Do testate amoebae communities recover in concordance with vegetation after restoration of drained peatlands?

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SUMMARY

The environmental importance of peatlands has stimulated efforts to restore their specific ecosystem structure and functions. Monitoring and assessment of the ecological state of the peatland is fundamental in restoration programmes. Most studies have focused on the responses of vegetation and, to a lesser extent, on testate amoebae (TA). To our knowledge, none have investigated whether these two groups show concordance in the context of restoration of drained peatland. Here we assess community concordance between TA and vegetation in boreal peatlands belonging to four different land use management classes (natural, drained, restored 3–7 years ago, and restored 9–12 years ago). TA and vegetation communities were concordant when all of the studied sites were compared. However, there was no concordance within management classes except for sites restored 3–7 years ago. We found that TA and vegetation communities are not surrogates of one another when measuring the success of restoration, and that thorough studies of both communities are required to build a holistic understanding of the changes during restoration from an ecosystem perspective. TA seemed to respond faster to changes caused by restoration and, hence, could be better early indicators of restoration success than plants. Furthermore, studies of the relationships between TA and plant communities could provide important insights to aid understanding of the link between the recovery of ecosystem structure and the reinstatement of ecosystem functions.

KEY WORDS: assessment, ecological state, monitoring, indicators of restoration, taxa surrogates

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INTRODUCTION

Peatlands of the boreal and subarctic regions cover only 3 % of the global land area. Due to the accumulation of organic matter as peat during hundreds to thousands of years, they store *ca*. 500 Gt of C corresponding to one third of the global soil C (Yu 2011, Yu 2012). Like many other ecosystems, peatlands have been heavily exploited. In Finland, more than 50 % of the total peatland area has been drained for forestry, 2.6 % for agriculture and 0.6 % for peat mining (Lappalainen 1996, Vasander *et al.* 2003). Peatland use is mainly concentrated in central and southern Finland where natural peatlands now occupy less than 25 % of their original area (Aapala *et al.* 1996). The increasing threat of environmental degradation has raised awareness of ecological restoration as a component of conservation programmes (Dobson *et al.* 1997). The environmental importance of peatlands has led to a growing number of attempts to restore or partially reinstate surface water retention, the carbon sink, and specific flora and fauna (Lunn & Burlton 2013).

Monitoring and assessment of ecological state is a fundamental part of peatland conservation and restoration programmes (Trepel 2007). Studies based on the assessment of plant community composition after restoration have shown promising results (e.g. Haapalehto *et al.* 2011, Laine *et al.* 2011, Hedberg *et al.* 2012, Poulin *et al.* 2013). However, little is known about changes in the microorganism communities of restored peatlands. Testate amoebae (TA) are a polyphyletic group of shell-building unicellular protists (Meisterfeld 2002), commonly associated with peatland plants, and especially abundant in *Sphagnum* mosses (Tolonen 1986). In peatlands, the number of TA can be as high as 16×10^6 individuals per m², making them a significant component of the heterotrophic soil community (Sleigh 1989). TA diversity and distribution in bogs is mainly controlled by

hydrological variables (e.g. moisture content and water table depth), and in fens by water pH, oxygen concentration and peat composition (Charman 1997, Bobrov *et al.* 1999). Depending on taxa and environmental conditions, their generation time ranges from days to weeks, while that of bryophytes and vascular plants is much longer (Schönborn 1986). Under natural conditions, TA communities are stable between seasons (Warner *et al.* 2007), but when conditions change, they can change within months (Marcisz *et al.* 2014).

Koenig *et al.* (2015) found that TA provide more accurate information on microenvironmental conditions than vegetation, and that valuable ecological information can be obtained without knowing all of the TA taxa. Thus, TA communities have been proposed as a tool for monitoring and assessment of peatland conditions, but to date TA have been employed in relatively few studies (e.g. Jauhiainen 2002, Davis & Wilkinson 2004, Raabe & Lamentowicz 2012, Turner & Swindles 2012, Koenig *et al.* 2015).

