition of many Swiss bogs is far from optimal, and their quality is still decreasing as a result of intact drainage systems, which lower the water table (Bergamini *et al.* 2019). In this study, we present the long-term effects of restoration measures in a formerly drained bog in the Swiss Plateau. We studied changes in vegetation and site conditions 30 years after restoration measures were implemented. The studied bog had been monitored before, namely 10 years and 30 years after restoration, and is therefore appropriate to study the long-term development of a raised bog after restoration. We asked the following questions:

(1) How does restoration affect site conditions, as expressed by ecological indicator values and life strategies of the vegetation, and are there differences between areas within former peat-cutting pits and areas outside those pits?

(2) What are the impacts of restoration measures on the species richness of vascular plants and bryophytes and on individual species?

(3) Is the development of the vegetation during the first 10 years after restoration (1989–1999) different from its development 10 to 30 years after restoration (1999–2020)?

METHODS

Study site

The raised bog Hagenmoos is situated at a mean elevation of 600 m a.s.l. in the Swiss Plateau in the canton of Zurich (47° 14' 07" N, 9° 31' 18" E). Today the bog covers an area of 3.75 ha (BAFU 2017). From 1981 to 2010, the annual precipitation in the area was 1,100–1,300 mm and the mean monthly temperature ranged from 18 to 21 °C in July and from 0 to 3 °C in January (MeteoSchweiz 2020). Manual peat extraction and drainage of the Hagenmoos bog started in the 18th century and continued into the Second World War (Lüönd & Göttlich 1982). The peat extraction created two peat-cutting pits: a small pit of 70 × 100 m in the south-east and a large pit of 100 × 200 m in the south-west of the Hagenmoos bog (Figures 1 and 2; Geissbühler 2000). Today, the surface of the two peat pits is approximately 1.2 m below the adjacent bog surface (digital terrain model with 0.5 m resolution; www.swisstopo.admin.ch/en/geodata/height/alti3d.html; Figure A1 in the Appendix). After peat extraction stopped, the area was abandoned for several decades and especially the larger of the two pits became encroached with woody plants, which further increased evapotranspiration and enhanced drying of the bog. Moreover, the intact bog surface became drier because of drainage systems and the elevation difference to the peat pits (Lüönd & Göttlich 1982). To stop this development, restoration measures were taken: between 1987 and 1988, trees and shrubs within the large pit were cut. The aim of this measure was to reduce evapotranspiration and enhance the growth of light-demanding plants. In 1991, drainage pathways were blocked. The aim of this measure was to raise the water table and thus to promote the establishment of typical bog vegetation (Geissbühler 2000).

Vegetation

The effects of the restoration measures were monitored in permanent plots (1 × 1 m), which were established at the intersections of a 25 × 25 m raster within the bog and a 50 × 50 m raster in the surrounding forest (Geissbühler 2000). The vegetation

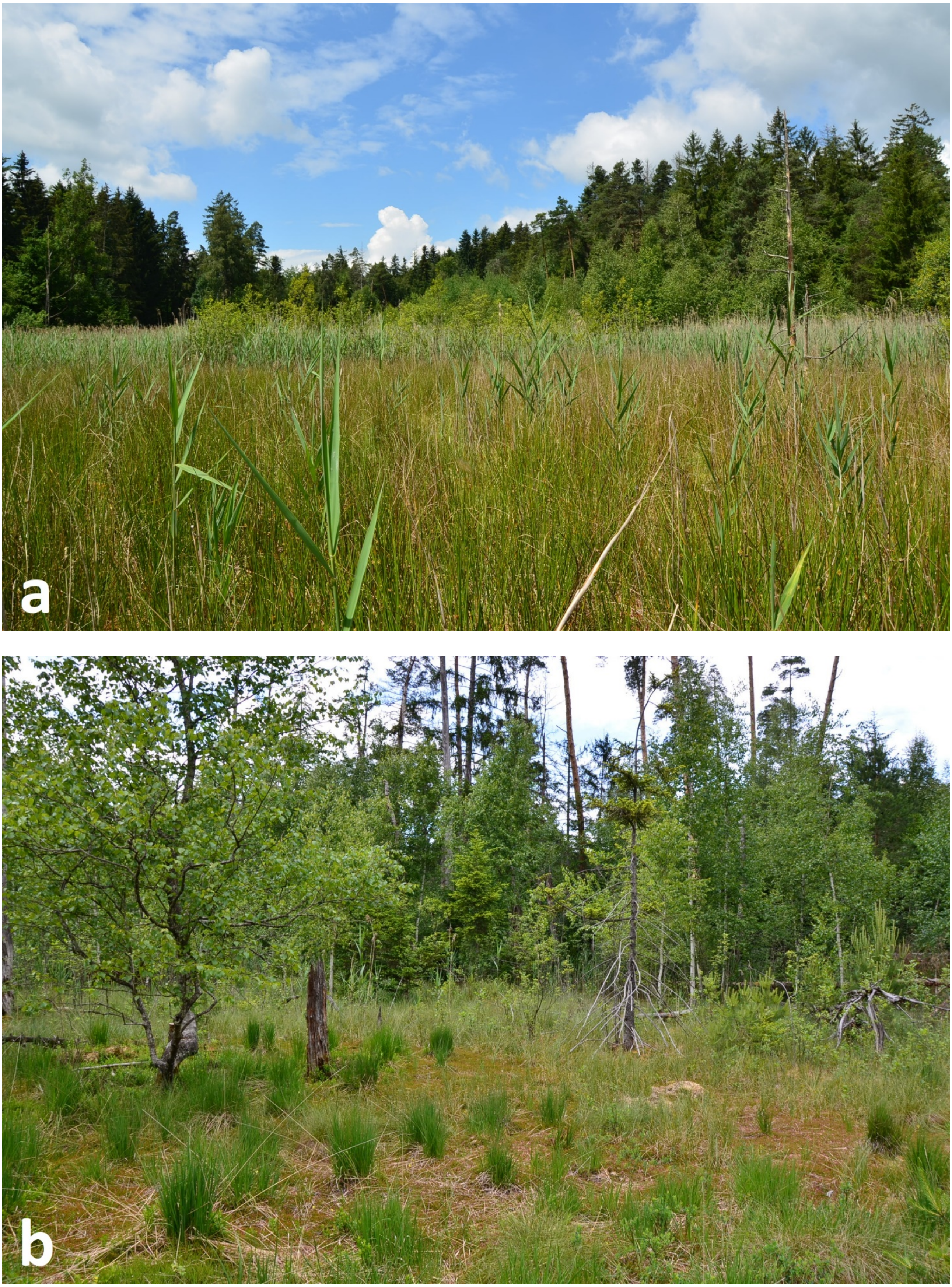

Figure 1. Impressions of the Hagenmoos raised bog, a bog of national importance, in 2020: (a) area within the large peat pit, (b) area outside the peat pits (photos: S. Frei).

