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The effect of peatland restoration on bryophyte and vascular plant species richness, community composition and community dispersion

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Summary

The diminishing area of pristine nature combined with the degraded stage of human altered landscapes has led to international targets of restoring degraded areas to safeguard ecosystems and their services. Because from the viewpoint of the communities restoration is another disturbance the effect of restoration on community assembly processes might be similar to that of disturbance. We used boreal peatlands representing three peatland types (spruce mires, pine mires and fens) with two levels of productivity to test whether this is the case. Half of the sites are in pristine stage and half had been restored after being drained for forestry for several decades. We sampled bryophyte and vascular plant species before (n = 120), two years after restoration (n = 115) and five years after restoration (n = 52).). In addition we analyzed a few alkaline fens in which we did not have different productivity levels. On the basis of our previous study of the changes in peatland community assembly processes after disturbance (Elo *et al.* 2014) we predict that restoration i) has no influence on species richness, ii) has an effect on community composition, and iii) has no influence on community dispersion (i.e. variation in community composition among sites). We used linear mixed models, permutational multivariate analysis, and the test of homogeneity of multivariate to analyze changes in species richness, community composition and dispersion in two and five years after restoration. Restoration increased *Sphagnum* moss abundance in spruce mires and decreased forest moss abundance in spruce mires and in alkaline fens. In addition, vascular plant communities in pine mires were affected by restoration. Despite of these changes, the general effect of restoration on bryophyte and vascular plant species richness, community composition and dispersion are still very subtle and inconsistent after five years. Thus, a long-term monitoring in order to determine whether restoration affects community assembly processes is clearly required.

Introduction

Over the past centuries human impact in ecosystems have been increasing in accelerated rate, currently reaching the point where only a quarter of the terrestrial landscape can be considered as wildlands (Ellis *et al.* 2010). This diminishing area of pristine nature combined with the degraded stage of human altered landscapes has led to international targets of restoring 15 % of the degraded areas by the year 2020 in order to safeguard ecosystems and their services (Convention on Biological Diversity 2010). Thus, although restoration has belong to conservation practitioners toolbox for quite a while it is likely that it is going to be put to use more often. Unfortunately, not all of the restoration activities are successful (Lockwood & Pimm 1999; Rey Benayas *et al.* 2009; Maron *et al.* 2012). Knowledge of the processes dominating in community assembly could help to predict how community response to restoration, and thus improve the chances of a successful outcome.

The processes determining all patterns in community ecology are speciation, drift, selection and dispersal (Vellend 2010). Speciation adds new species to the species pools and is thus the original source of variation in species richness which is further shaped in local communities by drift, selection and dispersal. Drift leads to random changes in species relative abundances and following random extinctions whereas selection leads into fitness differences among individuals of different species. Dispersal is movement of individuals and it may be completely stochastic or deterministic and interact with drift and selection (Vellend *et al.* 2014). Insights of which of these processes are dominating in a particular community can be achieved by studying community composition and particularly community dispersion (i.e. variation in community composition among sites, often called also as beta diversity) (Passy & Blanchet 2007; Vellend *et al.* 2007; Houseman *et al.* 2008; Murphy & Romanuk 2012; Elo *et al.* 2014). If communities are shaped by selection, restoration acts changing local environmental conditions lead to change in the direction or magnitude of selection. This is what is commonly assumed in restoration projects (Hilderbrand, Watts & Randle 2005). However, depending on whether local environmental conditions, and hence the direction of selection, become uniform or heterogenic, the result may be either increased or decreased community dispersion. Also, as disturbance may change the relative importance of selection and drift (Chase 2007) the same may be true for restoration. For instance, restoration acts may drop species out of the regional species pool which increases the relative importance of selection and decreases community dispersion.

But if the changes in communities are detectable only after the restoration has been conducted how can we predict these changes? From the viewpoint of the newly formed communities in degraded sites restoration is another disturbance: *'…a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established´* (Sousa 1984). Thus, we could use the knowledge of the processes underlying the changes in community assembly after disturbance to predict how communities will respond to restoration (Suding, Gross & Houseman 2004; Murphy & Romanuk 2012).

Here we tested whether the effect of restoration on community assembly processes is similar to that of disturbance. We used a set-up of 120 boreal peatlands of which half are in pristine stage and half had been restored after being drained for forestry for several decades, and sampled bryophyte and vascular plant species before restoration, two years after restoration and five years after restoration. We have previously shown that communities in these drained and pristine peatlands did not differ in species richness before restoration (Elo *et al.* 2014). Instead, drained and pristine peatlands had different community compositions, yet similar community dispersions. Altogether, this indicates a directional selection due to disturbance and no change in the relative strength of selection and drift. Hence, we suggested that restoration of the original physical properties, i.e. hydrological regime in the case of peatlands, may be enough for restoring the community composition, the key assumption made in several restoration projects (Hilderbrand, Watts & Randle 2005). Of course, this assumption rests on whether the pool of original species is still available in the landscape to recolonize the communities. On the basis of our previous study on the changes in peatland community assembly processes after disturbance (Elo *et al.* 2014) we predicted that restoration i) has no influence on species richness, ii) has an effect on community composition, and iii) has no influence on community dispersion.