The biological indicators that are used in assessment and monitoring of ecosystem health, i.e. the ecosystem's ability to maintain its structure and function when facing external stress (Costanza & Mageau 1999), are usually well-known taxonomic groups. However, the degree to which certain taxonomic groups actually mirror trends among other groups and can be used as surrogates is still unknown, and studies based on the surrogate-taxa approach have repeatedly been questioned (e.g. Paavola *et al.* 2003, Bilton *et al.* 2006). Most bioassessment studies focus on single taxonomic group responses to environmental factors while few have addressed parallel group responses (i.e. concordance). Community concordance describes the degree of similarity in distributions and abundances of different taxonomic groups across a region and emerges when different communities show similar responses to environmental changes (Infante *et al.* 2009). Studies that have investigated concordance have mostly focused on lakes and fluvial systems (e.g. Heino 2002, Mykrä *et al.* 2008, Infante *et al.* 2009, Jyväsjärvi *et al.* 2014) and very few have examined such patterns for peatland ecosystems (Mitchell *et al.* 2000b, Lamentowicz *et al.* 2010, Hájek *et al.* 2014, Koenig *et al.* 2015, Hunter Jr *et al.* 2016).

The factors that drive community concordance include strong species interactions within and between communities (Heino 2002) and co-losses of species in response to environmental stress, including that caused by anthropic stressors (Mykrä

et al. 2008, Yates & Bailey 2010). Life histories and reproductive and dispersal capabilities of taxa could influence the extent to which different environmental factors and biotic interactions drive spatial patterns of community composition and, subsequently, community concordance (Shurin *et al.* 2009). Because it is based on species identities rather than only the number of species, community concordance provides a wider understanding of similarities between communities than richness measures alone (Pawar *et al.* 2007). Furthermore, when concordance among taxonomic groups does not occur at a specific geographical scale, the use of a single group as an indicator for the state of the ecosystem may not be appropriate (Paavola *et al.* 2006).

Studies of the success of peatland restoration generally focus on the recovery of vegetation, but whether important microorganisms such as TA are concordant in their responses to restoration and how these responses are linked to general ecosystem functions remains an open question. Because TA are especially common in *Sphagnum* and other mosses, they are potentially concordant with peatland vegetation. Therefore, we assessed concordance of the changes in TA and plant community structures among natural, ditched and restored boreal peatlands. We specifically aimed i) to analyse changes and concordance between TA and plant communities in response to restoration processes, and ii) to determine which environmental variables drive the changes in these two communities.

METHODS

Study sites
The study sites were located in the south boreal climatic-phytogeographical zone of southern Finland (latitude 61° 53′–62° 51′ N, longitude 22° 53′–25° 26′ E). The larger peatland formations in this region are mainly raised bogs, while small weakly minerotrophic *Sphagnum*-dominated mires are typically found in a landscape mosaic with coniferous forests. Sampling sites were located *ca.* 150 m above sea level with mean annual temperature +4 °C and precipitation *ca.* 650 mm. We selected 19 study sites divided in four land use management classes: i) natural ($n = 5$), ii) drained ($n = 4$), iii) drained and restored 3–7 years before sampling ($n = 5$), and iv) drained and restored 9–12 years before sampling ($n = 5$). For brevity, the management classes will hereafter be referred to as Natural, Ditched, Res05 and Res10, respectively.

Pine fen sites of low minerotrophy were selected on the basis of field observations, and historic aerial photographs were used to ensure that the original tree stands of the drained and restored sites were similar. Sites with naturally similar vegetation were located in a mosaic of ombro-mesotrophic peatland vegetation where *Sphagnum* was the main peat-forming plant genus. Surface water flow was considered independently for each management class, on the basis of topographic data and field observations. The thickness of the peat layer ranged from 95 cm to more than 200 cm and the underlying soil was till or sand.