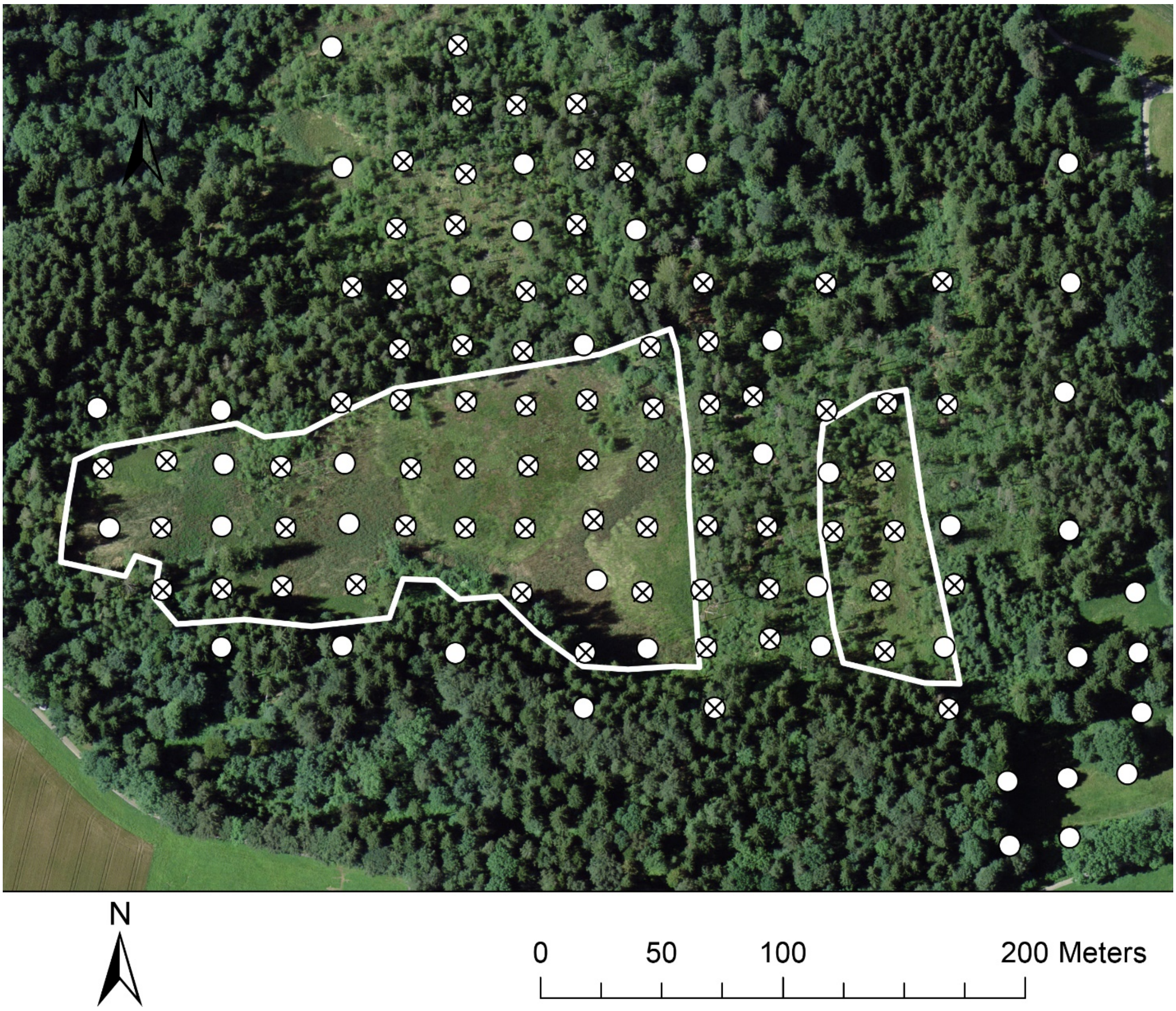

Figure 2. Location of all 113 plots in the Hagenmoos raised bog (white dots) and the 72 plots re-surveyed in 2020 (black crosses), as well as outline of the two peat-cutting pits (white lines).

within all 113 plots (Figure 2) was surveyed in 1989, before drainage pathways were blocked, and in 1999, 10 years after restoration. In 2020, 30 years after restoration, a selection of these plots was re-surveyed. For the re-survey, we did not consider 4 plots in the south and 13 plots in the east of the bog as these plots were in spruce forests or fens that were not in the area potentially affected by the restoration measures. The selection of the plots was based on a cluster analysis conducted in R version 4.0.2 (R Core Team 2020) by means of the function 'agnes' in the *cluster* package (Mächler *et al*. 2019), using the Ward method with Euclidean distances. The plots were clustered according to their plant species composition in 1999 (abundances considered). In the cluster dendrogram 4 distinct clusters were distinguished, and 60 plots were randomly selected proportional to cluster size. An additional 12 plots were selected randomly within the two pits to increase the number of plots there, leading to a total of 72 plots surveyed in 2020 (34 plots within the two peat-pits and 38 plots outside the two peat-pits; Figure 2).

All vegetation surveys were conducted between June and August. In the three surveys, all vascular plant species and bryophyte species were recorded and the cover of each species was estimated. In 2020, species cover was estimated according to a modified dominance scale following Braun-Blanquet (1964). In 1989 and 1999 a different scale was used. Thus, all cover estimates were transformed to presence/absence data prior to statistical analyses. Nomenclature followed Lauber *et al*. (2018) for vascular plants and Meier *et al*. (2013) for bryophytes.

Ecological indicator values and reference data

To interpret vegetation changes in terms of site conditions, we calculated unweighted mean ecological indicator values according to Landolt *et al.* (2010) for humus, light, moisture, nutrients, soil pH, temperature and stress tolerance. Indicator values of Landolt *et al.* (2010) are very similar to the well-known Ellenberg indicator values where each species is assigned a value between one and nine for each indicator (Ellenberg 1992). The values of Landolt *et al.* (2010) range from one to five (except stress tolerance, see below) with higher values indicating higher values of the environmental factor. For the calculations of mean indicator values per plot, species not identified with certainty were excluded. Stress tolerance as given by Landolt *et al.* (2010) and based on Grime (1979, 2001) and Frank & Klotz (1990), was translated into numeric values ranging from 0 to 3, reflecting the number of the corresponding letters in the strategy code given by Landolt *et al.* (2010). For example, a species with the code 'sss', indicating high stress tolerance, received a stress-tolerance value of 3, whereas a species with the code 'crs' was assigned a value of 1. The numeric values were used similarly to ecological indicator values. For each plot, mean indicator and stress-tolerance values were calculated based on presence/absence data. While both vascular plants and bryophytes were considered for calculating mean indicator values, mean stress-tolerance values were only calculated for vascular plants. No stress-tolerance values are assigned to bryophytes in Landolt *et al.* (2010).

Additionally, for each indicator value and the stress-tolerance value, a reference value was calculated to compare the values in the Hagenmoos bog to the values of typical bog vegetation, which is the target vegetation for the restored Hagenmoos bog. We calculated the reference values using a dataset of 21 selected vegetation relevés, which were conducted in typical open raised bogs, raised bog mountain pine forests and transitional forms between these two habitat types. The area of these relevés was 10 m^2. All 21 relevés were conducted in Switzerland between 2011 and 2017 and are part of a larger monitoring project on fens and bogs (Bergamini *et al.* 2019). The 21 selected relevés were randomly chosen out of those relevés with the highest floristic similarity to the corresponding habitats defined in Delarze *et al.* (2015).

Species richness

We determined the total number of vascular plant species and the total number of bryophyte species per plot. For this, species not identified with certainty were included as they contributed to the number of species on the plot level. Furthermore, we separately identified the number of vascular and bryophytes species typical for bogs. As bog specialist species, we considered the plant species listed as character species of raised bogs by Feldmeyer-Christe & Küchler (2018; for details see Table A1). In the following, the total number of species (vascular plant and/or bryophyte species) per plot is referred to as species richness.

Single species

For a more detailed insight into vegetation changes, we analysed trends of selected species, namely *Phragmites australis*, *Sphagnum magellanicum* aggr., *Sphagnum palustre*, *Sphagnum recurvum* aggr. and *Vaccinium oxycoccos*. *Phragmites australis* often increases in frequency as a result of inundation caused by restoration measures in bogs (Wheeler & Shaw 1995) and is of concern if it becomes abundant (Güsewell & Edwards 1999). *Sphagnum magellanicum* aggr. and *Vaccinium oxycoccos* are typical bog species (Feldmeyer-Christe & Küchler 2018), and an increase in their abundance after bog restoration is considered a successful outcome. We also included *Sphagnum palustre*, as it is known to be one of the first peat mosses to establish in fens and thus promotes the transition to raised bogs (Sliva 1997). Trends of *Sphagnum recurvum* aggr. are of particular interest, as species in this group are known to be effective in bog restoration processes (Grosvernier *et al.* 1997) but are slowly outcompeted by, e.g., *Sphagnum magellanicum* aggr. when the site develops towards typical bog vegetation. In the survey in 2020 all *S. recurvum* aggr. specimens belonged to *S. angustifolium.* However, in the older surveys *S. recurvum* aggr. was not identified to the species level and herbarium specimens from the older surveys were not available. We therefore treated *S. angustifolium* samples as *S. recurvum* aggr. when analysing trends, but as *S. angustifolium* when only recent data were analysed.

Statistical analyses

All statistical analyses were performed in R. We applied separate linear mixed-effects models to test the effects of year (1989, 1999, 2020) on mean indicator values. To analyse the effects of year on different types of species richness, we built generalised linear mixed-effects models with a Poisson distribution. We analysed trends of single species with generalised linear mixed-effects models with a binomial distribution, as species data were available as presence/absence data only. All linear and generalised linear mixed-effects models were implemented with the package *lmerTest* (Kuznetsova *et al*. 2017).

To identify non-linear developments, year was included as a linear and a quadratic term in all models. Furthermore, the linear and quadratic terms were first scaled by subtracting their means and dividing them by their standard deviation. If the quadratic term was not statistically significant (i.e. $p > 0.05$), it was removed from the model. Plot identity was included as a random effect to take plot-specific differences into account. As we expected that plots within the two peat pits would show different trends after restoration than plots outside the peat pits, all statistical analyses were performed for three different subsets of plots: all plots (A), plots within the two pits (within, W) and plots outside the two pits (outside, O). Differences amongst these groups in 2020 were tested with two-sided t-tests.

RESULTS

Ecological indicator values

When considering all 72 plots, all mean indicator values and stress-tolerance values showed significant changes over time (Table 1, Figures 3 and 4). Mean indicator values for nutrients, pH and temperature increased over the whole 30-year period, while light and moisture increased during the first 10 years, between 1989 and 1999, and showed hardly any changes afterwards. Mean indicator values for humus decreased across the whole period. Mean values for stress tolerance increased during the first 10-year period and decreased during the second (20-year) period. Within the pits, trends of mean indicator values were very similar to trends of mean indicator values in all plots. Outside the pits, there was a linear increase for moisture, pH and temperature indicator

Table 1. Estimates of slopes and associated p-values of the predictor variables Year and Year^2 from linear mixed-effects models with mean indicator values per plot as the dependent variable. The estimates refer to scaled predictors. The quadratic predictor was excluded from models when it was not statistically significant (i.e. $p > 0.05$). Models were built for all plots (A), for plots within the pits (W) and for plots outside the pits (O). p-values ≤ 0.05 are highlighted in bold.

