A decade of vegetation development on two revegetated milled peatlands with different trophic status

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SUMMARY

Milled peatlands in the Northern Hemisphere are frequently restored in order to mitigate negative effects of climate change and to benefit biodiversity. The aims of this study are to analyse the development of vegetation on milled peatlands in Estonia after restoration using the moss layer transfer technique (MLTT), relate the plant functional type cover with peat chemical factors, and study correlations between bryophyte and vascular plant cover on sites with different vegetation composition. Nutrient-poor (NP) Viru and nutrient-rich (NR) Ohtu milled peatlands in Northern Estonia were restored via MLTT between 2006 and 2008. Plant species cover was determined annually or biannually from 2009 to 2018, on permanent plots established during the restoration of both sites. Plant functional type cover was assessed in relation to peat chemical properties and time since restoration. The nutrient status of the restoration site plays a major role in vegetation succession, even if similar restoration methods have been applied. Vascular plant cover, especially evergreen shrubs, increased with time since restoration, while bryophyte (mainly *Sphagnum*) cover increased at the NP site and decreased at the NR site. At the NR site bryophyte cover decreased with increasing vascular plant cover, while the opposite pattern was observed at the NP site.

KEY WORDS: moss-layer-transfer technique, peat nutrient content, peatland restoration, plant functional types, *Sphagnum* spp.

INTRODUCTION

Peat milling is ongoing across vast areas of the Northern Hemisphere and has a detrimental effect on peatland ecosystems. Estimated losses due to peat extraction range from about 0.1 % (Clarke & Rieley 2019) up to 10 % of the global mire area (Joosten & Clarke 2002). About 6 % of the peatland area in Estonia has been (directly or indirectly) affected by peat mining (Ilomets 2017), leaving mainly bare peat areas which are emitting large quantities of CO_2 to the atmosphere. Karofeld *et al.* (2016) emphasise the need to prioritise the peatland restoration in Baltic countries in comparison with other reclamation options (e.g. afforestation, berry plantation, biomass production). This reclamation option mitigates the climate impact of milled peatlands. Abandoned milled peatlands may remain largely unvegetated for long periods if not restored. Although vegetation development after restoration activities can be rapid (Tuittila *et al.* 2000, Poulin *et al.* 2013), species composition may remain dissimilar to pristine bogs even decades following restoration (Pouliot *et al.* 2012). The indicator of successful peatland restoration activities is considered to be the recovery of *Sphagnum* or true moss dominated vegetation in nutrient-poor and nutrient-rich sites respectively (Rochefort 2000). Plant functional types (PFTs) are used for classification of plant species according to their physical, phylogenetic and phenological characteristics for describing the ecosystem behaviour. PFTs such as *Sphagnum*, true mosses, but also vascular PFTs e.g. shrubs, sedges and forbs differ in their stoichiometry (Wang & Moore 2014) and also carbon exchange (Ward *et al.* 2009, Kuiper *et al.* 2014, Purre *et al.* 2019). In primary mire succession, plant species richness and functional diversity generally increase with time during the fen–bog transition in northern peatlands (Laine *et al.* 2018). Active restoration of milled peatlands supports the re-establishment of peatland-specific plant species, while unrestored sites are dominated by ruderal species (Poulin *et al.* 2013).

During natural succession of bare peat surfaces, the abundance of pioneer plant species increases and then decreases rapidly. Plants which are abundant after the pioneer species have large interannual fluctuations, while abundant plant species during the later stages of succession increase their cover steadily (Feldmeyer-Christe *et al*. 2011). There are two main successional pathways (towards fen or raised bog vegetation), which depend on the properties of the residual peat layer (Triisberg *et al*. 2014, Renou-Wilson *et al*. 2019). *Sphagnum* and ombrotrophic sedges prevail in nutrient-poor (NP) areas while minerotrophic sedges and true mosses are more dominant at more nutrient-rich (NR) milled peatlands (Gagnon *et al*. 2018, Kozlov *et al*. 2018, Zając *et al*. 2018, Renou-Wilson *et al*. 2019). Vegetation development in NP peatlands is slower than in NR peatlands (Kozlov *et al*. 2018). Additional insight is needed as to how similar restoration activities applied to different milled peatlands with varying trophic status affect revegetation dynamics and therefore restoration success.

Site specific conditions such as type, thickness of the residual peat layer, and nutrient availability influence the restoration outcome. After restoration, the first species to arrive are those that are distributed by wind or through active restoration, while plant species that are resilient to harsh conditions (water table fluctuations, frost heave and so on) increase their cover more steadily (Triisberg-Uljas *et al*. 2018). Application of the moss layer transfer technique (MLTT) (Rochefort *et al*. 2003) has been considered likely to be beneficial according to a synthesis by Taylor *et al*. (2019). But it depends on site specific and management factors and can result in vegetation dominated by *Sphagnum* and other peatland species, but also bare peat or *Polytrichum strictum* (González *et al*. 2013, González & Rochefort 2014), which could evolve in the direction of *Sphagnum* domination with time (González & Rochefort 2014).

Knowledge about the long-term development of peatland vegetation after the restoration of milled peatlands with MLTT remains limited in Europe relative to North America. In Europe, MLTT has mainly been applied on *Sphagnum* farming sites (Beyer & Höper 2015, Gaudig *et al*. 2017, Krebs *et al*. 2017), where environmental conditions are kept favourable for *Sphagnum* growth and active management measures are applied throughout the studies. Such high-level management activities are not cost-effective to apply on large-scale peatland restoration sites, where active management is not carried out after initial restoration practice, and this distinguishes restoration sites from the *Sphagnum* farming sites. In Europe, restoration works are mainly done using rewetting and without spreading of bryophyte fragments and mulching (Tuittila *et al*. 1999, Tuittila *et al*. 2000, Wilson *et al*. 2007, Soini *et al*. 2010, Beyer & Höper 2015, Wilson *et al*. 2016), which does not support the recolonisation of typical hummock *Sphagnum* (Smolders *et al*. 2003, González *et al*. 2014a). Only a few studies conducted in milled peatlands in Europe analyse different aspects of restoration success on sites, where MLTT or other ways of *Sphagnum* reintroduction have been applied for experimental or restoration purposes (Smolders *et al*. 2003, Tuittila *et al*. 2004, Karofeld *et al*. 2015, Järveoja *et al*. 2016, Purre & Ilomets 2018, Purre *et al*. 2019, Karofeld *et al*. 2020, Purre *et al*. 2020).