Material & methods

Study sites & sampling

We used bryophyte and vascular plant data from 120 peatlands from National Peatland Restoration Monitoring Network established by Metsähallitus Natural Heritage Services and University of Jyväskylä (see Elo *et al.* 2014 for a detailed description). A significant part of the study sites were established under Boreal Peatland LIFE project by Metsähallitus Natural Heritage Services. The study set-up is a balanced design where the sites represent three peatland types (spruce mires, pine mires, fens) each of which are further divided according to their productivity (low, high) (Fig. 1). In addition we analyzed a few alkaline fens in which we did not have different productivity levels. Half of the sites are in a pristine state and the other half had been drained for forestry by the state during 1960s and 1970s. Generally, drainage leads to a drop of water level by 20 - 60 cm (Laine & Vanha-Majamaa 1992; Haapalehto *et al.* 2011, 2014b) which in turn results in complex changes in pH, and the amount and availability of different nutrients (Laiho, Sallantaus & Laine 1999; Haapalehto *et al.* 2011, 2014b). Peatland restoration is conducted by damming or filling in the ditches with peat and by removing the trees grown after drainage (Hedberg *et al.* 2012). These actions have been shown to result in a rise of the water-table and consequent changes in peat chemistry even within a few years after restoration (Jauhiainen, Laiho & Vasander 2002; Laine *et al.* 2011; Haapalehto *et al.* 2011, 2014b).

Bryophyte and vascular plant species were sampled during the years 2007-2014 by 10 of 1-m^2 permanent plots at each site (see Elo *et al.* 2014 for a detailed description), and abundance as a % cover for all plant species was recorded from each plot based on visual estimation (in the analyses the mean abundance of each species in 10 plots, i.e. data was pooled to a site-level data). After the first sampling, the drained sites were restored by filling in the ditches and, in some cases, by removal of the trees grown after drainage (Aapala, Similä & Penttinen 2013). The permanent plots were sampled again two (n = 115) and five (n = 52) years after restoration (Fig. 1).

Statistical methods

We used linear mixed models to infer whether restoration had an effect on bryophyte and vascular plant species richness. First, we modeled species richness for each of the three peatland types separately to see whether the results were consistent among spruce mires, pine mires and fens. We set 'site' as a random factor to account the fact that each site was sampled twice, and treatment (drained, pristine) and year (before restoration, two and five years after restoration) as fixed factors. As we had previously found that productivity significantly affected both species richness and community composition (Elo *et al.* 2014), we added also productivity (low, high,) as well as all two-way and three-way interactions as fixed factors. A significant interaction of year and treatment would denote that restoration had an effect on species richness.

To infer whether the restoration had an effect on combined abundance of *Sphagnum* mosses, and typical forest mosses (*Dicranum majus, D. polysetum, D. scoparium, Pleurozium schreberi, Pohlia nutas* and *Polytrichum commune*), we set both 'peatland type' and 'site', nested in the effect 'peatland type', as random factors. As before, we set productivity (low, high), treatment (drained, pristine), year (before restoration, two years after restoration, five years after restoration) as well as their two-way and three-way interactions as fixed factors.

To test whether productivity, treatment, year or their interactions had an effect on community composition we used permutational multivariate analysis of variance (Anderson 2001). It is a non-parametric test relying on permutations and can be based on any dissimilarity measure. To infer whether possible changes were due to changes in species occupancies or abundances we used Bray-Curtis dissimilarity index both with incidence (BC_i) and abundance data (BC_a). Permutational multivariate analysis is sensitive to differences in the dispersion of sites, even though the locations do not differ (Anderson 2001). Hence, we used additionally the distance-based test for homogeneity of multivariate dispersions (Anderson 2006). Basically, it is a multivariate extension of Levene's test of homogeneity, and like permutational multivariate analysis, it can be based on any dissimilarity measure. The procedure counts the distance of each site to multivariate centroid of the group, and statistical significance is tested by permutation of residuals (999 permutations) (Anderson 2006). We performed all analyses with R (R Core Team 2014) using packages 'lme4' (Bates *et al.* 2014) and 'vegan' (Oksanen *et al.* 2013).

Results

Species richness

Generally, species richness was affected only by productivity (Table 1; Figs 2,3): high productivity sites had higher species richness than low productivity sites. Drained sites had similar species richness than pristine sites and restoration did not affect species richness. This result was rather consistent across peatland types and for both bryophytes and vascular plants. The exceptions were bryophytes in spruce mires where none of the studied factors affected species richness and vascular plants in pine mires where the interaction of productivity and treatment was a significant factor. In alkaline fens (where there were not different productivity levels) bryophyte species richness was affected by year whilst vascular plant species richness was not associated by any of the factors.

Abundance of Sphagnum *and forest mosses*

Combined abundance of *Sphagnum* mosses was affected by treatment: their abundance was higher in pristine than in drained or restored areas, as expected (Table 2, Fig.4), although in alkaline fens this was not the case. Moreover, in spruce mires the interaction of year and treatment had an effect: restoration increased *Sphagnum* moss abundance in restored sites. Abundance of forest mosses was affected by multiple factors, and notably, restoration decreased their abundance in spruce mires and in alkaline fens (Table 2, Fig.5).

Community composition

Generally, with both BC_i and BC_a bryophyte and vascular plant communities in spruce mires, pine mires and fens were separated by productivity and treatment, accompanied in several cases by their interaction (Table 3). The only exception was BC_a of vascular plant communities in pine mires where treatment and year had an interaction denoting the effect of restoration. In alcaline fens there was no interaction between treatment and year indicating that restoration had no effect on the community composition.

Community dispersion

There was heterogeneity of dispersions among the eight groups (drained low productivity, pristine low productivity, drained high productivity, pristine high productivity: before, two and five years after restoration) in multiple studied cases (Table 3). However, only in one case drained sites showed different dispersion before and after restoration: with BC_i bryophyte communities in low productivity pine mires decreased in their dispersion five years after restoration.