Indicator value	Stratum	Number of plots per year	Predictors: Year		Predictors: Year^2	
			Slope	p-value	Slope	p-value
Humus	A	72	-0.051	**0.020**	-	-
	W	34	-0.119	**0.001**	-	-
	O	38	0.010	0.695	-	-
Light	A	72	0.122	**<0.001**	-0.118	**<0.001**
	W	34	0.112	**<0.001**	-0.133	**0.001**
	O	38	0.131	**<0.001**	-0.103	**0.005**
Moisture	A	72	0.123	**<0.001**	-0.101	**<0.001**
	W	34	0.197	**<0.001**	-0.163	**0.001**
	O	38	0.039	**0.008**	-	-
Nutrients	A	72	0.082	**0.001**	-	-
	W	34	0.154	**<0.001**	-	-
	O	38	0.018	0.460	-	-
pH	A	70	0.070	**<0.001**	-	-
	W	33	0.043	0.083	-	-
	O	37	0.094	**<0.001**	-	-
Temperature	A	72	0.042	**<0.001**	-	-
	W	34	0.066	**<0.001**	-	-
	O	38	0.020	**0.014**	-	-
Stress tolerance	A	65	0.026	0.365	-0.140	**0.001**
	W	33	0.077	**0.019**	-0.196	**<0.001**
	O	32	-0.060	0.127	-	-

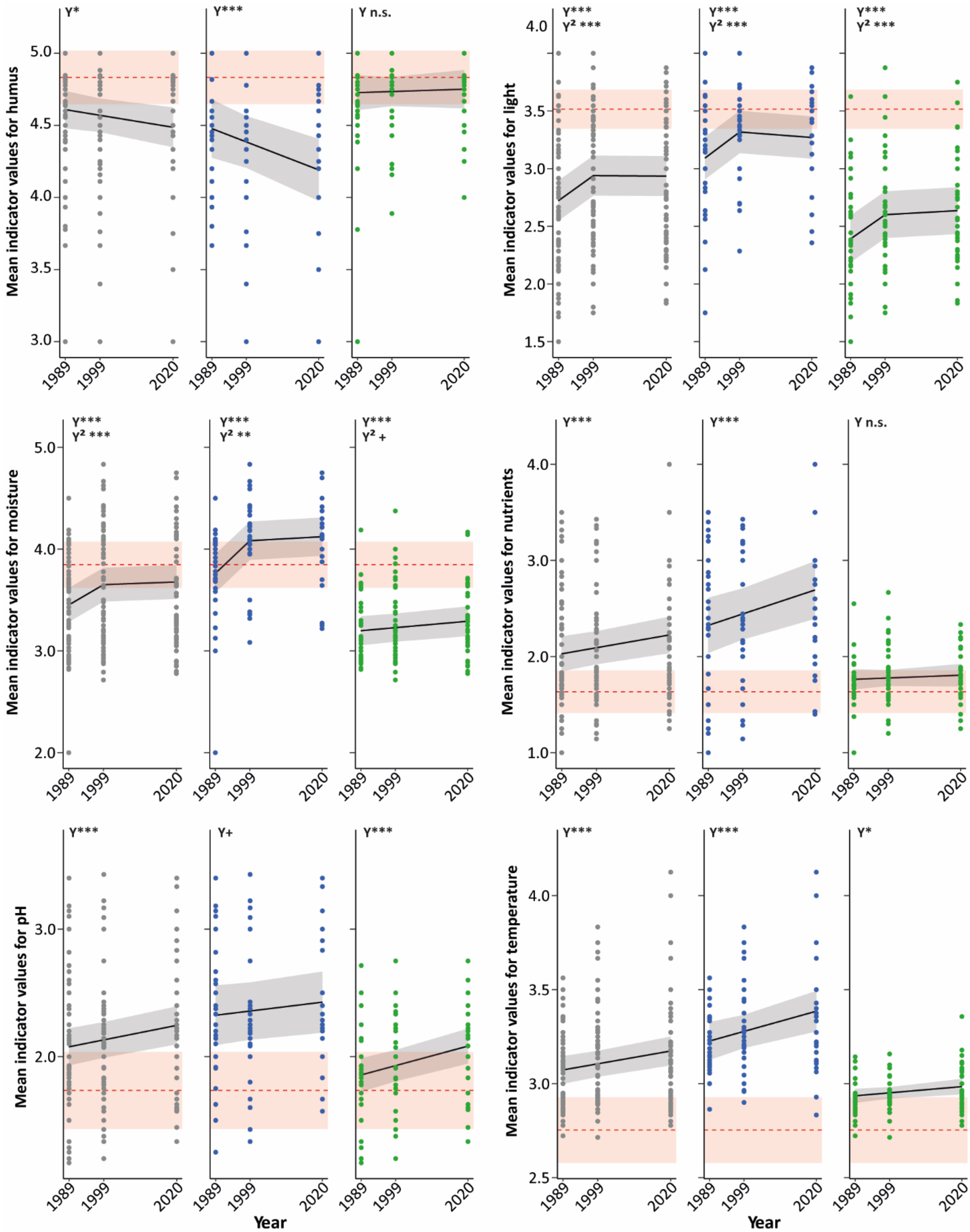

Figure 3. Temporal trends of indicator values for humus, light, moisture, nutrients, pH and temperature. Each dot represents the mean indicator value of one plot. For each indicator value, the three subfigures show all plots (grey; n = 72; pH: n = 70), plots within the pits (blue; n = 34; pH: n = 33) and plots outside the pits (green; n = 38; pH: n= 37). Black lines are regression lines based on linear mixed-effects models and grey areas show 99 % confidence intervals around regression lines. Red lines represent reference values derived from the reference dataset and red areas show ± 1 standard deviations of the reference values. Y: year; Y^2: year to the power of 2; n.s.: $p > 0.1$; +: $p \leq 0.1$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

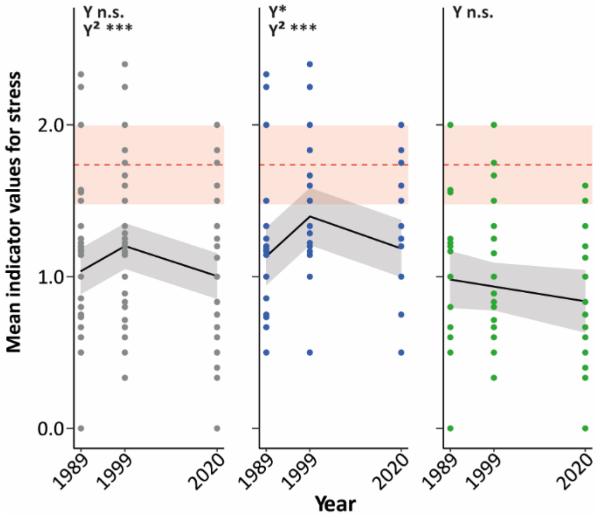

Figure 4. Temporal trends of stress-tolerance values. Each dot represents the mean stress-tolerance value of one plot. The three subfigures show all plots (grey; n = 65), plots within the pits (blue; n = 33) and plots outside the pits (green; n = 32). Black lines are regression lines based on linear mixed-effects models and grey areas show 99 % confidence intervals around regression lines. Red lines represent reference values derived from the reference dataset and red areas show ± 1 standard deviations of the reference values. Y: year; Y^2: year to the power of 2; n.s.: $p > 0.1$; +: $p \leq 0.1$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

values, while light indicator values mainly increased during the first 10-year period. The other indicator values did not show any significant changes outside the pits over time.

For all indicator values means in 2020 were significantly different within and outside the pits. The mean humus indicator value was lower within than outside the pits. All other indicator values were higher within than outside the pits (Table 2).

Light and moisture indicator values became increasingly similar to the reference values within and outside the pits over time. In 2020, both indicators were closer to the reference values within than outside the pits. Furthermore, within the pits the reference value was within the confidence interval of the regression line of mean moisture indicator values, i.e., the reference value and the mean were not different from each other. Within the pits, indicator values for humus and nutrients showed trends of moving away from the reference values over time, while pH indicator values remained relative stable at values slightly higher than the reference value. Outside the pits, pH indicator values showed a clear trend of moving away from the reference value over time. Temperature indicator values moved away from the reference values over time, both within and outside the pits. In 2020, humus, nutrient, pH and temperature indicator values were closer to the reference values outside the pits than within the pits.

Table 2. Mean indicator values and mean species richness in 2020 for different groups in plots within and plots outside the pits. P-values are according to two-sided t-tests, with p-values ≤ 0.05 highlighted in bold.