Previously we have demonstrated that two milled peatland sites restored using MLTT but having different peat chemistry vary by their bryophyte biomass production and we related production of different bryophyte groups to variations in differences in peat chemical factors (Purre & Ilomets 2018) and the effect of different treatments of MLTT to restoration outcome based on plant biomass (Purre *et al*. 2020). The current paper provides insight to the development of vegetation cover, including bryophyte and vascular PFTs and their temporal variations after the restoration activities in these two sites in relation with peat chemical factors. The aims of the study are to (1) relate the plant functional type cover with peat chemical factors, (2) analyse the development of vegetation composition for over a decade on milled peatlands restored using MLTT at two sites, and (3) study relationships between bryophyte and vascular plant cover on sites with different vegetation composition.

METHODS

Study sites

The Ohtu (59° 17' 18" N, 24° 23' 11" E) and Viru (59° 28' 29" N, 25° 39' 28" E) sites, henceforth NR and NP respectively, are experimental restoration sites on milled peatlands in Northern Estonia. At NR (nutrient-rich), milling continued until *Sphagnum* - *Carex* peat was reached; whereas at NP (nutrient-poor), some less-decomposed *Sphagnum* peat was left in the residual peat layer. NR is bordered by drained peatland forest dominated by *Pinus sylvestris* on one side and by active milled peatland on the other sides. NP is located in the middle of rewetted milled peatland (rewetted in 2011–2013) bordered with *P. sylvestris* dominated forests and adjoins an old peat transportation road flanked by *Betula pendula*.

All sparse vegetation that was present before restoration was removed with the upper 10 cm layer of mineralised peat from both sites. Restoration by MLTT (Rochefort *et al*. 2003) was carried out in 2006 in NR and 2008 in NP, correspondingly two and 23 years after peat extraction. Plant material for spreading on both sites was collected from raised bogs in a natural state. *Dactylis glomerata* hay was used for mulching in NR and straw was used in NP. The area of each experimental site is about 0.05 ha. The uppermost peat layer at the NR site has higher ash and moisture content and pH, but also higher nutrient (N, P, K, PO_4-P) contents than at the NP experimental site, which has led to higher *Sphagnum* biomass on that site, while forest mosses dominate in NR (Purre & Ilomets 2018). The range of water table depth fluctuations is mainly 20–30 cm at NR and 20–40 cm at NP.

Plant cover determination

Square (25 × 25 cm) permanent plots were established at each site during restoration (75 plots at Ohtu (NR) in 2006; 60 plots at Viru (NP) in 2008) and marked with white plastic pipes. Some plots were left out of analysis during subsequent years due to loss of permanent plot markers as a result of human vandalism or animal activities.

Cover (%) of plant species, lichen, bare peat, mulch and litter was determined visually from permanent plots for six years at NR and seven years at NP (Table 1). Rochefort *et al.* (2013) support the use of permanent plots to determine cover changes of key plants on restored peatlands as it is reliable and cost-efficient.

Substrate sampling and analysis

Peat samples (30 samples from either site) were collected from both sites in autumn 2015. The topmost (0–5 cm) peat samples were collected using a polyvinyl chloride (PVC) cylinder with a diameter of 5 cm. During sampling, peat pH was measured in every sampling point with a “Knick Portamess” (Knick, Germany) pH-meter. The moisture content (%) at 60 °C was determined in the laboratory by drying about 65 g of wet peat sample (exact weight of each sample was recorded) in an oven at 60 °C for 48 hours. The ash content of the dried peat was then determined through combustion of the samples on 550 °C for 6 h (Chambers *et al.* 2011).

The Ca content (%) was measured in the Laboratory of Chemical Analysis in Tallinn Technological University using atomic absorption spectrophotometry using “SpectrAA 220F” (Varian, USA) spectrophotometer. N (%), P (%), K (%), and P-PO_4 contents (mg kg^{-1}) of peat were determined in the Laboratory of Plant Biochemistry at the Estonian University of Life Sciences. The Kjeldahl method (Parkinson & Allen 1975) was used to determine N and P content, PO_4-P content was measured by ammonium lactate solubility and K content of the peat was analysed using the ammonium lactate extraction method. Chemical analyses are described in more detail in Purre & Ilomets (2018).

Table 1. Plant cover estimation dates and number of permanent plots at the study sites. n.d. indicates years when plant cover photographs were not captured.

	Nutrient-rich site		Nutrient-poor site	
Year	Date	No. plots	Date	No. plots
2009	29 Oct	59	19 Nov	73
2010	n.d.		n.d.	
2011	02 Nov	57	21 Sep	40
2012	n.d.		11 Oct	40
2013	24 Aug	54	14 Aug	39
2014	09 Sep	54	n.d.	
2015	24 Sep	54	12 Oct	39
2016	n.d.		n.d.	
2017	n.d.		19 Sep	39
2018	20 Jun	51	07 Jun	39

Data analysis

The data were analysed using IBM SPSS Statistics ver. 23 software. All results were considered statistically significant when $p < 0.05$. All results in the text are presented as mean ± *SE*. Shapiro-Wilk tests revealed deviations from the normal distribution of variables; therefore, nonparametric methods were used for data analysis. For the analysis of variance we used the Kruskal-Wallis test, and for the pair-wise comparison of variables the Mann-Whitney U test. This was used to test the differences in vegetation variables between the sites. Spearman correlation coefficient was used to relate vegetation and substrate cover to years since restoration, and bryophyte cover to vascular plant abundance. Fisher $r-z$ transformation (Fisher 1928) was used to analyse the similarity of correlation between two sites.

PC-ORD 7.0 software was used for redundancy analysis (RDA) on vegetation data for the year 2018, detrended correspondence analysis (DCA) and Mantel randomisation test. Explanatory variables with r lower than 0.20 were excluded. RDA was used to relate peat chemical properties to plant functional type (PFT) cover. Plant taxa was also divided to oligotrophic peatland species, minerotrophic peatland species, generalist species and mineral soil species according to Kask (1982) for vascular plants and Kannukene & Kask (1982) for bryophytes. Division of plant taxa by PFTs and by peatland specific, mineral soil and generalist plant taxa is shown in Table 2. Variation partitioning using multiple RDAs was done based on Borcard *et al.* (1992). DCA was used to find the main gradients in plant species data, as we used data from all of the study years in the analysis and added time since restoration as a supplementary variable. Shannon diversity index based on PFTs abundance was calculated according to Shannon (1948) also in PC-ORD 7.0:

$$H' = \sum_{i=1}^{R} p_i ln p_i \quad [1]$$

where H' is Shannon diversity index, and p_i is proportion of PFT i in permanent plot.