Discussion

In general, bryophyte and vascular plant species richness, community composition or community dispersion did not change consistently in two or five years after restoration. As drained and pristine peatlands did not differ in their species richness or community composition (Elo *et al.* 2014) we did not expect a major change in these features due to restoration, either. The lack of marked changes in community composition in two or five years after restoration, although in contrast to our predictions, was to be expected: even though some recovery of community composition in forestry drained peatlands after restoration has been reported (Mälson, Backéus & Rydin 2008; Laine *et al.* 2011; Haapalehto *et al.* 2011; Hedberg *et al.* 2012) five to 10 years is required for clear recovery (Haapalehto *et al.* 2014a).

Restoration increased *Sphagnum* abundance in spruce mires and decreased forest moss abundance in spruce mires and in alkaline fens. This positive response of *Sphagnum* and negative response of forest moss abundances have been shown also in other peatland restoration studies (e.g. Haapalehto *et al.* 2011). Community composition, when based on species occupancies only, differed between productivity levels and whether pristine or drained, as found also in our previous study (Elo *et al.* 2014). The lack of an effect of restoration was expected as it has been previously shown that recovery of wetland communities are mainly driven by changes in species abundances, rather than by their identities (Moreno-Mateos *et al.* 2012; Haapalehto *et al.* 2014a). However, in majority of the cases there were no significant changes after restoration in community composition when based on species abundances, either. The only case where restoration had an effect on community composition was vascular plant communities in pine mires. Thus, peatland types may differ in how rapidly they respond to restoration: unlike in spruce mires and fens, in pine mires the first effects of restoration were detectable after a few years. The general lack of a significant effect of restoration on community composition indicates that either the changes in species abundances after restoration were very subtle or towards random directions. If the changes in species abundances were random this would cause community dispersion in restored sites to increase. This was not true in majority of the cases and thus the latter option can be rejected, and we are left with the explanation that changes in species abundances two or five years after restoration are very modest.

To conclude, although there were some changes, two or five years after restoration the effects on bryophyte and vascular plant species richness, community composition and dispersion were still very subtle and inconsistent in general. The inconsistency may be partly due to some small variability in the restoration acts but it may also indicate that communities in different peatland types are affected slightly different community assembly processes. It is inevitable in the light of the study presented here as well as previous ones (Mälson, Backéus & Rydin 2008; Haapalehto *et al.* 2011; Hedberg *et al.* 2012) that whether restoration succeeds in reversing the effects of peatland drainage can't be fully judged at the basis of short-term data. Although changes in water level and in peat chemistry occur even within a few years after restoration (Jauhiainen, Laiho & Vasander 2002; Laine *et al.* 2011; Haapalehto *et al.* 2011, 2014b) the subsequent changes in vegetation communities take substantially longer time. Even after 10 years the signs of recovery of vegetation communities ranged from weak to non-existing, depending on the original stage of the degradation (Haapalehto *et al.* 2014a). Thus, a long-term monitoring lasting up to 15 or even 20 years is required in order to prevent premature conclusions of the uneffectiveness of restoration. Indeed, there is an urgent need for funding of long-term studies internationally (Birkhead 2014), particularly in case of restoration studies (Brewit & Holl 2014) as without proper long-term monitoring we are left with the most important question unanswered: were our actions effective?

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Table 1 Linear mixed effects model of the effects of productivity (L = low, H = high), treatment (D = drained, P = pristine), year (before restoration, two and five years after restoration) and their interactions on bryophyte and vascular plant species richness for spruce mires, pine mires and fens. Productivity(L), treatment(D) and year(0) were used as baselines. See figure 1 for number of mires in each category.