	Mean within the pits	Mean outside the pits	p-value
Indicator value			
Humus	4.2	4.8	**<0.001**
Light	3.3	2.6	**<0.001**
Moisture	4.1	3.3	**<0.001**
Nutrients	2.7	1.8	**<0.001**
pH	2.5	2.1	**0.001**
Temperature	3.4	3.0	**<0.001**
Stress tolerance	1.2	0.8	**<0.001**
Species richness			
Vascular plants	3.5	3.7	0.746
Bryophytes	2.9	6.2	**<0.001**
Vascular plant bog specialists	0.2	0.1	0.431
Bryophyte bog specialists	0.8	1.1	0.281

Outside the pits, the reference values for humus, nutrient and pH were included in the confidence interval of the regression lines (Figure 3). Stress-tolerance values within the pits became more similar to the reference value during the first period but showed trends away from the reference later on. Mean stress-tolerance values in 2020 were lower than the values from the reference dataset within and outside the pits (Table 2, Figure 4).

Species richness

Full species lists are given in Tables A2 and A3 in the Appendix. Vascular plant species richness decreased continuously across the whole bog, whereas bryophyte species richness increased after the restoration measures in 1989 but decreased after 1999 (Table 3, Figure 5). Similar trends were found outside the pits, although vascular plant richness showed no significant change. Bryophyte richness outside the pits was almost the same in 2020 as in 1989. Within the pits, vascular plant richness and bryophyte richness decreased continuously (Table 3, Figure 5). In 2020, mean bryophyte richness was significantly lower within than outside the pits. Mean vascular plant richness showed no differences between within and outside the pits (Table 2). Bog specialist richness of vascular plants and of bryophytes showed no significant changes over time (Table 3, Figure 5). The mean proportion of bog specialist vascular plant and bryophyte species in 2020 was 0.07 and 0.27, respectively, within the pits and 0.04 and 0.18, respectively, outside the pits.

Selected species

Phragmites australis and *Sphagnum magellanicum* aggr. showed an increase when considering all plots. *Sphagnum palustre* only increased outside the pits, whereas *S. recurvum* aggr. increased when considering all plots and those outside the pits. *Vaccinium oxycoccos* decreased over time when considering all plots (Table 4).

In 2020, *P. australis* had a high mean cover within the pits (10.6 %), which was significantly higher than its cover outside the pits (0.6 %). When considering all plots, the mean cover was 10.7 % for *Sphagnum magellanicum* aggr. 6.6 % for *S. palustre* and 11.9 % for *S. angustifolium*. The mean cover of *S. angustifolium* was significantly lower within than outside the pits. *Sphagnum magellanicum* aggr. and *S. palustre* also tended to have higher covers within the pits, but differences between within and outside the pits were not significant. *Vaccinium oxycoccos* had a very low mean cover (1.4 %) across all plots, as well as within and outside the pits (Table 5).

Table 3. Estimates of slopes and associated p-values of the predictor variables Year and Year^2 from generalised linear mixed-effects models with different types of species richness per plot as the dependent variable. The estimates refer to scaled predictors. The quadratic predictor was excluded from models when it was not statistically significant (i.e. $p > 0.05$). Models were built for all plots (A; n = 72), for plots within the pits (W; n= 34) and for plots outside the pits (O; n = 38). p-values ≤ 0.05 are highlighted in bold.

Species richness	Stratum	Predictors			
		Year		Year^2	
		Slope	p-value	Slope	p-value
Vascular plants	A	-0.109	**0.001**	-	-
	W	-0.196	**<0.001**	-	-
	O	-0.019	0.689	-	-
Bryophytes	A	-0.019	0.600	-0.135	**0.006**
	W	-0.144	**0.007**	-	-
	O	0.035	0.430	-0.180	**0.003**
Vascular plant bog specialists	A	-0.258	0.067	-	-
	W	-0.240	0.174	-	-
	O	-0.289	0.217	-	-
Bryophyte bog specialists	A	-0.053	0.421	-	-
	W	-0.122	0.225	-	-
	O	0.001	0.991	-	-

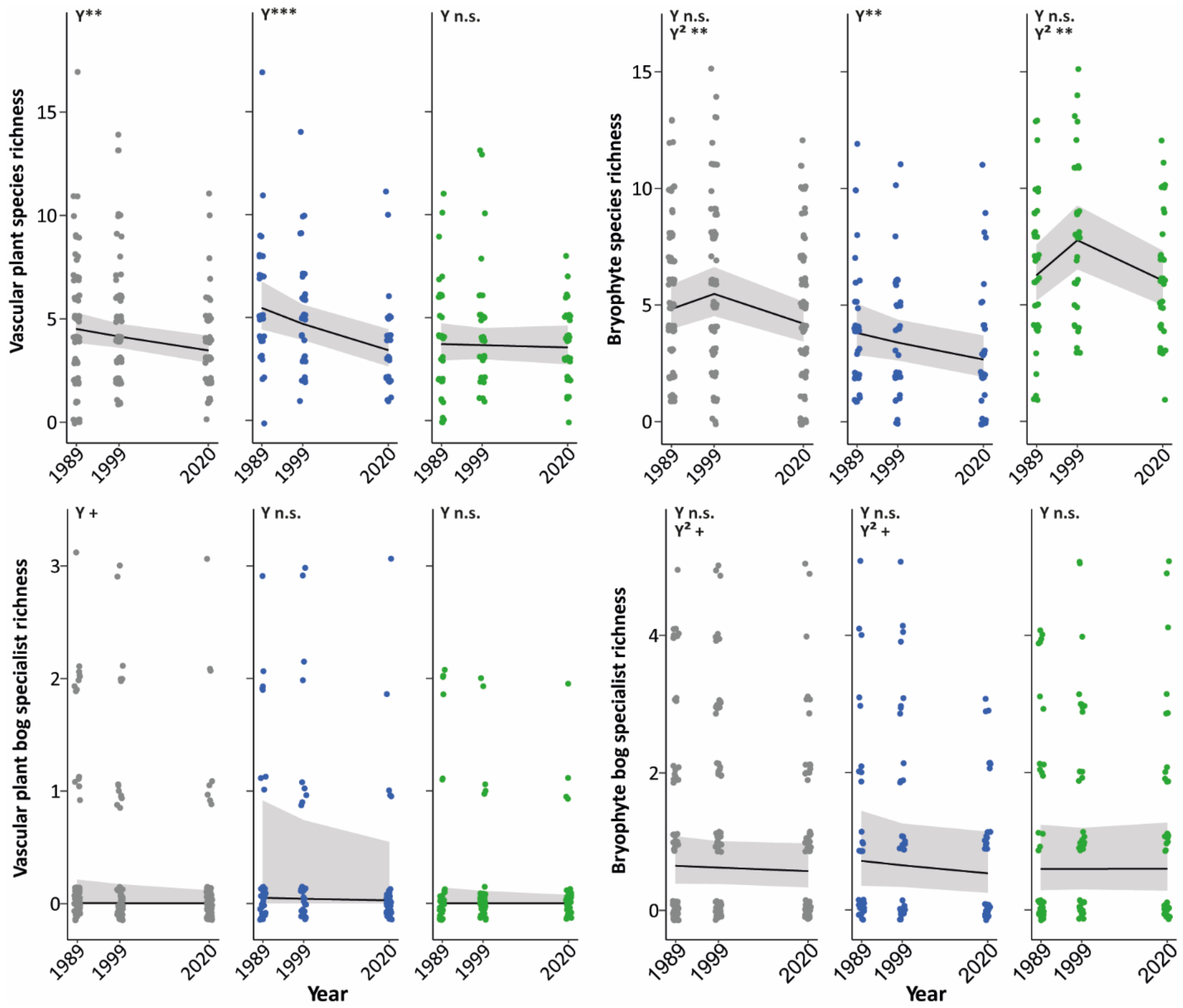

Figure 5. Temporal trends of vascular plant richness, bryophyte richness, richness of vascular plant bog specialists, and richness of bryophyte bog specialists. Each dot represents the value of one plot. Dots have been jittered for clarity. For each type of species richness, the three subfigures show all plots (grey; n = 72), plots within the pits (blue; n = 34) and plots outside the pits (green; n = 38). Black lines are regression lines based on generalised linear mixed-effects models and grey areas show 99 % confidence intervals around regression lines. Y: year; Y^2: year to the power of 2; n.s.: $p > 0.1$; +: $p \leq 0.1$; *: $p \leq 0.05$; **: $p \leq 0.01$; ***: $p \leq 0.001$.

DISCUSSION

Although the restoration of bogs is a well-established conservation tool (Andersen *et al.* 2017) there is not much long-term data on the outcome of restoration measures. Here we had the opportunity to revisit vegetation plots established in 1989 just before hydrological restoration measures were implemented in a bog. Our findings regarding a range of indicators suggest that the restoration measures improved the condition of the bog. At the same time, our results demonstrate that the bog still has not reached the conservation target, i.e. typical raised bog vegetation, 30 years after the restoration effort.