Table 2. Average vegetation coverage (%) at the study sites in 2018 between the nutrient-rich and the nutrient-poor site, and species type according to Kask (1982) and Kannukene & Kask (1982). The statistical significance of the difference between the sites is shown according to results of Mann-Whitney test. OP indicates species typical to oligotrophic peatlands; MP indicates species typical to minerotrophic peatlands; G indicates generalist species; MS indicates species typical to mineral soils; + indicates that species is present but with very low (< 0.5 %) cover; - indicates that species or plant functional type is absent from the site.

	Nutrient-rich site	Nutrient-poor site	Statistical significance	Species type
Hummock *Sphagna* (%)	-	17 ± 4	Z = 5.3; p < 0.01	
S. fuscum (%)	-	12 ± 3	Z = 5.1; p < 0.01	OP
S. rubellum (%)	-	5 ± 2	Z = 3.8; p < 0.01	OP
Lawn *Sphagna* (%)	5 ± 2	39 ± 6	Z = 5.0; p < 0.01	
S. angustifolium (%)	4 ± 2	28 ± 6	Z = 3.5; p < 0.01	OP
S. magellanicum (%)	1 ± 1	11 ± 4	Z = 4.2; p < 0.01	OP
***Sphagnum* (%)**	5 ± 2	56 ± 6	Z = 7.2; p < 0.01	
True moss (%)	15 ± 4	8 ± 2	Z = 0.3; p > 0.05	
Polytrichum strictum (%)	+	7 ± 2	Z = 4.8; p < 0.01	OP
Aulacomnium palustre (%)	8 ± 2	+	Z = 3.1; p < 0.01	MP
Pleurozium schreberi (%)	8 ± 2	+	Z = 2.9; p < 0.01	G
Dicranum polysetum (%)	+	1 ± 1	Z = 1.3; p > 0.05	G
Evergreen shrub (%)	76 ± 3	30 ± 4	Z = 6.7; p < 0.01	
Vaccinium oxycoccus (%)	8 ± 2	3 ± 1	Z = 2.0; p > 0.05	OP
Calluna vulgaris (%)	68 ± 3	26 ± 4	Z = 6.4; p < 0.01	G
Andromeda polifolia (%)	-	1 ± 0	Z = 3.1; p < 0.01	OP
Empetrum nigrum (%)	+	-	Z = 1.3; p > 0.05	OP
Rhododendron tomentosum (%)	+	1 ± 0	Z = 0.5; p > 0.05	OP
Deciduous shrub (*Vaccinium uliginosum*) (%)	+	1 ± 0	Z = 0.8; p > 0.05	G
Ombrotrophic forb (*Drosera rotundifolia*) (%)	-	+	Z = 2.6; p < 0.05	OP
Minerotrophic forb *(Epilobium angustifolium)* (%)	+	-	Z = 1.8; p > 0.05	MS
Minerotrophic grasses (*Phragmites australis***)** (%)	+	-	Z = 1.8; p > 0.05	G
Ombrotrophic sedge (*Eriophorum vaginatum*) (%)	12 ± 3	5 ± 1	Z = 1.1; p > 0.05	OP
Minerotrophic sedge (*Carex spp*.)	+	-	Z = 1.6; p > 0.05	MP
Evergreen tree (*Pinus sylvestris*)	7 ± 2	2± 1	Z = 2.0; p < 0.05	G
Deciduous tree (%)	5 ± 1	+	Z = 4.3; p < 0.01	
Betula pendula (%)	24± 1	+	Z = 4.0; p < 0.01	MS
Salix spp. (%)	+	-	Z = 1.3; p > 0.05	MP
Populus tremula (%)	1 ± 0	-	Z = 1.3; p > 0.05	MP
Lichen (%)	-	4 ± 2	Z = 3.5; p < 0.01	
Litter (%)	12 ± 2	9 ± 3	Z = 2.1; p < 0.05	
Bare peat (%)	+	32 ± 5	Z = 7.7; p < 0.01	

RESULTS

Vegetation cover and peat chemical factors

By the end of the study period in 2018, the two sites differed significantly by their vascular plant and bryophyte cover, but the sites differed also significantly by their peat chemistry (Tables 2 and 3). Sum of vascular plant species coverage was significantly higher in NR (102 ± 3 %; NP 37 ± 4 %; $Z = 8.0$; $p < 0.01$), whereas bryophyte cover was higher in NP (NR 20 ± 4 %; NP 64 ± 4 %; $Z = 5.6$; $p < 0.01$). *Sphagnum* was widespread in NP but made up only about one third of bryophyte cover in NR. The cover of litter was higher at NR, while cover of lichens and bare peat was higher at the NP site.

RDA analysis including peat chemical characteristics and site explained about 38 % of variation in PFT compositions during the last measurement year while about 62 % of variance was undetermined. The first axis of RDA correlated strongest with Ca, N and pH while the second axis correlated with P-PO_4 and K contents (Figure 1). Cover of different PFTs was mostly explained by differences in peat N content and pH, but also peat Ca, P, P-PO_4 and moisture contents. Peat K and ash contents, and especially peat decomposition levels had weakest effect on vegetation development (Table A1 in the Appendix). According to RDA, higher cover of vascular plant PFTs are related to higher pH values and nutrient content in the peat, whereas *Sphagnum* cover is higher in NP, with lower peat ash and higher moisture content. According to randomisation tests of RDA species - environment correlations and eigenvalues for individual axes were significant ($p < 0.05$). Variation partitioning showed that “site” itself explained about 14 % variation in PFT matrix, while including only peat chemistry variables (Ca, N, K, P, ash and moisture contents, and pH), about 35 % of variation in PFT matrix was explained. The Mantel test indicates that the environmental and PFT matrices have positive relationship ($r = 0.26$; $p < 0.01$) in 2015 when both peat chemistry and plant coverages were analysed.

DCA solution of substrate cover throughout the study period was significant according to randomisation test ($p < 0.05$; Figure 2). First axis in DCA corresponds to differences in time since restoration and site nutrient content, while the second axis can be explained with differences in moisture conditions indicating wetter conditions in the positive end of the axis. Similarly, to correlation analysis, DCA shows, that with time since restoration, substrate cover of permanent plots succeeds from mulch and bare peat, to bryophytes, and then to vascular plants (mainly tree and shrub species) at NR site and peatland plant communities at NP site.

Table 3. Average species group coverage (%) at the study sites in 2018, and peat chemical properties according to Purre & Ilomets (2018) between the nutrient-rich and the nutrient-poor site. The statistical significance of the difference between the sites is shown according to results of Mann-Whitney test. * indicates data from Purre & Ilomets (2018); species were grouped according to Kask (1982) and Kannukene & Kask (1982), see Table 2.