		Bryophytes					Vascular plants				
		Value	SE	df	t	*P*	Value	SE	df	t	*P*
Spruce mires	Intercept	**12.0**	**1.2**	**48**	**10.0**	**<0.001**	**8.9**	**1.7**	**50**	**5.2**	**<0.001**
	Productivity(H)	0.8	1.7	36	0.5	0.636	**7.5**	**2.4**	**36**	**3.1**	**0.004**
	Treatment(P)	-1.6	1.7	36	-1.0	0.348	2.3	2.4	36	1.0	0.343
	Year	0.3	0.3	48	0.8	0.408	0.4	0.3	50	1.6	0.115
	Productivity(H)*Treatment(P)	2.0	2.4	36	0.8	0.408	2.1	3.4	36	0.6	0.553
	Productivity(H)*Year	-0.2	0.5	48	-0.5	0.645	-0.4	0.3	50	-1.2	0.232
	Treatment(P)*Year	0.1	0.5	48	0.3	0.767	-0.2	0.3	50	-0.6	0.532
	Productivity(H)*Treatment(P)*Year	0.4	0.6	48	0.6	0.539	0.4	0.5	50	0.9	0.373
Pine mires	Intercept	**8.4**	**0.8**	**52**	**10.8**	**<0.001**	**11.5**	**1.0**	**52**	**11.8**	**<0.001**
	Productivity(H)	**3.1**	**1.1**	**36**	**2.9**	**0.007**	**3.3**	**1.4**	**36**	**2.4**	**0.022**
	Treatment(P)	-0.3	1.1	36	-0.3	0.782	-0.3	1.4	36	-0.2	0.822
	Year	0.2	0.2	52	0.9	0.394	0.0	0.1	52	-0.2	0.829
	Productivity(H)*Treatment(P)	0.4	1.5	36	0.3	0.782	**4.7**	**1.9**	**36**	**2.4**	**0.020**
	Productivity(H)*Year	0.1	0.3	52	0.3	0.765	-0.1	0.2	52	-0.3	0.780
	Treatment(P)*Year	-0.3	0.3	52	-0.9	0.380	0.3	0.2	52	1.6	0.114
	Productivity(H)*Treatment(P)*Year	-0.1	0.4	52	-0.2	0.818	-0.3	0.3	52	-1.0	0.332
Fens	Intercept	**7.7**	**0.9**	**53**	**8.1**	**<0.001**	**10.6**	**0.8**	**53**	**13.2**	**<0.001**
	Productivity(H)	**6.0**	**1.3**	**36**	**4.5**	**<0.001**	**3.3**	**1.1**	**36**	**2.9**	**0.006**
	Treatment(P)	-0.2	1.4	36	-0.2	0.879	0.8	1.2	36	0.7	0.474
	Year	0.2	0.3	53	0.6	0.559	-0.1	0.1	53	-0.8	0.411
	Productivity(H)*Treatment(P)	-1.8	1.9	36	-1.0	0.344	1.1	1.6	36	0.7	0.499
	Productivity(H)*Year	-0.7	0.4	53	-1.7	0.094	-0.2	0.2	53	-1.2	0.232
	Treatment(P)*Year	-0.1	0.4	53	-0.3	0.740	0.3	0.2	53	1.1	0.267
	Productivity(H)*Treatment(P)*Year	0.8	0.6	53	1.4	0.173	0.0	0.3	53	0.1	0.886
Alkaline fens	Intercept	**15.7**	**1.9**	**12**	**8.2**	**<0.001**	**26.0**	**2.9**	**12**	**9.0**	**<0.001**
	Treatment(P)	1.3	2.7	12	0.5	0.647	4.7	4.1	12	1.1	0.276
	Year	**1.6**	**0.6**	**8**	**2.7**	**0.026**	-0.3	0.3	8	-1.0	0.351
	Treatment(P)*Year	-0.6	0.8	8	-0.7	0.519	0.7	0.4	8	1.8	0.111

Table 2 Linear mixed effects model of the effects productivity (L = low, H = high), treatment (D = drained, P = pristine), year (before restoration, two years after restoration, five years after restoration) and their interactions on abundance of *Sphagnum* mosses and typical forest mosses. Productivity(L) and treatment(D) were used as baselines

		Abundance of *Sphagnum* mosses					Abundance of forest mosses				
		Value	SE	df	t	*P*	Value	SE	df	t	*P*
Spruce mires	Intercept	**20.0**	**8.8**	**48**	**2.3**	**0.029**	**27.4**	**3.9**	**48**	**7.1**	**<0.001**
	Productivity(H)	-9.7	12.5	36	-0.8	0.442	**-15.9**	**5.5**	**36**	**-2.9**	**0.007**
	Treatment(P)	**59.8**	**12.5**	**36**	**4.8**	**<0.001**	**-17.8**	**5.5**	**36**	**-3.3**	**0.003**
	Year	**2.8**	**0.8**	**48**	**3.4**	**0.002**	**-3.5**	**0.8**	**48**	**-4.3**	**<0.001**
	Productivity(H)*Treatment(P)	-0.4	17.7	36	0.0	0.982	8.0	7.8	36	1.0	0.313
	Productivity(H)*Year	-0.3	1.1	48	-0.2	0.811	2.0	1.1	48	1.8	0.075
	Treatment(P)*Year	**-3.7**	**1.1**	**48**	**-3.3**	**0.002**	**3.2**	**1.1**	**48**	**2.9**	**0.005**
	Productivity(H)*Treatment(P)*Year	0.0	1.5	48	0.0	0.992	-1.9	1.5	48	-1.2	0.219
Pine mires	Intercept	**41.5**	**7.0**	**52**	**5.9**	**<0.001**	**38.2**	**5.7**	**52**	**6.7**	**<0.001**
	Productivity(H)	5.4	9.9	36	0.5	0.589	**-23.4**	**8.1**	**36**	**-2.9**	**0.007**
	Treatment(P)	**47.2**	**9.9**	**36**	**4.7**	**<0.001**	**-34.8**	**8.1**	**36**	**-4.3**	**<0.001**
	Year	0.7	0.7	52	1.1	0.296	**-1.6**	**0.6**	**52**	**-2.7**	**0.009**
	Productivity(H)*Treatment(P)	-8.6	14.1	36	-0.6	0.547	**25.9**	**11.5**	**36**	**2.3**	**0.031**
	Productivity(H)*Year	0.7	1.0	52	0.7	0.462	-0.3	0.8	52	-0.4	0.680
	Treatment(P)*Year	-0.7	1.0	52	-0.7	0.508	1.2	0.8	52	1.5	0.149
	Productivity(H)*Treatment(P)*Year	-0.6	1.4	52	-0.4	0.683	0.5	1.1	52	0.4	0.678
Fens	Intercept	**52.5**	**7.0**	**53**	**7.5**	**<0.001**	**2.5**	**1.0**	**53**	**2.4**	**0.019**
	Productivity(H)	10.0	9.8	36	1.0	0.315	**3.7**	**1.4**	**36**	**2.6**	**0.015**
	Treatment(P)	**43.3**	**10.1**	**36**	**4.3**	**<0.001**	-2.4	1.5	36	-1.6	0.113
	Year	1.4	1.1	53	1.3	0.200	-0.3	0.2	53	-1.4	0.159
	Productivity(H)*Treatment(P)	-14.0	14.0	36	-1.0	0.323	-3.3	2.0	36	-1.6	0.117
	Productivity(H)*Year	-1.4	1.6	53	-0.9	0.360	**-0.7**	**0.3**	**53**	**-2.6**	**0.013**
	Treatment(P)*Year	-3.2	1.8	53	-1.8	0.075	0.3	0.3	53	0.9	0.397
	Productivity(H)*Treatment(P)*Year	2.4	2.3	53	1.0	0.299	0.8	0.4	53	1.8	0.070
Alkaline fens	Intercept	**38.9**	**9.7**	**12**	**4.0**	**0.002**	4.1	2.1	12	2.0	0.072
	Treatment(P)	15.3	13.8	12	1.1	0.289	-1.6	3.0	12	-0.6	0.589
	Year	-1.2	2.7	8	-0.5	0.660	-0.2	0.1	8	-1.5	0.173
	Treatment(P)*Year	-0.5	3.9	8	-0.1	0.903	**0.4**	**0.1**	**8**	**2.9**	**0.019**