Changes in site conditions

As we expected, the mean indicator values for light and moisture increased over time after restoration. In 2020, mean light and moisture indicator values within the pits showed values similar to the reference dataset we compiled, and which consisted of a set of plots from typical open raised bogs, raised bog mountain pine forests and transitional forms between these two habitat types. Moreover, mean light and moisture indicator values within the pits were significantly higher than outside the pits. This indicates that the bog outside the pits was not in the desired condition regarding conservation targets, even 30 years after restoration. Its vegetation indicated that the conditions

Table 4. Estimates of slopes and associated p-values of the predictor variables Year and Year^2 from generalised linear mixed-effects models with single species typical of raised bogs as the dependent variable. The estimates refer to scaled predictors. The quadratic predictor was excluded from models when it was not statistically significant (i.e. $p > 0.05$). Models were built for all plots (A; n = 72), for plots within the pits (W; n = 34) and for plots outside the pits (O; n = 38). p-values ≤ 0.05 are highlighted in bold. NA: model could not be calculated because there were too few observations.

Species	Stratum	Predictors			
		Year		Year^2	
		Slope	p-value	Slope	p-value
Phragmites australis	A	1.002	**0.008**	-	-
	W	0.368	0.296	-	-
	O	NA	NA	NA	NA
Sphagnum magellanicum aggr.	A	0.687	**0.046**	-	-
	W	1.175	**0.050**	-	-
	O	0.336	0.442	-	-
Sphagnum palustre	A	0.531	0.081	-	-
	W	-0.278	0.398	-	-
	O	6.137	**0.001**	-	-
Sphagnum recurvum aggr.	A	1.097	**0.003**	-	-
	W	0.281	0.449	-	-
	O	3.058	**0.006**	-2.086	**0.041**
Vaccinium oxycoccos	A	-1.121	**0.031**	-	-
	W	-0.761	0.151	-	-
	O	NA	NA	NA	NA

were too dry and too dark. Due to the difference in elevation between the pits and the surface outside the pits, the water table outside the pits was most likely lowered as well (Holden *et al.* 2006), at least up to a certain distance from the edge of the pits. Dry conditions can delay the recovery of degraded bogs (Hancock *et al.* 2018), and thus it would be necessary to raise the water table in the whole Hagenmoos bog to increase soil moisture and ensure recovery outside the pits. Furthermore, temperatures already increased considerably since the mid-18th century and dry periods in summer were extremely common during the last 15 years. As it is expected that these trends continue, i.e., that future summers in Switzerland will become warmer and drier due to climate change (BAFU 2020), it is relevant to restore the hydrology of the Hagenmoos bog as soon as possible. It is, however, important that the water table is raised gradually to avoid inundating the current vegetation within the pits and to ensure enough time for gradual adaptation. A rapid inundation would flood the two peat pits, the current vegetation would most likely be destroyed, and possibly floating mats would establish (Poschlod *et al.* 2007). It will therefore take considerable time until the water table is sufficiently raised to substantially improve the conditions outside the two pits. A long-term commitment of authorities to nature conservation measures in this bog is thus required. In addition, if the water table of a bog is too low, the growth of woody plants and especially trees increases (Murphy *et al.* 2009, Cedroa & Lamentowicz 2011). Thus, the light conditions outside the pits should be monitored and the establishment of woody plants (e.g. *Frangula alnus*) must be controlled until the water table is sufficiently raised. How fast the water table effectively can be raised without destroying the established *Sphagnum* carpets in the two pits should be further evaluated and discussed with the nature conservation authorities. If conditions outside the pits deteriorate too quickly, the strategy should be adjusted, and the water raised more quickly. It is thus important to monitor the site and to adopt an adaptive management strategy (McCarthy & Possingham 2007).

Table 5. Mean cover and standard errors for single species in 2020. Mean cover was calculated for all plots (A; n = 72), for plots within the pits (W; n = 34) and for plots outside the pits (O; n = 38). P-values are according to two-sided t-tests for the mean cover within and outside the pits, with p-values ≤ 0.05 highlighted in bold.

Species	Mean cover and standard error [%]			p-value
	A	W	O	
Phragmites australis	5.3 ± 1.3	10.6 ± 2.5	0.6 ± 0.2	**<0.001**
Sphagnum magellanicum aggr.	10.7 ± 2.4	12.7 ± 3.6	8.9 ± 3.1	0.423
Sphagnum palustre	6.6 ± 2.0	9.9 ± 3.7	3.6 ± 1.9	0.138
Sphagnum angustifolium	11.9 ± 2.9	22.1 ± 5.5	2.7 ± 1.4	**0.002**
Vaccinium oxycoccos	1.4 ± 0.6	1.4 ± 0.8	1.4 ± 1.0	0.983

In contrast to our expectations, mean indicator values for nutrients increased within the peat pits after restoration. A similar development was also observed in other restored bogs (Haapalehto *et al.* 2014, Lundin *et al.* 2017, Gaffney *et al.* 2018). Gaffney *et al.* (2018) observed an increase of certain nutrients within the pore-water of bogs in Scotland three years after restoration. However, nutrient concentrations decreased during the next 14 years of monitoring, whereas within the pits of the Hagenmoos bog the indicator values for nutrients increased over the 30 years of monitoring. Similarly, Lundin *et al.* (2017) reported an initial increase of phosphorus in soil water after the rewetting of a peat extraction site in Sweden, followed by a decrease in the subsequent years. Haapalehto *et al.* (2014) observed an increased concentration of nitrogen and phosphorus in the pore-water of restored bogs in comparison to pristine bogs in Finland. They suggested that the increase of nutrients was caused by the rewetting of the surface soil layer, which consisted of highly decomposed peat. Highly decomposed peat has a large amount of oxidising substances and organic matter, which act as electron donors and thus cause a large mobilisation of nitrogen and phosphorus after rewetting (Zak & Gelbrecht 2007). As a result, plants with high nutrient values initially increase after the blocking of drainage pathways. These observations (Zak & Gelbrecht 2007, Haapalehto *et al.* 2014) are consistent with the development in the Hagenmoos bog: mean nutrient indicator values increased only within the pits, where soil moisture increased most. In 2020, values within the peat pits were significantly higher than those for the reference dataset, indicating that nature conservation objectives had not yet been accomplished.

Interestingly, mean pH indicator values increased slightly but not significantly within the peat pits, whereas they increased significantly outside the pits. It is not clear why they increased outside the pits. It may be that although mean pH indicator values increased, the soil pH did in fact not increase. Nature conservation measures such as logging and thinning of trees outside the pits may have temporally favoured disturbance-tolerant species, which may have higher pH indicator values. In species-poor ecosystems, such as bogs, a single species can strongly influence the mean indicator value of a plot. Such increases in disturbance-tolerant species might partly explain the increase in mean pH indicator values outside the pits.

One important aim when rewetting peat bogs is to reactivate peat formation. We therefore expected the mean indicator values for humus to increase over time if restoration measures were successful. However, no change in the mean indicator values for humus was observed outside the pits. Within the pits the mean humus indicator values even decreased. One species particularly common in these plots in 2020 was *Phragmites australis*, which has a lower humus indicator value (3; Landolt *et al.* 2010) compared with that of species typical of raised bogs. Within the pits, the number of plots dominated by *Phragmites* and thus the number of plots with lower humus indicator values increased over time. These plots were partially responsible for the decrease in mean humus indicator values. Nevertheless, in 2020 many plots with a moderate cover of *Phragmites* had a high cover of *Sphagnum* species (up to 100 %), mainly *S. angustifolium* but also *S. magellanicum* aggr. The latter is a main peat builder, because it decomposes relatively slowly (Turetsky *et al.* 2008, Bengtsson *et al.* 2016).

We expected mean indicator values for temperature to remain constant or increase slightly over time. In fact, mean temperature indicator values increased within as well as outside the peat pits. It is not fully clear why this was the case. Indicator values for temperature are interdependent with indicator values for light, as high light radiation also means high radiation (Landolt *et al.* 2010). However, temperature and light indicator values showed different developments in the Hagenmoos bog. A partial explanation may be the high abundance of *Phragmites australis* in 2020, which has a comparatively high indicator value for temperature (4; Landolt *et al.* 2010).

All mean indicator values in the present study were calculated based on presence/absence data, i.e., all species present in a plot were weighted equally. In a study on 74 species-rich sites, mean indicator values for moisture, nutrients and pH, calculated using presence/absence data, differed only slightly from values calculated using abundance data (Schaffers & Sýkora 2000). For species-poor sites, however, the authors recommended using abundance data. Bedolla (2018) performed statistical analyses for all 113 plots in the Hagenmoos bog from 1989 to 1999 using indicator values weighted according to species cover. Her analyses generally showed the same trends as observed in our study, indicating that our results are robust and would likely show similar trends if cover-weighted indicator values were used.

Changes in species richness and single species

We predicted that there would be a decrease in species richness over time if the measures were successful, as raised bogs are typically species-poor ecosystems (Rydin & Jeglum 2013). Within the pits, we observed a decrease in vascular plant and bryophyte species richness over time, but the number of bog specialists stayed constant. This also held true for bog specialists outside the pits. The decrease in vascular plants within the pits was expected due to the rewetting as a result of the closure of the main ditches. However, we would have also expected an increase in the number of bog specialists, which did not (yet) take place. Unfortunately, and as explained above, we could not analyse trends in cover values, which would have given additional insight. Regarding the presence of individual species of interest, we anticipated a decrease of *Phragmites australis* over time if restoration measures were successful, as *Phragmites* indicates eutrophic and weakly basic to weakly acidic conditions (Landolt *et al.* 2010, Packer *et al.* 2017), i.e., conditions not found in intact raised bogs (Vitt 2006). Furthermore, we expected to observe an initial increase of species typical of transitional bogs and species known to benefit from restoration measures, such as *Sphagnum palustre* and especially *S. recurvum* aggr. (Grosvernier *et al.* 1997, Sliva 1997). Additionally, we anticipated that typical bog specialists such as *S. magellanicum* aggr. and *Vaccinium oxycoccos* would increase in the longer term.