	Nutrient-rich site	Nutrient-poor site	Statistical significance
Oligotrophic peatland species (%)	26 ± 3	72 ± 6	Z = 5.3; p < 0.01
Minerotrophic peatland species (%)	8 ± 2	0 ± 0	Z = 4.0; p < 0.01
Generalist species (%)	83 ± 4	29 ± 4	Z = 6.9; p < 0.01
Mineral soil species (%)	5 ± 1	0 ± 0	Z = 4.3; p < 0.01
Peat moisture content (%)*	80.2 ± 0.6	84.4 ± 0.6	Z = 4.5; p < 0.01
Peat ash content (%)*	4.9 ± 0.4	1.4 ± 0.1	Z = 7.5; p < 0.01
Peat decomposition level (von Post)*	H2 – H8	H3 – H6	Z = 0.6; p > 0.05
pH*	4.1 ±0.1	3.1 ± 0.0	Z = 6.4; p < 0.01
N (%)*	1.40 ± 0.05	0.90 ± 0.02	Z = 5.1; p < 0.01
P (%)*	0.06 ± 0.00	0.05 ±0.00	Z = 4.1; p < 0.01
K (%)*	0.04 ± 0.00	0.03 ± 0.00	Z = 3.3; p < 0.01
Ca (g kg^{-1})*	303 ± 20.9	92.3 ± 6.2	Z = 6.6; p < 0.01
P-PO_4 (mg kg^{-1})*	60.9 ± 3.4	45.7 ± 3.0	Z = 3.0; p < 0.01

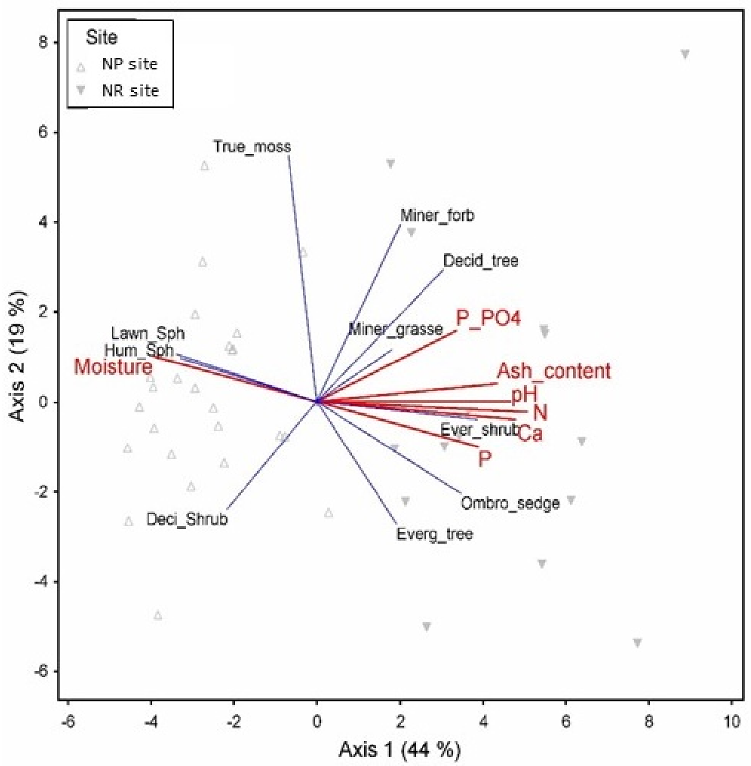

Figure 1. Redundancy analysis of substrate properties and PFT cover. Eigenvalues for the first and second axis are 4.4 and 1.9 respectively. Decid_tree = deciduous trees; Everg_tree = evergreen trees; Deci_Shrub = deciduous shrubs; Ever_shrub = evergreen shrubs; Miner_grasse = minerotrophic grasses; Miner_forb = minerotrophic forbs; Ombro_sedge = ombrotrophic sedges; Lawn_Sph = lawn *Sphagnum*; Hum_Sph = hummock *Sphagnum*. Minerotrophic sedges and ombrotrophic forbs were left out from the analysis due to their very low occurrence at the study sites. Peat decomposition and K content were left out during forward selection of variables for RDA.

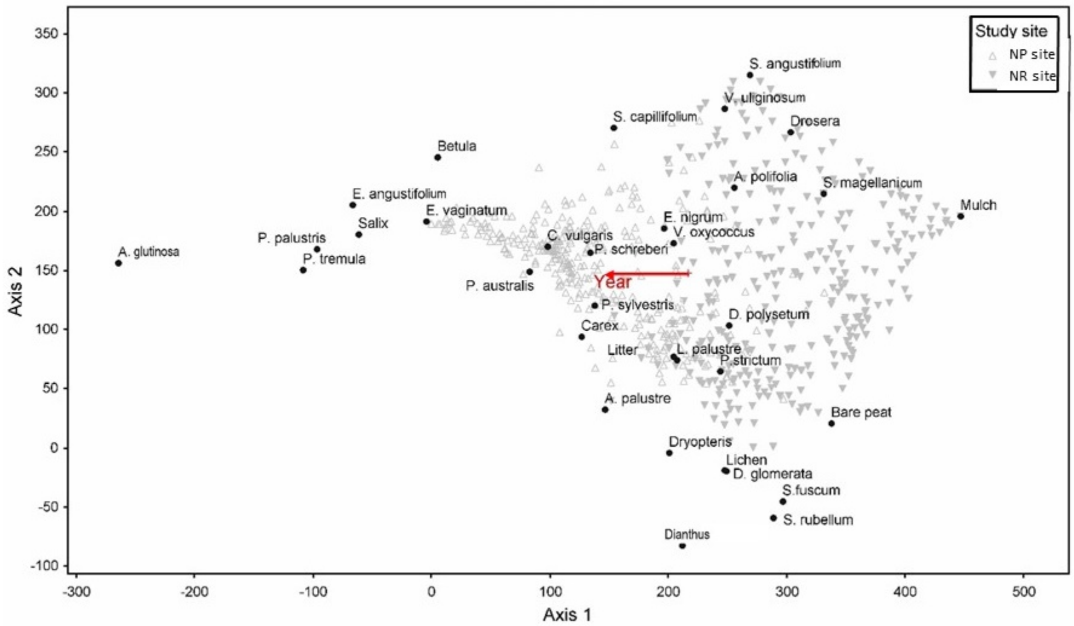

Figure 2. Detrended correspondence analysis (DCA) of plant species at the study sites during the study period. Eigenvalues for the first and second axes are 0.636 and 0.413, respectively. Gradient lengths for the first and the second axes are 4.469 and 3.092, respectively.