Table 3 Permutational multivariate analyses of the effect of productivity (low, high), treatment (pristine, drained) and year (before restoration, two years after restoration, five years after restoration) and their interactions for bryophytes and vascular plant communities in spruce mires, pine mires and fens. F values and their statistical significance (*P*) from permutation analyses. Degrees of freedom: df_1=1 for all cases, df_2=*84 for bryophytes, 86 for vascular plants, **88, ***89, ****20

		Bryophytes				Vascular plants			
		Incidence-based		Abundance-based		Incidence-based		Abundance-based	
		F	*P*	F	*P*	F	*P*	F	*P*
Spruce mires*	Productivity	**8.9**	**<0.001**	**21.3**	**<0.001**	**16.7**	**<0.001**	**54.6**	**<0.001**
	Treatment	**14.0**	**<0.001**	**18.4**	**<0.001**	**5.1**	**<0.001**	**12.5**	**<0.001**
	Year	2.1	0.058	2.0	0.063	0.4	0.947	0.3	0.969
	Productivity * Treatment	**2.3**	**0.031**	**5.8**	**<0.001**	**3.9**	**0.002**	**8.6**	**<0.001**
	Productivity * Year	1.0	0.425	0.7	0.658	0.8	0.630	0.5	0.863
	Treatment * Year	0.1	0.990	0.4	0.926	0.4	0.915	0.5	0.885
	Productivity * Treatment * Year	0.2	0.980	0.9	0.471	0.5	0.846	0.3	0.977
Pine mires**	Productivity	**27.9**	**<0.001**	**26.5**	**<0.001**	**31.3**	**<0.001**	**38.3**	**<0.001**
	Treatment	**16.5**	**<0.001**	**16.4**	**<0.001**	**17.6**	**<0.001**	**13.6**	**<0.001**
	Year	1.4	0.201	0.6	0.785	0.7	0.635	1.4	0.180
	Productivity * Treatment	**1.1**	**0.402**	**5.4**	**0.002**	2.1	0.082	6.6	**<0.001**
	Productivity * Year	1.8	0.098	0.6	0.691	0.8	0.560	0.5	0.852
	Treatment * Year	1.7	0.132	0.8	0.629	0.3	0.864	2.3	**0.032**
	Productivity * Treatment * Year	0.4	0.843	0.4	0.918	0.5	0.756	0.1	0.997
Fens***	Productivity	**24.0**	**<0.001**	**26.3**	**<0.001**	**25.1**	**<0.001**	**38.6**	**<0.001**
	Treatment	**12.6**	**<0.001**	**13.3**	**<0.001**	**19.8**	**<0.001**	**14.1**	**<0.001**
	Year	1.6	0.144	0.5	0.825	1.1	0.370	1.9	0.096
	Productivity * Treatment	1.9	0.086	**6.2**	**<0.001**	**4.1**	**0.003**	**8.2**	**<0.001**
	Productivity * Year	0.7	0.641	0.6	0.813	0.7	0.610	-0.1	1.000
	Treatment * Year	1.4	0.210	1.0	0.417	1.3	0.255	1.9	0.087
	Productivity * Treatment * Year	1.0	0.476	0.7	0.689	0.1	0.972	0.0	1.000
Alkaline fens****	Treatment	1.9	0.064	**2.4**	**0.021**	**2.2**	**0.014**	**3.5**	**0.002**
	Year	1.0	0.446	0.7	0.637	**1.9**	**0.048**	0.7	0.715
	Treatment * Year	0.7	0.677	0.4	0.913	1.2	0.305	0.6	0.815

Table 4 Homogeneity of dispersions of pristine low productivity, drained low productivity, pristine high productivity and drained high productivity sites before, two and five years after restoration, for bryophytes and vascular plants in spruce mires, pine mires, and fens. F values, degrees of freedom (df 1, df 2) and statistical significance (*P*) from permutation (999 permutations) analyses