Sites whose hydrology has not been altered by ditches or other direct measures represent the least impacted management class and are subsequently referred to as "Natural". We acknowledge that forestry measures in distant parts of Natural site catchments may have slight impacts on their hydrology (Tahvanainen 2011), but such effects were not obvious. Ditched and Restored sites were drained for forestry purposes during the 1960s and 1970s. During the 1980s, peatlands were restored by filling in the ditches and removing trees from areas where drainage had significantly increased tree growth. More detailed information about the studied peatlands is given in Haapalehto *et al.* (2014).

Field sampling and sample processing
A grid of $20 \times 1m^2$ plots was established at each site (Figure 1). Plots at the Ditched and Restored sites were arranged in five parallel transects, spaced four metres apart, running perpendicular to the ditch. Within each transect there were plots at 5, 10 and 15 metres from the ditch. A 15 m × 20 m grid of plots was used at each Natural reference site. The location of the first plot at each study site was randomised.

For water chemistry analyses at the Natural sites, three 32 mm diameter polypropylene pipe wells with 2 mm slits spaced at 2–3 cm intervals and polypropylene filter gauges were distributed in the central part of the sampling grid. At the Ditched and Restored sites filter gauges were set at a distance of 15 m from the ditch and 10 m apart (Figure 1). Water samples were collected in August 2007. Redox potential (Eh_7), electrical conductivity (EC) and pH were measured 2–5 hours after sample collection using a Consort SP50X meter with SP50X, SK10T and SP10B electrodes, respectively. The samples were then stored in darkness at +4 °C until further analysis. Cation concentrations (Al, Ca, Fe, K, Mg, Na) were obtained after filtration with 0.45 µm pore size filters and analysed with a Perkin Elmer Optima 4300 DV inductively coupled plasma
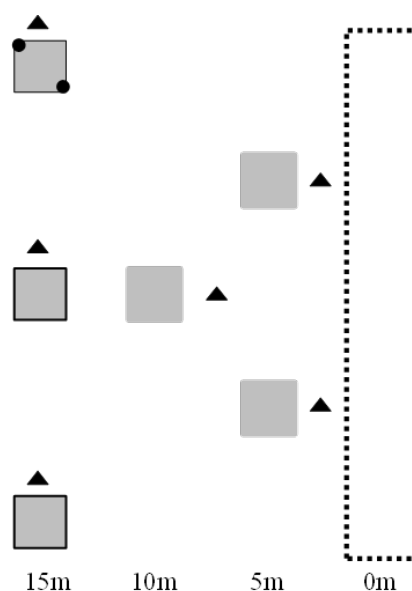
Sampling plots, Natural sites.
Sampling plots, Ditched, Res05 and Res10 sites.
Pipe wells for WTD measurement. Two/sampling plot.
Pipe well for water samples.
Ditch (ditched sites), filled ditch (restored sites).

Figure 1. Sampling design for testate amoebae, plants and environmental variables. Distances (m) refer to distances of the 1m² plots from ditches at the Ditched and Restored sites. At Natural sites, a similar arrangement of plots was used. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.

optical emission spectrometer. Water table depth (WTD) was measured five times (in May, June, July, August and September) during 2008 in two permanent polypropylene pipe wells at selected plots. WTD values were corrected for the natural slope (see Haapalehto *et al.* 2014) and averaged to absolute levels throughout the site. WTD is usually recorded as negative values, but to facilitate readability, inverse positive values are used here.

Plants and TA were sampled at the plots located adjacent to the polypropylene pipe wells (three plots at each site). We estimated the relative abundance (percentage cover) of each taxon of vascular plants, bryophytes and some lichens for each sampled plot. Sampling was done during July and August 2007. To obtain TA, approximately 10cm³ of bryophyte mass was extracted (see also Booth *et al.* 2010). Samples were stored in plastic Ziploc bags, frozen, defrosted and oven dried, stored in paper bags and analysed in 2013 using the protocol proposed by Booth *et al.* (2010). To retain TA, each sample was

boiled for ten minutes in distilled water with one tablet of *Lycopodium clavatum* spores (batch 1031) standard preparation from Lund University (Sweden), and sieved through a 300 µm mesh to remove coarse materials and onto a 7 µm mesh. Retained TA were centrifuged at 3000 rpm for five minutes and stored in distilled water. At least 150 TA were counted and identified using 40× magnification (Olympus BX41 microscope). As the standing plant community is the result of several years of development, non-living TA were also included in the analysis to integrate the accumulation of tests over the entire time period. TA identification was based on characteristics of the shell following several different taxonomic keys (e.g. Charman *et al.* 2000 with modifications by Booth 2008, Meisterfeld 2002, Clarke 2003, Mitchell 2002, Mitchell 2003, Mazei & Tsyganov 2006).