Development of vegetation cover

Time since restoration correlated significantly with some PFTs cover (Figure 3, Table A2). Evergreen shrub cover has increased in both sites with time after the restoration, while *Sphagnum* cover increased in NP while decreased in NR. Mulch cover vanished in both sites completely during the first few years after restoration. Lichens were present in low abundance at NP but were absent from the NR site (Figure 4).

From NR throughout the study period, 29 plant taxa were found, compared to 17 different taxa at NP (Table A2). Although averaged during the experiment, the amount of PFTs (NR 3.4±0.1; NP 2.9±0.1; Z = 5.7; $p < 0.01$) and Shannon diversity index calculated based on PFTs cover (NR 0.8±0.0; NP 0.7±0.0; Z = 3.5; $p < 0.01$) was significantly higher at NR. By the end of experiment in 2018 the amount of PFTs (NR 3.3±0.2; NP 3.6±0.2; Z = 1.0; $p > 0.05$) and Shannon diversity index (NR 0.8±0.1; NP 0.9±0.1; Z = 1.5; $p > 0.05$) were higher at the NP site. Shannon diversity index was positively correlated with time since restoration at NP (r = 0.44; $p < 0.01$), while no such correlation was found at NR (r = –0.05; $p > 0.05$) (Figure 5).

The NP site was dominated by the oligotrophic peatland species, while during the end of the experiment some small increase in generalist plant species was observed in this site (Figure 6). At the NR site, abundance of peatland specific species has declined, and generalist species have increased their abundances. Over the study period at the NR site also mineral soil species have increased their abundances slowly.

Vascular plants and bryophytes

At NR, increasing vascular plant cover throughout the study period and all plots correlates with decreasing bryophyte (r = -0.65; $p < 0.01$) and *Sphagnum* (r = -0.24; $p < 0.01$) cover (Figures 3, 4). Conversely higher vascular plant cover correlates positively with bryophyte (r = 0.23; $p < 0.01$) and *Sphagnum* (r = 0.19; $p < 0.01$) cover at NP. Differences in those correlations were statistically significant ($Z < -12.72$; $p < 0.01$) according to Fisher's $r – z$ transformation.

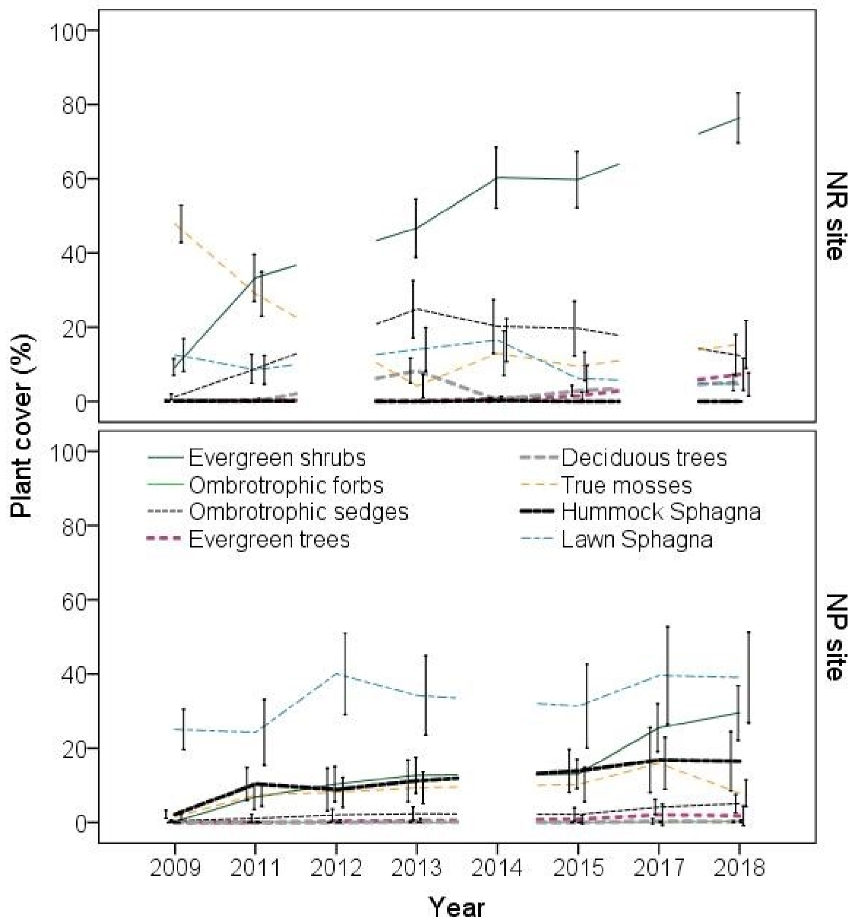

Figure 3. Changes in PFT cover at the study sites. Average values are brought with ±95 % confidence intervals. Deciduous shrubs, minerotrophic grasses, minerotrophic forbs and minerotrophic sedges were excluded from the figure due to their very low cover on all years and sites.