			$F_{df\,1,df\,2}$	*P*
Bryophytes	Incidence-based	Spruce mires	$\mathbf{2.1_{11,\,80}}$	**0.029**
		Pine mires	$\mathbf{2.7_{11,\,84}}$	**0.005**
		Fens	$1.8_{11,\,85}$	0.056
		Alkaline fens	$1.1_{3,18}$	0.378
	Abundance-based	Spruce mires	$\mathbf{2.0_{11,\,80}}$	**0.043**
		Pine mires	$1.0_{11,\,84}$	0.464
		Fens	$0.4_{11,\,85}$	0.925
		Alkaline fens	$1.5_{3,18}$	0.249
Vascular plants	Incidence-based	Spruce mires	$\mathbf{3.5_{11,\,82}}$	**0.003**
		Pine mires	$\mathbf{2.6_{11,\,84}}$	**0.007**
		Fens	$\mathbf{2.0_{11,\,85}}$	**0.032**
		Alkaline fens	$1.0_{3,18}$	0.457
	Abundance-based	Spruce mires	$0.9_{11,\,82}$	0.474
		Pine mires	$\mathbf{2.3_{11,\,84}}$	**0.017**
		Fens	$\mathbf{1.6_{11,\,85}}$	**0.108**
		Alkaline fens	$1.0_{3,18}$	0.41

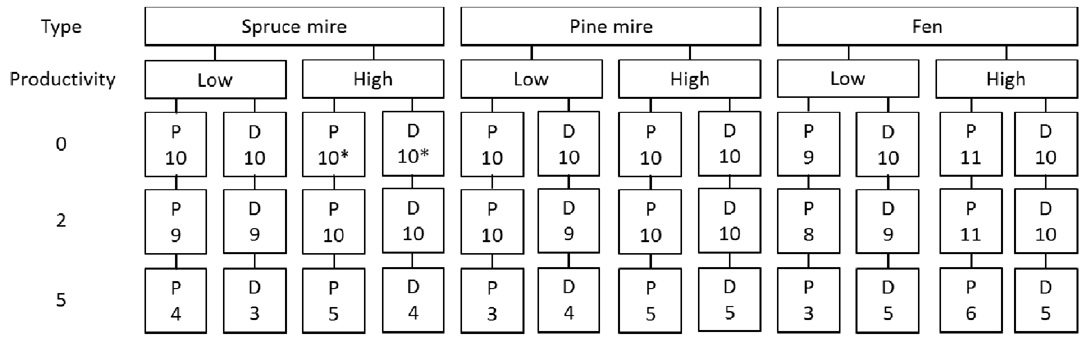

Fig. 1 The study involved three peatland types (spruce mires, pine mires, fens) which were further divided according to their productivity (low, high) from which half were pristine (P) and half drained (D). Number of sites sampled before restoration (0), two years after restoration (2) and five years after restoration (5) are shown. *9 sites for bryophytes. In addition we had a few alkaline fens that are not shown in the figure

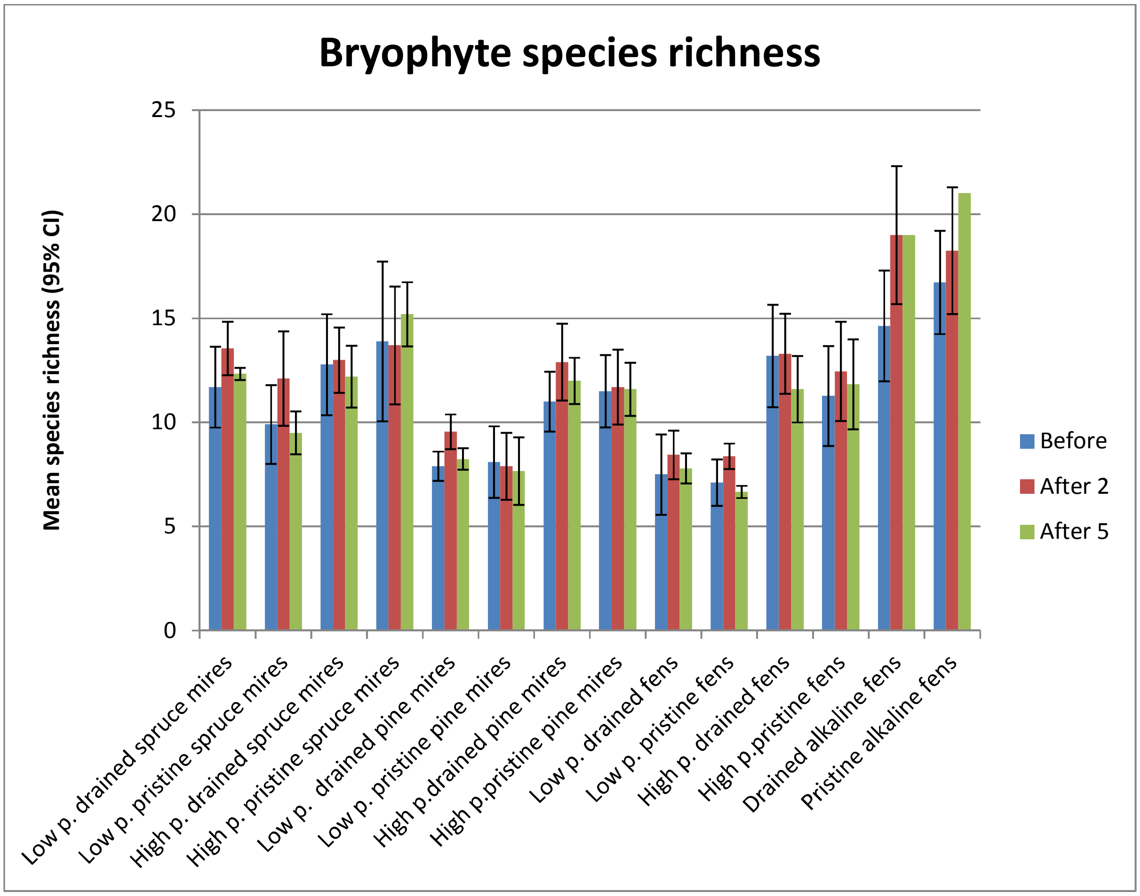

Fig. 2 Bryophyte species richness (mean ± 95% Confidence Interval) in sites with different treatments (drained, pristine) and productivity levels (low, high) before restoration, two years after restoration and five years after restoration in different peatland types (spruce mires, pine mires, fens, alkaline fens)