Data analysis

We calculated species richness, Shannon diversity index and relative abundances of TA and plant communities for each site (using plot averages), and averaged by management classes. For TA communities, density was estimated using the *Lycopodium* count as an external marker (see Stockmarr 1971 for details) and relative abundance was calculated as a percentage of the total counted. ANOVA and Tukey's (HSD) post hoc test were performed to assess differences in species richness and Shannon diversity index between management classes. Due to the unbalanced design, permutational MANOVA (PerMANOVA) was used to test the significance of the differences in structure and composition among the communities in the four management classes. Differences in water chemistry and WTD were analysed using ANOVA or Kruskal-Wallis depending on whether the data met the normality and homoscedasticity assumptions. To summarise variability in the communities, a Non-metric Multidimensional Scaling (NMDS) based on Sørensen's (Bray-Curtis) distance was performed. We used NMDS to examine the degree of concordance of water chemistry variables with community ordinations. WTD was not included in the community ordinations, as these data were not collected at exactly the same time as the biological samples. A two dimensional NMDS solution achieved a moderate stress level for plant communities but not for TA communities; however, for simplicity of comparison we retained the two dimensional TA solution. Concordance between TA and plant communities was tested using the PROTEST analysis (Peres-Neto & Jackson 2001).

All calculations were done using R version 3.0.2 (R Core Team 2013) and the vegan package for NMDS and PROTEST analyses (Oksanen *et al.* 2015).

RESULTS

Community data

Altogether, 44 TA and 45 plant taxa were found in our study. TA taxon richness at Natural sites ($\bar{X} = 17.7$ range 14–24, SE = 0.71) was higher than at Ditched, Res05, and Res10 sites (ANOVA $F_{[1,3]} = 15.79$, $p < 0.001$) whereas no differences were found among Ditched, Res05, and Res10 sites (Table 1, Figure 2a). The Shannon diversity index for TA was generally higher at Natural sites, where the highest value was 2.56, while the lowest values were found at Res05 sites (Figure 2c). We observed differences in TA diversity only between Natural-Res05 and Natural-Res10 sites (Table 1). The highest cell density was found at Res10 sites ($\bar{X} = 24953$ cells/10cm³) and the lowest at Ditched sites ($\bar{X} = 6767$ cells/10cm³).

No differences were found in the mean number of plant taxa between management classes (Figure 2b). In general, plant diversity tended to be higher at Res05 sites but, overall, there were no significant differences between classes (F = 0.9, $p = 0.46$; Table 1, Figure 2d). TA community structure and composition differed between classes except between Res05 and Res10 (Table 2). For plant communities, only Natural sites differed from all other classes (Table 2, see also Haapalehto 2014).

On average, TA communities in Natural, Res05, and Res10 sites were mainly dominated by *Arcella catinus* and *Bullinularia indica*. At Ditched sites, *Trigonopyxis arcula* was the most widely dominant taxon followed by *A. catinus*. More than 50 % of the TA species were found across all sites regardless of management class, but some species displayed more restricted distributions. For example, *Arcella artocrea, Centropyxis ecornis, Difflugia leidyi, Difflugia lithophila, Hyalosphenia minuta* and *Pseudodifflugia fascicularis* were present at Natural sites only; while *Hyalosphenia elegans* and *Physochila griseola* were absent from Ditched and Res05 sites (Table 3). The plant communities at all sites were dominated by *Sphagnum angustifolium* regardless of management class. However, densities were highly variable. *Pleurozium schreberi* was the second most dominant species at Res05 and Ditched sites, while at Res10 and Natural sites *S. magellanicum* and *S. fuscum* were more abundant (see Haapalehto 2014).