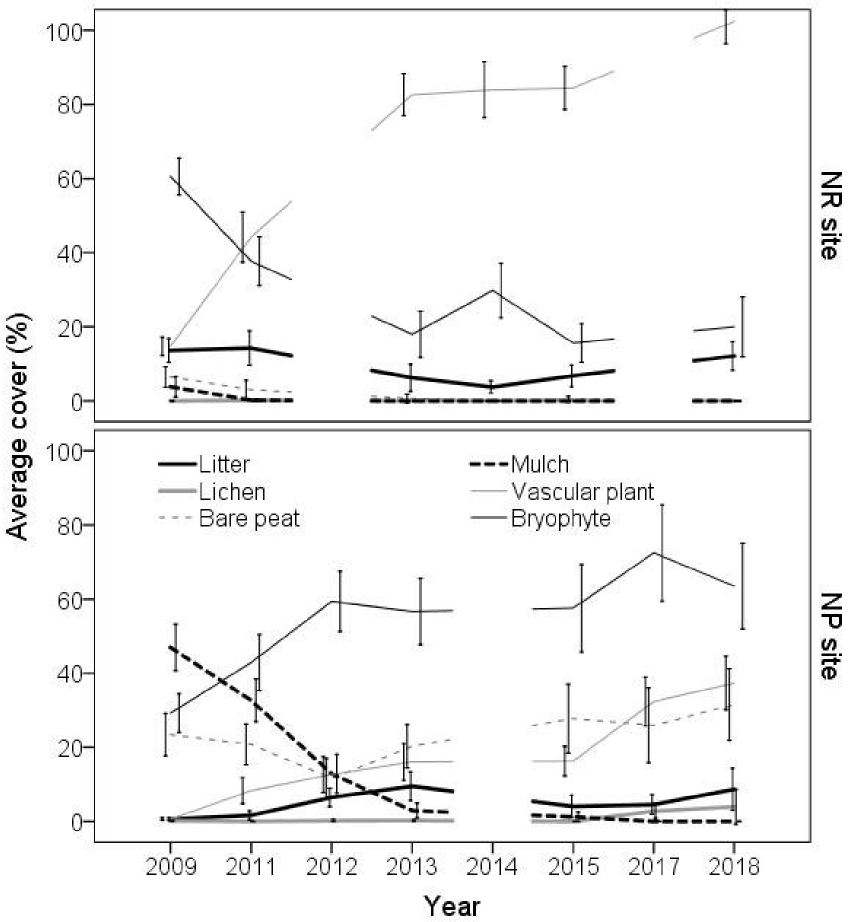

Figure 4. Changes in substrate cover at the study sites. Average values are shown with ±95 % confidence intervals.

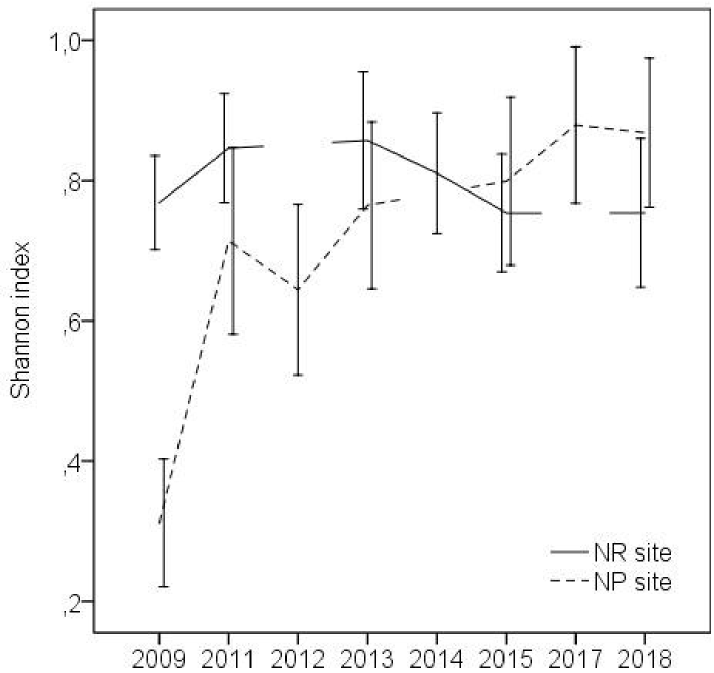

Figure 5. Shannon diversity index of PFTs at the study sites. Average values are shown with ±95 % confidence intervals.

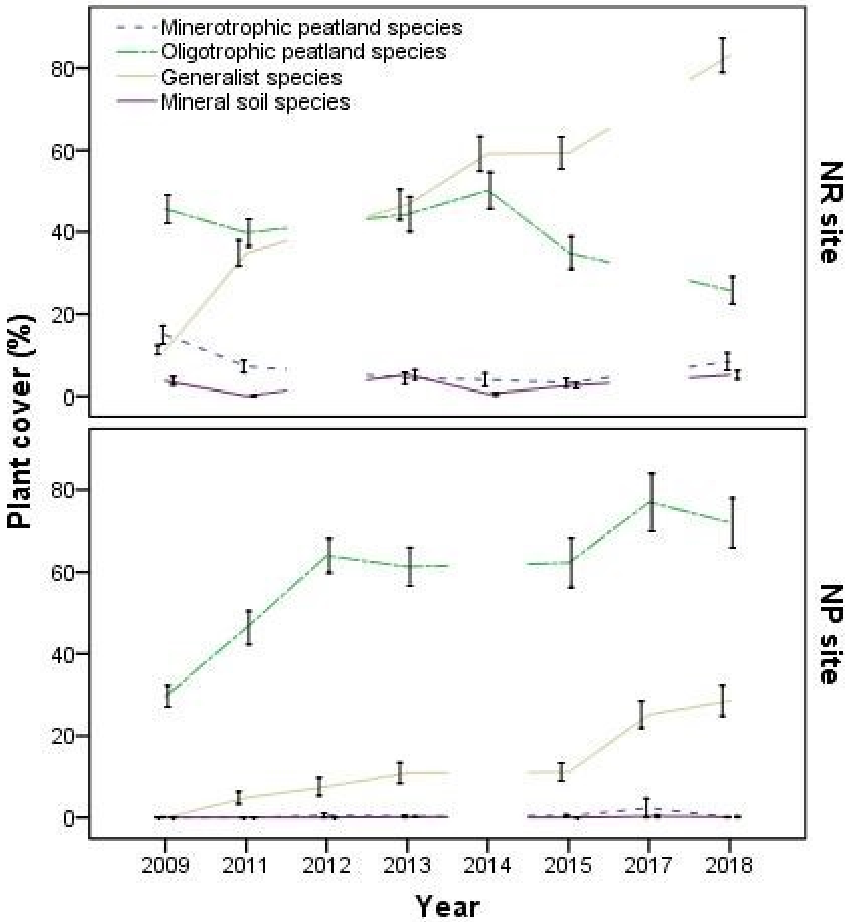

Figure 6. Changes in cover of minerotrophic and oligotrophic peatland, generalist and mineral soil species at the study sites throughout the study period. Average values are shown with ±95 % confidence intervals.

DISCUSSION

Vegetation and peat chemistry

The two restored milled peatland sites with different peat nutrient contents differ by their vegetation composition - the NR site has higher cover of vascular plants while the NP site is dominated by *Sphagnum*. Cover of different PFTs in the study sites were mainly explained by peat Ca and N contents and pH. According to Hájková & Hájek (2004) and Gagnon *et al.* (2018), pH creates the main environmental gradient on peatlands, so creating conditions for the development of different plant communities - lower pH leads to vegetation similar to bogs, while higher pH to dominance of fen vegetation. This pattern was also observed in the current study, as increased vascular plant PFTs cover, presence of minerotrophic peatland and mineral soil species were connected with higher pH and nutrient contents, while *Sphagnum* and oligotrophic peatland species were in the other end of the gradient. Similar results were reached by Triisberg *et al*. (2014), Paal *et al*. (2016) and Renou-Wilson *et al.* (2019). Typical dominants on restored peatlands like *Polytrichum strictum*, *Calluna vulgaris* and *Eriophorum vaginatum* communities, which were abundant at the NR site, are in the middle part of the pH and nutrient gradient (Triisberg *et al*. 2014).