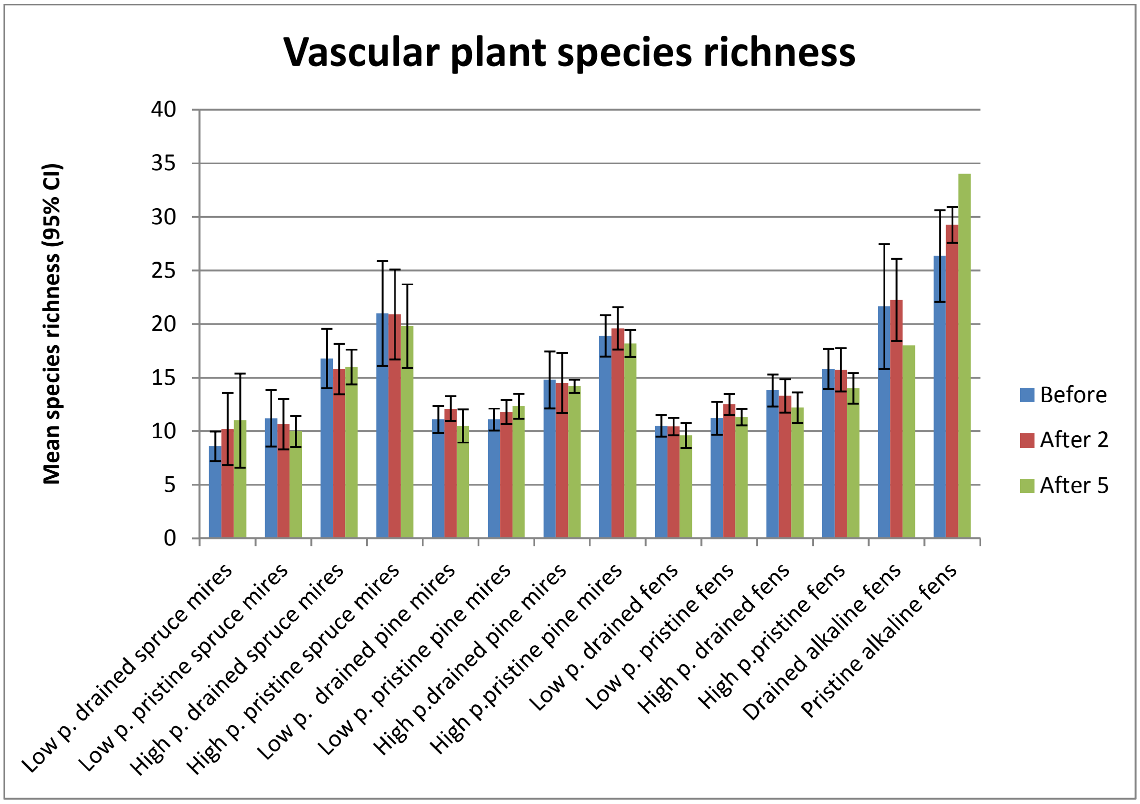

Fig. 3 Vascular plant species richness (mean ± 95 % Confidence Interval) in sites with different treatments (drained, pristine) and productivity levels (low, high) before restoration, two years after restoration and five years after restoration in different peatland types (spruce mires, pine mires, fens, alkaline fens)