Table 1. Tukey's (HDS) results for TA taxon richness and Shannon diversity. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.

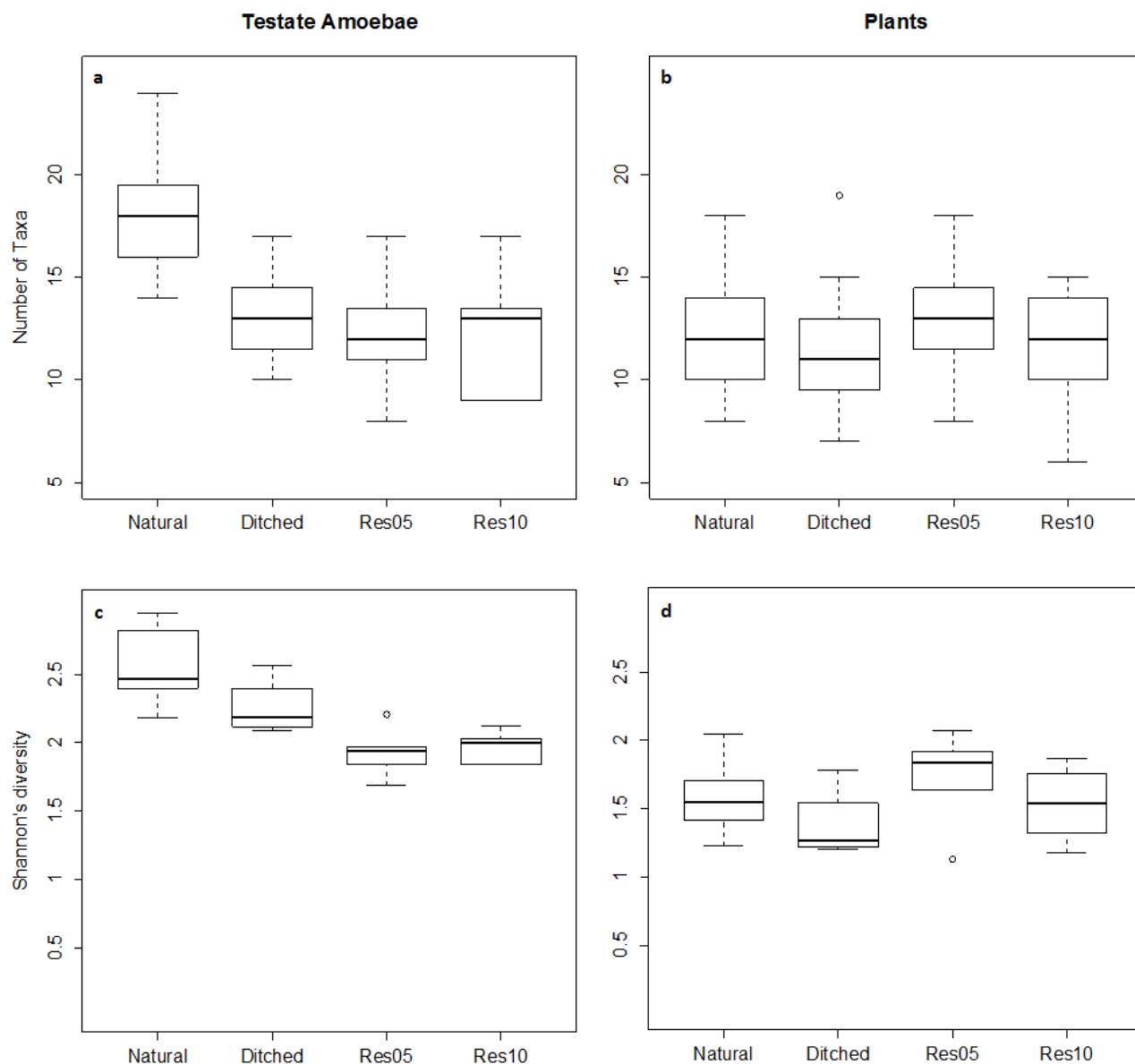|		Richness				Shannon Diversity			
		Difference	lower bound	Upper bound	*p*	Difference	lower bound	Upper bound	*p*
Natural	Res05	5.47	3.00	7.94	<0.001	0.64	0.23	1.04	0.002
	Res10	-5.47	-7.94	-3.00	<0.001	-0.60	-1.00	-0.19	0.003
	Ditched	4.64	1.96	7.33	<0.001	0.31	-0.12	0.74	0.205
Res05	Res10	0.00	-2.47	2.47	1.000	0.04	-0.37	0.44	0.993
	Ditched	-0.82	-3.51	1.86	0.847	-0.33	-0.76	0.10	0.171
Res10	Ditched	-0.82	-3.51	1.86	0.847	-0.29	-0.72	0.14	0.253