In contrast to our expectations, *Phragmites australis* increased when all plots were considered. Outside the peat pits, *Phragmites* had a low mean cover in 2020 (0.6 %) and was therefore of minor concern. Within the pits, however, its mean cover in 2020 was 10.6 %. Poschlod *et al.* (2007) also observed the establishment of *Phragmites* in two formerly drained and exploited raised bogs after rewetting. *Phragmites* became abundant in areas with upwelling mineral water or where peat had become connected to groundwater due to heavy peat extraction. This might also be the case in the Hagenmoos. As *Phragmites* can form very long roots (Marks *et al.* 1994, Packer *et al.* 2017), our results may also indicate that this species experiences site conditions different from those of the species found in its immediate proximity. The development of *Phragmites* in the Hagenmoos bog should be further monitored, as it may shade typical bog species (e.g. *Sphagnum* spp.) or cover them with its litter. This could be done, for example, by analysing orthophotos taken by drones. If the cover of *Phragmites* continues to increase, measures such as frequent mowing could be considered (Güsewell 2003).

Outside the peat pits, *S. palustre* and *S. recurvum* aggr. presences increased continuously over time. *Sphagnum palustre* typically occurs at bog margins and in at least partly forested habitats (Rapp 2020), as well as in fens, promoting the transition to raised bogs (Sliva 1997). Its increase outside the pits may thus indicate either increased shade or the succession of fen vegetation towards raised bog vegetation. In 2020, however, its mean cover outside the pits was only 3.6 %. The same is true for *S. recurvum* aggr., which increased only outside the pits but remained at a low mean cover value in 2020 (2.7 %). Species included in the *Sphagnum recurvum* aggr. such as *S. angustifolium* and *S. fallax* are well known pioneer species in restored bogs and may rapidly expand when bogs are rewetted (Grosvernier *et al.* 1997, Bedolla *et al.* 2019). Within the pits, both *S. palustre* and *S. recurvum* aggr. had much higher cover values in 2020 (9.9 % and 22.1 %, respectively) than outside the pits, but there were no significant changes in the frequency of these two species over the 30 years since restoration.

The increase of *S. magellanicum* aggr. within the two peat pits may indicate a transition towards open raised bog vegetation, as *S. magellanicum* aggr. is a typical bog specialist and indicates rather high water tables (Feldmeyer-Christe & Küchler 2018). Similarly, *V. oxycoccos* increased when all plots were considered. This increase is also considered an indication of successful restoration, as *V. oxycoccos* is a typical specialist of open raised bogs (Küchler 2018).

Temporal trends in vegetation development

Most trends in vegetation changes were the same in the first 10 years after restoration as they were 10 to 30 years after restoration. Within the peat pits, however, indicator values for light and moisture mainly increased during the first 10 years and showed no changes afterwards, which was reflected in an accompanying increase of stress-tolerance values during the first period only. Similarly, Hancock *et al.* (2018) observed a stagnation in vegetation development six years after restoration in a bog in Scotland. Outside the pits, bryophyte richness increased during the first period and decreased during the second period. The restoration measures taken in the Hagenmoos bog may partly explain the initial increase in bryophyte richness, as the measures caused disturbance. An initial increase in vascular plant richness, however, was not observed in plots outside the pits.

Our results demonstrate that the vegetation was still in development 30 years after restoration. To develop a detailed concept for future restoration measures, a long-term hydrological monitoring would be helpful. Furthermore, it should also be thought about including other groups of taxa in the monitoring which are also in the focus of nature conservation (e.g. insects such as dragonflies, amphibians, reptiles) as habitat demands of different taxa may be different. Regrading climate warming, it seems important that the Hagenmoos is well monitored so that unwanted trends are recognised early on and adapted counter measures can be initiated such as a more rapid increase of the water level in the peat pits, mowing of *Phragmites* or more frequent cutting of bushes such as *Frangula alnus*.

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AUTHOR CONTRIBUTIONS

SF, AB and RH conceived the study. SF conducted the fieldwork and did the statistical analyses with support of AB and RH. SF wrote the manuscript with contributions from AB and RH.

DATA AVAILABILITY STATEMENT

All data necessary to replicate the analyses are accessible at https://www.envidat.ch/dataset/data-hagenmoos-1989-2020. These data include mean indicator values and species richness data, as well as complete species lists (vascular plants and bryophytes) for each plot and year.

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Appendix

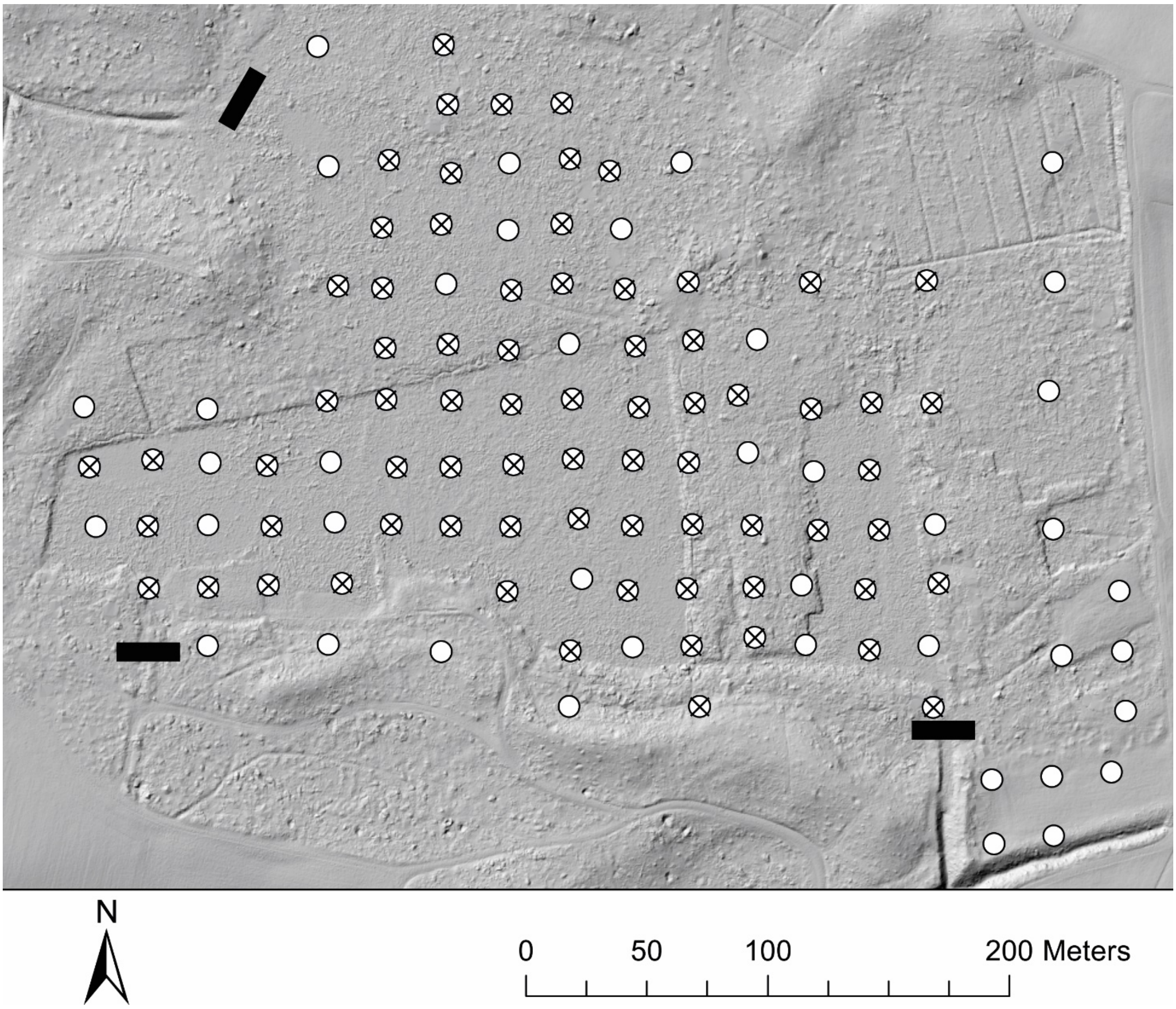

Figure A1. Digital terrain model (source: https://www.swisstopo.admin.ch/en/geodata/height/alti3d.html) of all 113 plots in the Hagenmoos raised bog (white dots) and the 72 plots re-surveyed in 2020 (black crosses). Black bars mark the places where main ditches have been blocked in 1991.

Table A1. List of bog character species, according to Feldmeyer-Christe & Küchler (2018), found in at least one survey year in our study.