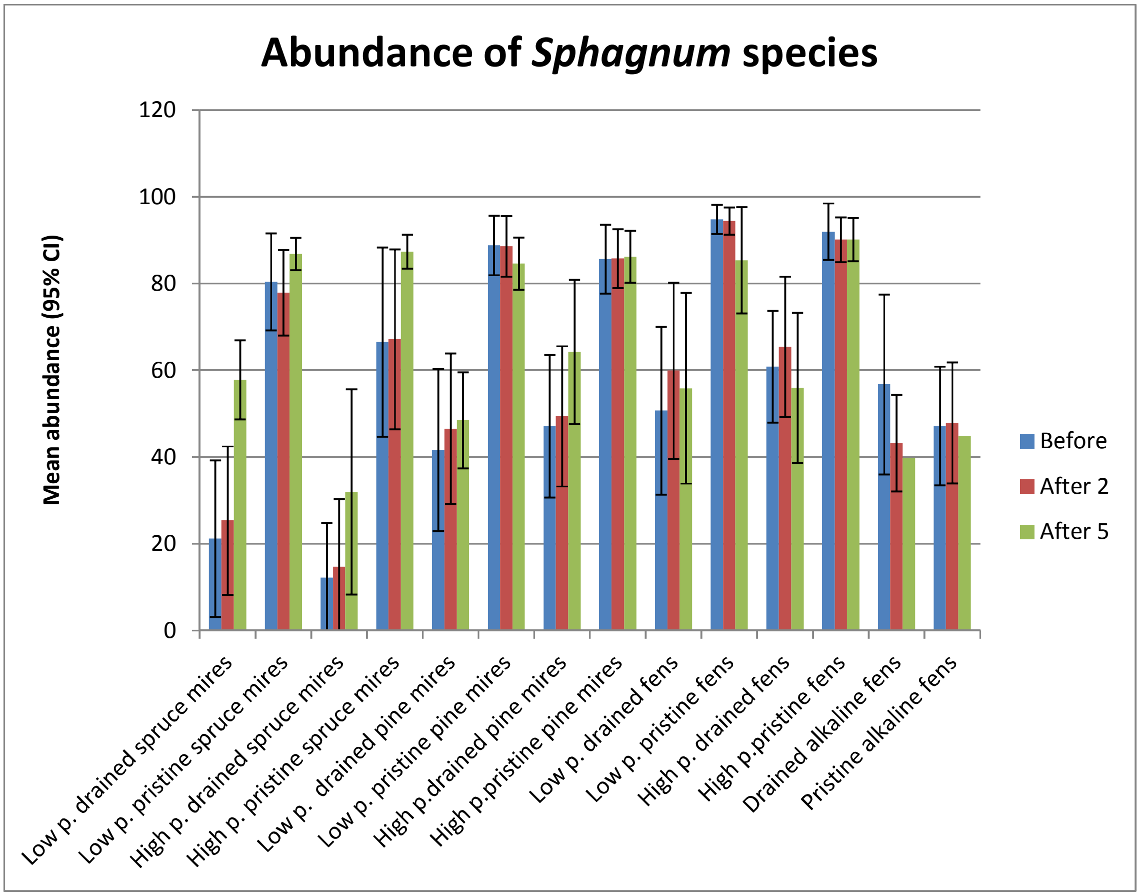

Fig. 4 Abundance of *Sphagnum* species (mean ± 95 % Confidence Interval) in sites with different treatments (drained, pristine) and productivity levels (low, high) before restoration, two years after restoration and five years after restoration in different peatland types (spruce mires, pine mires, fens, alkaline fens)

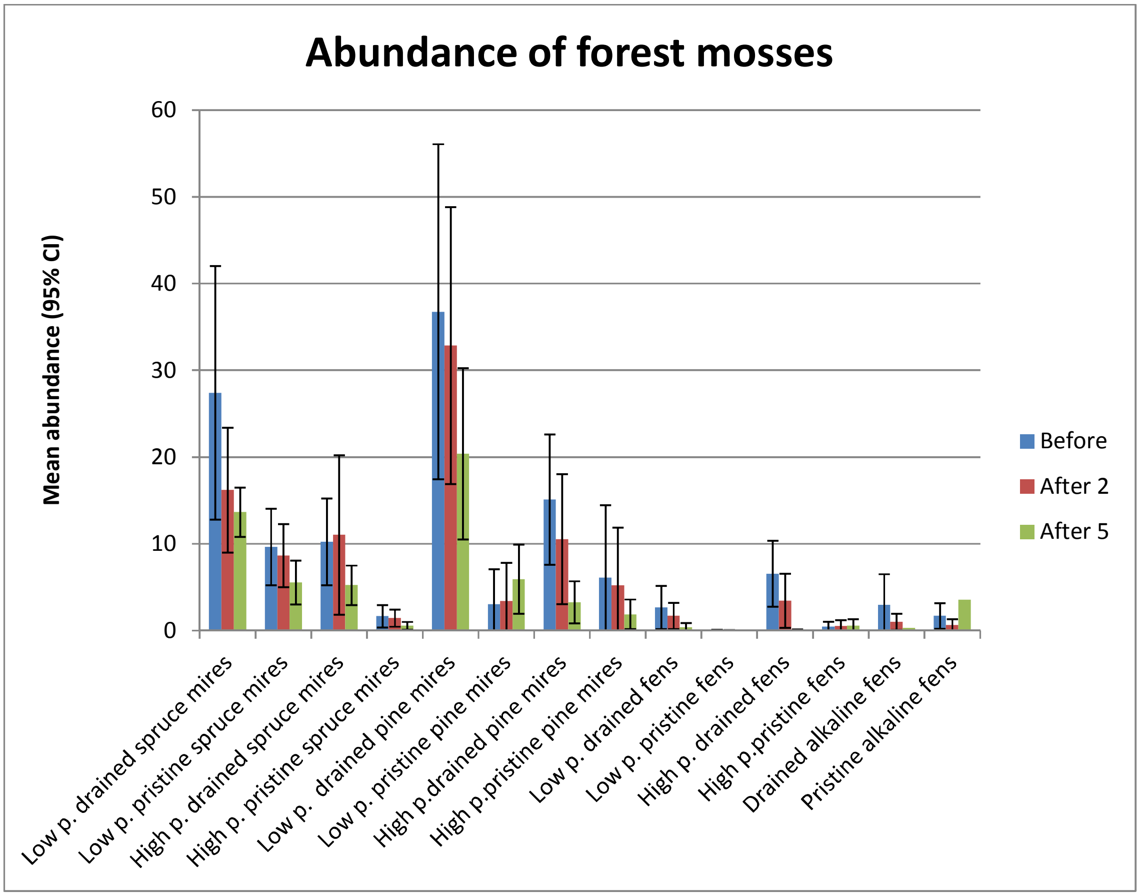

Fig. 5 Abundance of forest moss species (mean ± 95 % Confidence Interval) in sites with different treatments (drained, pristine) and productivity levels (low, high) before restoration, two years after restoration and five years after restoration in different peatland types (spruce mires, pine mires, fens, alkaline fens)