Figure 2. Taxon richness boxplots for testate amoebae (a) and vegetation (b). Shannon's diversity boxplots for testate amoebae (c) and vegetation (d) for each management class. Circles: outliers, upper whisker: maximum value excluding outliers, upper box line: upper quartile, middle line inside box: median, lower box line: lower quartile, lower whisker: minimum value excluding outliers. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.

Table 2. PerMANOVA pairwise comparisons for TA and plant community structure and composition. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.

				TA							Plants			
		df	SS	MS	Pseudo-F	r²	p	df	SS	MS	Pseudo-F	r²	p
Natural	Res05	1	0.28	0.28	2.74	0.25	0.021	1	0.44	0.44	3.23	0.29	0.042
	Res10	1	0.29	0.29	4.02	0.33	0.016	1	0.15	0.15	1.83	0.19	0.047
	Ditched	1	0.48	0.48	4.90	0.41	0.006	1	0.46	0.46	4.11	0.37	0.016
Res05	Res10	1	0.09	0.09	1.36	0.15	0.259	1	0.33	0.33	2.35	0.23	0.104
	Ditched	1	0.36	0.36	3.90	0.36	0.036	1	0.12	0.12	0.66	0.09	0.499
Res10	Ditched	1	0.59	0.59	10.17	0.59	0.010	1	0.35	0.35	2.98	0.30	0.093

Table 3. TA average relative abundances in percentage and standard deviations for each management class. (*) Taxa found just at natural sites; (**) taxa found at Natural and in sites restored 10 years ago; (***) taxa found at all but Ditched sites; (****) taxa found just at Ditched sites. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.