Aulacomnium palustre (Hedw.) Schwägr.	*Sphagnum cuspidatum* Hoffm.
Cephalozia connivens (Dicks.) Lindb.	*Sphagnum magellanicum* aggr.
Drosera rotundifolia L	*Sphagnum papillosum* Lindb.
Eriophorum vaginatum L.	*Straminergon stramineum* (Brid.) Hedenäs
Polytrichum strictum Brid.	*Vaccinium oxycoccos* L.
Rhynchospora alba (L.) Vahl	*Warnstorfia exannulata* (Schimp.) Loeske
Sphagnum capillifolium aggr.	*Warnstorfia fluitans* (Hedw.) Loeske

Table A2. List of all vascular plant species found, including their frequency (number of plots) per survey year (1989, 1999, 2020) and stratum (A = all plots, n = 72; W = within the pits, n = 34; O = outside the pits, n = 38).

Vascular plant species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Abies alba Mill.	1	0	1	1	0	1	1	0	1
Acer pseudoplatanus L.	8	2	6	3	0	3	2	1	1
Aegopodium podagraria L.	1	1	0	1	1	0	0	0	0
Agrostis canina L.	2	2	0	2	2	0	0	0	0
Agrostis stolonifera L.	0	0	0	1	1	0	1	1	0
Ajuga reptans L.	0	0	0	0	0	0	1	1	0
Aldrovanda vesiculosa L.	0	0	0	0	0	0	1	1	0
Angelica sylvestris L.	1	0	1	1	0	1	0	0	0
Betula pendula aggr.	10	7	3	7	1	6	20	9	11
Brachypodium sylvaticum (Huds.) P. Beauv.	1	0	1	1	0	1	0	0	0
Calamagrostis epigejos (L.) Roth	0	0	0	1	1	0	2	2	0
Calluna vulgaris (L.) Hull	6	2	4	1	1	0	1	0	1
Cardamine sp.	1	1	0	0	0	0	0	0	0
Carex acutiformis Ehrh.	4	4	0	4	4	0	2	2	0
Carex cf. *acutiformis* Ehrh.	0	0	0	1	1	0	0	0	0
Carex brizoides L.	3	3	0	2	2	0	0	0	0
Carex canescens L.	2	2	0	2	1	1	2	2	0
Carex cf. *canescens* L.	0	0	0	0	0	0	1	0	1
Carex echinata Murray	3	0	3	5	1	4	0	0	0
Carex elata All.	1	0	1	2	0	2	0	0	0
Carex elongata L.	0	0	0	0	0	0	2	1	1
Carex nigra (L.) Reichard	1	1	0	1	1	0	0	0	0
Carex cf. *nigra* (L.) Reichard	0	0	0	0	0	0	1	0	1

Vascular plant species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Carex pilulifera L.	0	0	0	1	0	1	0	0	0
Carex rostrata Stokes	8	7	1	22	18	4	16	14	2
Carex cf. *rostrata* Stokes	0	0	0	0	0	0	4	3	1
Carex sp.	2	2	0	0	0	0	3	3	0
Carex vesicaria L.	1	1	0	0	0	0	0	0	0
Cerastium fontanum subsp. *vulgare* (Hartm.) Greuter & Burdet	1	1	0	0	0	0	0	0	0
Circaea lutetiana L.	1	1	0	0	0	0	0	0	0
Cirsium palustre (L.) Scop.	1	1	0	1	1	0	0	0	0
Cladium mariscus (L.) Pohl	0	0	0	0	0	0	1	1	0
Colchicum autumnale L.	1	1	0	0	0	0	1	1	0
Corylus avellana L.	1	0	1	2	1	1	0	0	0
Crepis paludosa (L.) Moench	1	0	1	0	0	0	0	0	0
cf. *Crepis paludosa* (L.) Moench	0	0	0	0	0	0	1	1	0
Daucus carota L.	0	0	0	1	1	0	0	0	0
Deschampsia cespitosa (L.) P. Beauv.	0	0	0	1	0	1	0	0	0
Drosera rotundifolia L.	8	4	4	3	2	1	1	1	0
Dryopteris carthusiana (Vill.) H. P. Fuchs	1	0	1	5	0	5	1	1	0
Dryopteris dilatata (Hoffm.) A. Gray	3	2	1	0	0	0	1	0	1
Dryopteris sp.	0	0	0	1	1	0	1	0	1
Epilobium tetragonum L.	0	0	0	1	1	0	0	0	0
Epipactis sp.	0	0	0	0	0	0	2	2	0
Equisetum arvense L.	1	1	0	1	1	0	0	0	0
Equisetum fluviatile L.	0	0	0	0	0	0	1	1	0
Equisetum palustre L.	1	1	0	2	2	0	0	0	0
Equisetum sylvaticum L.	0	0	0	2	1	1	1	1	0
Eriophorum angustifolium Honck.	0	0	0	1	1	0	0	0	0

Vascular plant species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Eriophorum vaginatum L.	2	2	0	4	3	1	2	1	1
Fagus sylvatica L.	1	0	1	0	0	0	0	0	0
Filipendula ulmaria (L.) Maxim.	2	1	1	1	1	0	0	0	0
Frangula alnus Mill.	14	11	3	19	6	13	25	6	19
Fraxinus excelsior L.	2	1	1	2	0	2	0	0	0
Galeopsis tetrahit L.	1	1	0	0	0	0	0	0	0
Galium album Mill.	1	1	0	1	1	0	1	1	0
Galium palustre L.	8	8	0	6	4	2	4	4	0
Galium uliginosum L.	1	1	0	0	0	0	0	0	0
Hedera helix L.	2	0	2	2	0	2	2	0	2
Impatiens noli-tangere L.	2	2	0	0	0	0	0	0	0
Impatiens parviflora DC.	1	1	0	0	0	0	0	0	0
Impatiens sp.	2	2	0	0	0	0	0	0	0
Iris pseudacorus L.	1	1	0	2	2	0	1	1	0
Juncus articulatus L.	4	4	0	5	5	0	1	1	0
Juncus effusus L.	6	5	1	11	11	0	8	8	0
Knautia dipsacifolia Kreutzer	1	0	1	1	0	1	0	0	0
Lathyrus pratensis L.	2	2	0	1	1	0	0	0	0
Lemna minor aggr.	0	0	0	10	7	3	2	2	0
Leucanthemum vulgare Lam.	1	1	0	0	0	0	0	0	0
Listera cordata (L.) R. Br.	0	0	0	0	0	0	1	1	0
Luzula sylvatica (Huds.) Gaudin	1	0	1	0	0	0	0	0	0
Lysimachia vulgaris L.	12	11	1	9	9	0	3	3	0
cf. *Lysimachia vulgaris* L.	0	0	0	0	0	0	1	1	0
Lythrum salicaria L.	2	2	0	2	2	0	0	0	0
Maianthemum bifolium (L.) F. W. Schmidt	0	0	0	1	1	0	1	0	1

Vascular plant species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Melampyrum pratense L.	1	0	1	0	0	0	1	0	1
Mentha aquatica L.	5	5	0	3	3	0	0	0	0
Mentha longifolia (L.) Huds.	0	0	0	1	1	0	0	0	0
Molinia caerulea aggr.	21	11	10	19	7	12	14	2	12
Myosotis scorpioides L.	0	0	0	2	2	0	0	0	0
Oxalis acetosella L.	6	2	4	5	0	5	2	0	2
Paris quadrifolia L.	0	0	0	0	0	0	1	0	1
Phalaris arundinacea L.	1	1	0	2	2	0	0	0	0
Phragmites australis (Cav.) Steud.	22	20	2	25	23	2	30	23	7
Picea abies (L.) H. Karst.	28	4	24	26	2	24	22	3	19
Pimpinella major (L.) Huds.	1	1	0	0	0	0	0	0	0
Pinus sp.	22	14	8	2	1	1	0	0	0
Pinus sylvestris L.	0	0	0	1	0	1	3	2	1
Poa palustris L.	0	0	0	1	1	0	0	0	0
Populus tremula L.	0	0	0	1	1	0	0	0	0
Pteridium aquilinum (L.) Kuhn	0	0	0	0	0	0	1	0	1
Quercus robur L.	0	0	0	2	1	1	0	0	0
Ranunculus repens L.	1	1	0	0	0	0	0	0	0
Rhynchospora alba (L.) Vahl	1	1	0	1	1	0	1	1	0
Rubus fruticosus aggr.	5	1	4	5	0	5	9	1	8
Rubus idaeus L.	0	0	0	2	1	1	2	2	0
Salix cinerea L.	4	4	0	1	1	0	0	0	0
Scirpus sylvaticus L.	1	1	0	1	1	0	0	0	0
Solanum dulcamara L.	0	0	0	0	0	0	1	1	0
Sorbus aucuparia L.	8	1	7	9	0	9	6	0	6
Spirodela polyrhiza (L.) Schleid.	0	0	0	3	3	0	0	0	0

Vascular plant species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Stachys officinalis aggr.	1	1	0	1	1	0	0	0	0
Stellaria graminea L.	1	1	0	0	0	0	0	0	0
Tracheophyta sp.	0	0	0	2	1	1	0	0	0
Urtica dioica L.	1	1	0	0	0	0	0	0	0
Utricularia australis R. Br.	0	0	0	9	6	3	0	0	0
Vaccinium myrtillus L.	38	7	31	36	4	32	32	1	31
Vaccinium oxycoccos L.	13	7	6	14	9	5	9	5	4
Vaccinium uliginosum L.	3	1	2	1	0	1	2	0	2
Vaccinium vitis-idaea L.	1	0	1	1	0	1	0	0	0
Valeriana officinalis aggr.	0	0	0	0	0	0	1	1	0
Vicia cracca L.	0	0	0	1	1	0	0	0	0
Vicia hirsuta (L.) Gray	1	1	0	0	0	0	0	0	0
Viola riviniana Rchb.	0	0	0	1	0	1	0	0	0
Viola sp.	2	1	1	0	0	0	0	0	0

Table A3. List of all bryophyte species found, including their frequency (number of plots) per survey year (1989, 1999, 2020) and stratum (A = all plots, n = 72; W = within the pits, n = 34; O = outside the pits, n = 38).