Different vascular plant PFTs had somewhat different correlations with various peat nutrients. In the current study, higher evergreen shrub cover was on plots with higher P content similarly to Tuittila *et al.* (2000). Also cover of the ombrotrophic sedge *E. vaginatum* increased with peat P and C contents similarly to Sottocornola *et al.* (2007). Deciduous shrubs (represented by *Vaccinium uliginosum*) were the only vascular plant PFT with a negative correlation with nutrient contents of the peat. This species is usually found in the NP conditions of bog edges and bog forests (Krall *et al*. 2010).

The NR site had higher cover of plant litter, shrub and sedges, and low cover of *Sphagnum* similarly to mesotrophic peatland in the study by Renou-Wilson *et al.* (2019) indicating that higher nutrient concentrations in the upper peat layer of restored peatlands lead the succession to vascular plant dominated fen-like vegetation. PFT cover, especially *Sphagnum*, shrub and forbs, is similar to raised bog vegetation on rewetted NP milled peatlands (Zając *et al*. 2018, Renou-Wilson *et al*. 2019) as in the current study. This supports the previous studies relating higher *Sphagnum* production with higher peat moisture content (Potvin *et al*. 2015, Paal *et al*. 2016, Purre & Ilomets 2018), while true mosses (Sottocornola *et al*. 2007, Purre & Ilomets 2018) and vascular plants (Berendse *et al*. 2001, Limpens *et al*. 2003, Malmer *et al*. 2000) benefit from higher nutrient contents. Therefore, peat physical and chemical properties should be determined prior to restoration to ensure that a suitable approach is chosen which takes into account the peat properties of the site, and therefore whether the succession of the restored peatland is likely to be towards a fen or bog ecosystem.

Time since restoration

Abundances of various PFTs increased or decreased with time since restoration. Time since restoration is considered to be an important predictor of plant cover in restored peatlands (Chirino *et al*. 2006, Karofeld *et al*. 2015, Orru *et al*. 2016, Hancock *et al*. 2018, Triisberg-Uljas *et al*. 2018), whereas in the study by González *et al*. (2013) time since restoration explained only about 4 % of variation in vegetation composition. At our two sites, vascular plant cover increased significantly with time following restoration as also reported by González & Rochefort (2014) and Karofeld *et al*. (2015).

According to Triisberg *et al*. (2014), recently abandoned milled peatlands in Estonia are covered by *E. vaginatum*, *C. vulgaris* and *P. strictum* which evolve into communities that are characteristic to transitional mires and raised bogs with time. This coheres with our results from the NP site and another nutrient-poor restoration site in Estonia (Karofeld *et al*. 2015), while generalist species increased their abundances throughout the study period in the NR site.

Bryophyte cover increased at NP and decreased at NR with time. Therefore, NR site differed from the NP sites as described by Chirino *et al*. (2006), Rochefort *et al*. (2013), González & Rochefort (2014) in Canada and in Estonia by Karofeld *et al*. (2015). Generally, cover of PFTs in our study remain in the ranges of previous studies (González & Rochefort 2014, González *et al*. 2014a), while in some studies (Chirino *et al*. 2006, Karofeld *et al*. 2015), higher *Sphagnum* cover was obtained sooner after restoration, whereas vascular plant cover remained lower than in the current study.

In both study sites evergreen shrub cover, mainly *Calluna vulgaris*, has increased with time since restoration. The slower growth of shrubs than sedges and herbs has been widely reported by previous studies (Lavoie *et al*. 2005, Feldmeyer-Christe *et al*. 2011, Pouliot *et al*. 2012, González *et al*. 2013, González & Rochefort 2014). As ericaceous shrubs with mycorrhiza are characteristic of deeper groundwater levels (Laine *et al*. 2012, Potvin *et al*. 2015), high and increasing cover of *C. vulgaris* indicates the need for further restoration activities to raise the water table.

Hummock *Sphagnum* species were absent from NR, where they had not been actively dispersed during restoration, whereas their cover increased slowly but steadily at the NP site. González *et al*. (2014b) anticipate that more time since restoration is needed for establishment of hummock *Sphagnum* if they are not dispersed during restoration. However, hummock *Sphagnum* species like *Sphagnum fuscum* have good immigration potential (Campbell *et al*. 2003) and their absence at NR could also be explained by unfavourable conditions at the restored site, such as high nutrient contents and shading from vascular plants in the later stages of succession.

Shannon diversity index increased over time following restoration at NP similarly to results of Tuittila *et al*. (2000) while being stable at NR. In temperate peatlands, number of plant species tends to decrease with succession in a longer time-scale after the restoration from peat milling due to shading from woody species (Prach *et al*. 2014). At the NR site, increasing shading from vascular plants could be the cause of a reduction in bryophyte PFTs such as true mosses and lawn *Sphagnum*, and therefore a small decrease in Shannon index in the end of the study period. The difference between the sites could originate from differences in nutrient richness, as Kozlov *et al*. (2018) reported faster vegetation succession at NR sites as in the current study.

Vascular plants and bryophytes

At the NP site, where vascular plant cover was relatively low, it did not inhibit the development of moss layer. Some results suggest that the presence of vascular plants, especially *E. vaginatum*, could improve *Sphagnum* regeneration on restored milled peatlands by reducing frost heaving and improving moisture conditions on milled peatlands (Ferland & Rochefort 1997, Lavoie *et al*. 2003). The presence of shrubs is positively related to moss surface height, so supporting the development of microtopography on revegetated milled peatlands (Pouliot *et al*. 2012).

At NR site higher vascular plant cover resulted in lower *Sphagnum* and bryophyte cover. In case of high shrub and tree abundance, the shading and litter from vascular plants could reduce the abundance of *Sphagnum* and change the species composition of the moss layer (Paal *et al*. 2016). The negative impact of higher vascular plant cover on *Sphagnum* is probably site-specific (Limpens *et al*. 2004). Vascular plant litter cover was higher at NR, so corroborating the results of Berendse *et al*. (2001). High litter cover (exceeding 20 %) reduces *Sphagnum* cover (Gaudig *et al*. 2017), while in our study, average litter cover did not exceed that limit at any of the sites throughout the nine-year period of the study.