Bryophyte species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Amblystegium radicale (P. Beauv.) Schimp.	0	0	0	0	0	0	1	1	0
Amblystegium serpens (Hedw.) Schimp.	1	1	0	0	0	0	0	0	0
Aneura pinguis (L.) Dumort.	0	0	0	0	0	0	1	0	1
Atrichum undulatum (Hedw.) P. Beauv.	0	0	0	3	0	3	0	0	0
Aulacomnium palustre (Hedw.) Schwägr.	7	5	2	7	4	3	7	2	5
Bazzania trilobata (L.) Gray	1	0	1	0	0	0	0	0	0
Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	1	0	1	0	0	0	0	0	0
Brachythecium rivulare Schimp.	2	2	0	0	0	0	1	0	1
Brachythecium rutabulum (Hedw.) Schimp.	1	1	0	1	1	0	1	1	0
Brachythecium salebrosum (F. Weber & D. Mohr) Schimp., nom. cons.	1	1	0	0	0	0	1	1	0
Brachythecium cf. *salebrosum* (F. Weber & D. Mohr) Schimp., nom. cons.	0	0	0	1	0	1	0	0	0
Brachythecium sp.	1	1	0	0	0	0	0	0	0
Bryum pseudotriquetrum (Hedw.) G. Gaertn. & al.	0	0	0	0	0	0	1	1	0
Bryum sp.	0	0	0	1	1	0	0	0	0
Calliergonella cuspidata (Hedw.) Loeske	5	4	1	7	6	1	3	2	1
Calliergonella lindbergii (Mitt.) Hedenäs	0	0	0	0	0	0	1	1	0
Calypogeia azurea Stotler & Crotz	4	2	2	3	0	3	4	0	4
Calypogeia cf. *azurea* Stotler & Crotz	0	0	0	0	0	0	1	0	1
Calypogeia cf. *fissa* (L.) Raddi	0	0	0	0	0	0	1	0	1
Calypogeia integristipula Steph.	3	0	3	5	0	5	0	0	0
Calypogeia muelleriana (Schiffn.) Müll. Frib.	8	1	7	4	0	4	0	0	0

Bryophyte species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Calypogeia neesiana (C. Massal. & Carestia) Müll. Frib.	1	0	1	0	0	0	1	0	1
Campylopus flexuosus (Hedw.) Brid.	3	0	3	10	0	10	3	0	3
Campylopus pyriformis (Schultz) Brid.	2	1	1	1	0	1	0	0	0
Cephalozia bicuspidata (L.) Dumort.	0	0	0	1	0	1	0	0	0
Cephalozia connivens (Dicks.) Lindb.	3	0	3	4	0	4	3	0	3
Cephaloziella sp.	0	0	0	0	0	0	1	0	1
Cirriphyllum piliferum (Hedw.) Grout	2	2	0	2	2	0	2	2	0
Climacium dendroides (Hedw.) F. Weber & D. Mohr	3	3	0	0	0	0	0	0	0
Ctenidium molluscum (Hedw.) Mitt.	0	0	0	1	1	0	0	0	0
Dicranodontium denudatum (Brid.) E. Britton	25	0	25	24	1	23	23	3	20
Dicranum montanum Hedw.	4	0	4	1	0	1	0	0	0
Dicranum polysetum anon.	9	0	9	10	1	9	5	0	5
Dicranum scoparium Hedw.	12	2	10	12	1	11	7	1	6
Eurhynchium striatum (Hedw.) Schimp.	6	2	4	8	3	5	10	2	8
Herzogiella seligeri (Brid.) Z. Iwats.	2	0	2	3	0	3	2	2	0
Hygroamblystegium humile (P. Beauv.) Vanderp. & al.	1	1	0	0	0	0	1	1	0
Hylocomium splendens (Hedw.) Schimp.	10	2	8	12	2	10	8	0	8
Hypnum cupressiforme aggr.	18	2	16	30	4	26	26	2	24
Lepidozia reptans (L.) Dumort.	2	0	2	3	0	3	0	0	0
Leucobryum glaucum (Hedw.) Ångstr.	20	1	19	22	1	21	15	0	15
Lophocolea bidentata (L.) Dumort.	2	2	0	1	1	0	3	1	2
Lophocolea heterophylla (Schrad.) Dumort.	24	7	17	13	1	12	1	1	0
Metzgeria temperata Kuwah.	0	0	0	0	0	0	1	0	1

Bryophyte species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Mnium spinulosum Bruch & Schimp.	1	1	0	0	0	0	0	0	0
Orthotrichum lyellii Hook. &Taylor	0	0	0	0	0	0	1	0	1
Plagiomnium affine aggr.	5	4	1	4	2	2	6	1	5
Plagiomnium undulatum (Hedw.) T. J. Kop.	2	1	1	4	1	3	1	1	0
Plagiothecium laetum Schimp.	12	2	10	11	2	9	1	0	1
Plagiothecium nemorale (Mitt.) A. Jaeger	4	4	0	1	1	0	1	1	0
Plagiothecium undulatum (Hedw.) Schimp.	1	0	1	0	0	0	0	0	0
Pleurozium schreberi (Brid.) Mitt.	26	2	24	30	3	27	24	0	24
Pohlia nutans (Hedw.) Lindb.	0	0	0	1	1	0	0	0	0
Polytrichum commune Hedw.	9	9	0	11	11	0	5	5	0
Polytrichum formosum Hedw.	12	1	11	17	1	16	10	2	8
Polytrichum strictum Brid.	11	3	8	15	6	9	6	1	5
Pseudoscleropodium purum (Hedw.) M. Fleisch.	2	1	1	6	2	4	4	2	2
Ptilium crista-castrensis (Hedw.) De Not.	1	1	0	0	0	0	0	0	0
Radula complanata (L.) Dumort.	0	0	0	0	0	0	1	0	1
Rhizomnium punctatum (Hedw.) T. J. Kop.	6	5	1	0	0	0	1	1	0
Rhytidiadelphus loreus (Hedw.) Warnst.	1	0	1	1	0	1	1	0	1
Rhytidiadelphus squarrosus (Hedw.) Warnst.	4	2	2	4	2	2	3	2	1
Rhytidiadelphus triquetrus (Hedw.) Warnst.	0	0	0	0	0	0	2	0	2
Riccardia incurvata Lindb.	0	0	0	2	0	2	0	0	0
Riccardia multifida (L.) Gray	2	2	0	0	0	0	0	0	0
Riccardia palmata (Hedw.) Carruth.	0	0	0	2	0	2	2	1	1
Riccardia sp.	1	0	1	0	0	0	0	0	0

Bryophyte species	Frequency per year and stratum								
	1989			1999			2020		
	A	W	O	A	W	O	A	W	O
Sanionia uncinata (Hedw.) Loeske	2	2	0	0	0	0	0	0	0
Sphagnum capillifolium aggr.	21	8	13	25	9	16	18	4	14
Sphagnum cf. *capillifolium* aggr.	0	0	0	0	0	0	1	1	0
Sphagnum cuspidatum Hoffm.	5	3	2	7	5	2	2	1	1
Sphagnum magellanicum aggr.	22	10	12	26	11	15	28	14	14
Sphagnum palustre L.	16	14	2	17	14	3	21	12	9
Sphagnum papillosum Lindb.	0	0	0	0	0	0	1	1	0
Sphagnum recurvum aggr.	17	15	2	25	17	8	28	17	11
Sphagnum squarrosum Crome	0	0	0	3	2	1	2	1	1
Sphagnum teres (Schimp.) Ångstr.	1	1	0	0	0	0	0	0	0
Straminergon stramineum (Brid.) Hedenäs	5	5	0	9	9	0	3	3	0
Tetraphis pellucida Hedw.	3	0	3	6	1	5	1	1	0
Thuidium tamariscinum (Hedw.) Schimp.	8	1	7	17	2	15	25	3	22
Warnstorfia exannulata (Schimp.) Loeske	0	0	0	0	0	0	1	1	0
Warnstorfia fluitans (Hedw.) Loeske	0	0	0	1	1	0	0	0	0