One possibility to decrease the negative effects of vascular plants on development of moss layer could be removal of vascular plants. Guêné-Nanchen *et al*. (2017) showed that mowing of graminoids (*Eriophorum angustifolium*) had no effect on *Sphagnum* cover in a *Sphagnum* farm, while Gaudig *et al*. (2017) found that mowing of vascular plants was beneficial to *Sphagnum* productivity at *Sphagnum* farming sites where several different vascular PFTs were present. In our case, the main vascular plants at the NP site were *E. vaginatum*, which creates dense tussocks, and *C. vulgaris*, which shades the moss layer. *E. vaginatum* has also been reported to reduce the peat N and P contents (Kaštovská *et al.* 2018), so creating unsuitable conditions for other vascular plants. Initial removal of shrubs can result in increased shrub cover through re-sprouting, where there are relatively low water tables (Tuittila *et al.* 2000), and similar results have been found with birch (*Betula pubescens*, *Betula pendula*) removal, although it resulted in a short-term increase in the abundance of *Sphagnum* and other peatland species (Czerepko *et al.* 2018). Therefore, the effect of vascular plant removal is not uniform, and further studies should be conducted.

The current study demonstrates the importance of peat chemistry on restoration success on milled peatlands. Applied restoration activities were successful at the NP site where species composition typical to oligotrophic peatlands and *Sphagnum* carpet had formed. At the NR site, generalist vascular plant species dominated and therefore further restoration measures should be applied to support the development of minerotrophic vegetation composition. This is more in accordance with the nutrient-rich peat chemistry conditions in the site than oligotrophic peatland vegetation initially aimed at by applying the MLTT. High abundance of shrubs at the NR site indicates that the relatively deep water table (about 20–30 cm) does not support the development of (minerotrophic) peatland species, but communities evolve in direction of generalist vascular plants. At NR, if the main aim is to restore the bryophyte carpet, repeated mowing of vascular plants until dense bryophyte carpet has formed could have beneficial effect on restoration outcomes and should be studied further, simultaneously to applying additional measures for raising the water table.

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AUTHOR CONTRIBUTIONS

MI and LT designed and prepared the experimental sites. AHP, LT and MI planned the study. LT and AHP photographed the permanent plots throughout the years and AHP analysed the plant cover and was responsible for conducting and organising the peat chemistry analysis. AHP did the statistical analyses and prepared the manuscript with support of MI and LT. All authors contributed to the final version of the manuscript.

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Appendix

Table A1. Standardised regression coefficients according to RDA between plant functional type cover and peat chemistry at both study sites in 2015. * indicates $p < 0.05$; ** $p < 0.01$. Ombrotrophic forbs and minerotrophic sedges were not present on plots where peat chemistry samples were collected and were therefore omitted from the analysis.

	Ca_{peat}	N_{peat}	P_{peat}	K_{peat}	$P\text{-}PO_{4,\ peat}$	ASH_{peat}	$Moisture_{peat}$	pH_{peat}	$Decomposition_{peat}$	R^2
Evergreen shrubs	0.44**	0.41**	-0.11	-0.28	-0.03	0.14	-0.32*	-0.22	0.02	0.55
Deciduous shrubs	-0.15	-0.37*	0.16	0.37*	-0.05	-0.21	0.11	0.39*	0.02	0.11
Minerotrophic forbs	-0.48**	0.16	-0.19	-0.18	0.54**	0.16	0.24	0.72**	-0.18	0.67
Minerotrophic grasses	0.46**	0.49**	-0.04	-0.02	0.18	-0.17	0.33*	-0.38*	0.03	0.22
Ombrotrophic sedge	0.24	0.05	0.15	0.13	0.00	-0.30	-0.11	0.23	0.00	0.23
Evergreen trees	-0.07	-0.67**	0.40*	0.11	-0.53**	-0.11	-0.17	0.19	0.03	0.71
Deciduous trees	-0.18	0.44**	-0.39*	-0.12	0.34*	-0.08	-0.04	0.49**	-0.16	0.40
True mosses	-0.10	0.23	-0.13	-0.09	0.37*	0.57**	0.43**	-0.55**	0.05	0.20
Hummock *Sphagna*	-0.03	-0.29	0.23	0.08	0.11	-0.11	0.44**	-0.04	0.06	0.29
Lawn *Sphagna*	-0.13	0.15	-0.40	0.02	-0.06	-0.04	0.01	-0.06	0.01	0.19

Table A2. Spearman correlation coefficients between plant functional type, species and its group, and year since restoration. - indicates that species is absent from the site. * indicates $p < 0.05$; ** – $p < 0.01$.

	Nutrient-rich site	Nutrient-poor site
Hummock Sphagna	-0.09	0.20**
S. fuscum	-0.09	0.21**
S. rubellum	-	0.15**
Lawn Sphagna	-0.18**	0.06
S. angustifolium	-0.12*	-0.06
S. magellanicum	-0.31**	-0.15**
S. capillifolium	0.03	0.04
Sphagnum	-0.19**	0.30**
True moss	-0.47**	0.26**
Polytrichum strictum	-0.59**	0.24**
Aulacomnium palustre	-0.28**	0.05
Pleurozium schreberi	0.05	-0.02
Dicranum polysetum	-0.02	0.12*
Evergreen shrub	0.64**	0.65**
Vaccinium oxycoccus	0.24**	0.28**
Calluna vulgaris	0.58**	0.59**
Andromeda polifolia	-0.11*	0.23**
Empetrum nigrum	0.12*	-0.01
Rhododendron tomentosum	0.01	0.08
Deciduous shrub (*Vaccinium uliginosum*)	0.01	0.13*
Ombrotrophic forb (*Drosera rotundifolia*)	-	0.14*
Minerotrophic forb	0.01	-
Epilobium angustifolium	0.14*	-
Dianthus sp.	-0.11*	-
Thelypteris palustris	-0.11*	-
Potentilla palustris	0.01	-
Minerotrophic grasses	-0.22**	-
Phragmites australis	-0.03	-
Dactylis glomerata	-0.31*	-
Ombrotrophic sedge (*Eriophorum vaginatum*)	0.28**	0.35**
Minerotrophic sedge (*Carex spp.*)	-0.03	-
Evergreen tree (*Pinus sylvestris*)	0.28**	0.24**
Deciduous tree	0.34**	0.08
Betula pendula	0.35**	0.08
Salix spp.	0.02	-
Populus tremula	0.09	-
Alnus glutinosa	-0.01	-
Lichen	-0.08	0.25**
Litter	-0.25**	0.24**
Bare peat	-0.44**	0.07
Mulch	-0.26*	-0.83**
Oligotrophic peatland species (%)	-0.19**	0.43**
Minerotrophic peatland species (%)	-0.24**	0.05
Generalist species (%)	0.64**	0.61**
Mineral soil species (%)	0.15**	0.08