	Taxa	Treatments							
		Natural		Ditched		Res05		Res10	
		X̄	SD	X̄	SD	X̄	SD	X̄	SD
*	*Arcella artocrea*	0.78	1.56	0	0	0	0	0	0
*	*Centropyxsis ecornis*	0.09	0.33	0	0	0	0	0	0
*	*Difflugia leidyi*	0.05	0.17	0	0	0	0	0	0
*	*Difflugia lithophila*	0.04	0.17	0	0	0	0	0	0
*	*Hyalosphenia minuta*	0.53	0.85	0	0	0	0	0	0
*	*Pseudodifflugia fascicularis*	0.04	0.16	0	0	0	0	0	0
**	*Hyalosphenia elegans*	3.60	3.93	0	0	0	0	0.22	0.48
**	*Physochila griseola*	0.67	1.03	0	0	0	0	0.09	0.35
***	*Heleopera petricola*	2.56	3.76	0	0	0.34	0.63	0.12	0.34
****	*Arcella vulgaris*	0	0	0.11	0.37	0	0	0	0
****	*Euglypha compressa*	0	0	0.11	0.37	0	0	0	0
****	*Hyalosphenia subflava*	0	0	0.12	0.41	0	0	0	0
****	*Phryganella acropodia*	0	0	0.06	0.19	0	0	0	0
****	*Trigonopyxis minuta*	0	0	1.14	3.79	0	0	0	0
****	*Unidentified*	0	0	0.34	0.81	0	0	0	0
	Archerella flavum	6.02	6.27	0.06	0.19	0	0	0.53	1.71
	Arcella catinus	20.96	20.17	14.05	16.46	37.44	17.27	44.95	30.18
	Arcella discoides	0.13	0.49	0.41	1.03	0.48	1.17	0.16	0.63
	Argynnia vitrea	0.18	0.52	0	0	0.04	0.16	0	0
	Assulina muscorum	4.86	4.54	4.92	2.85	3.62	2.62	3.03	3.18
	Assulina seminulum	0.56	0.89	0.29	0.62	0.09	0.24	0.04	0.17
	Bullinularia indica	8.43	5.41	13.08	10.94	16.81	19.60	10.21	11.62
	Centropyxis aculeata	1.18	2.90	2.29	4.92	0.29	1.11	1.93	4.17
	Centropyxis cassis	0.05	0.17	6.61	6.38	2.02	5.41	0.24	0.65
	Centropyxis platystoma	0	0	0	0	0.04	0.17	0	0
	Corythion spp.	1.95	2.93	3.47	3.71	4.23	3.67	3.93	5.70
	Cyclopyxis arcelloides	0.48	0.66	6.01	5.82	0	0	0.35	0.66
	Difflugia globulosa	0.04	0.16	2.33	5.04	0	0	0.13	0.51
	Difflugia lucida	0.11	0.30	0.06	0.20	0.04	0.17	0	0
	Euglypha rotunda	3.55	4.16	0.97	1.61	0.83	1.04	3.00	3.39
	Euglypha strigosa	3.79	3.30	1.23	1.60	3.01	2.86	2.36	2.31
	Euglypha tuberculata	1.23	2.07	3.97	6.65	3.65	3.29	2.07	4.09
	Heleopera rosea	1.23	1.81	0.18	0.31	0.45	1.23	0.95	1.36
	Heleopera sphagni	5.86	9.24	0.28	0.74	0.68	1.24	0.22	0.48
	Heleopera sylvatica	3.02	4.12	0.18	0.43	0.68	1.28	0.47	0.56
	Hyalosphenia papilio	7.99	8.01	0.29	0.61	4.43	9.75	8.97	10.84
	Nebela bohemica	0	0	0	0	0.04	0.15	0.71	2.06
	Nebela flabellulum	0	0	0	0	0.04	0.16	0	0
	Nebela militaris	4.21	3.74	2.03	3.49	3.15	3.99	1.07	1.11
	Nebela parvula	1.12	1.86	0.17	0.57	0.22	0.86	0.27	0.55
	Nebela tincta	5.34	3.42	5.75	6.01	5.15	4.61	4.65	3.41
	Pseudodifflugia fulva	0.04	0.17	0.43	1.43	0	0	0	0
	Trigonopyxis arcula	5.13	5.80	26.61	15.36	7.24	5.86	3.22	3.63
	Trinema lineare	4.17	6.44	2.43	3.23	4.99	4.59	6.10	7.17

Community-environment relationships and community concordance

Water chemistry did not vary significantly between sites (Table 4). However, in some cases (mainly for Al and Mg) chemical concentrations were below the detection limits and were recorded as 0. In general, the highest mean values for studied elements apart from Fe were recorded at Ditched sites (Figure 3). WTD varied between the management classes (Table 4) and between months, with the lowest depths recorded at the Ditched sites (Figure 4).

A two-dimensional solution NMDS ordination of the TA communities produced the lowest stress $= 0.207$. Ca and K were significantly correlated with TA community variability ($p = 0.02$ and $p = 0.01$, respectively; Figure 5a). The ordination of the plant community resulted in a two-dimensional solution (final stress $= 0.168$) with significant relation to Fe ($p < 0.01$), K ($p < 0.01$) and Na ($p = 0.04$; Figure 5b).

Table 4. ANOVA (*) and Kruskal-Wallis (**) for water chemistry variables. Calculations are based on average values for each site over all management classes.

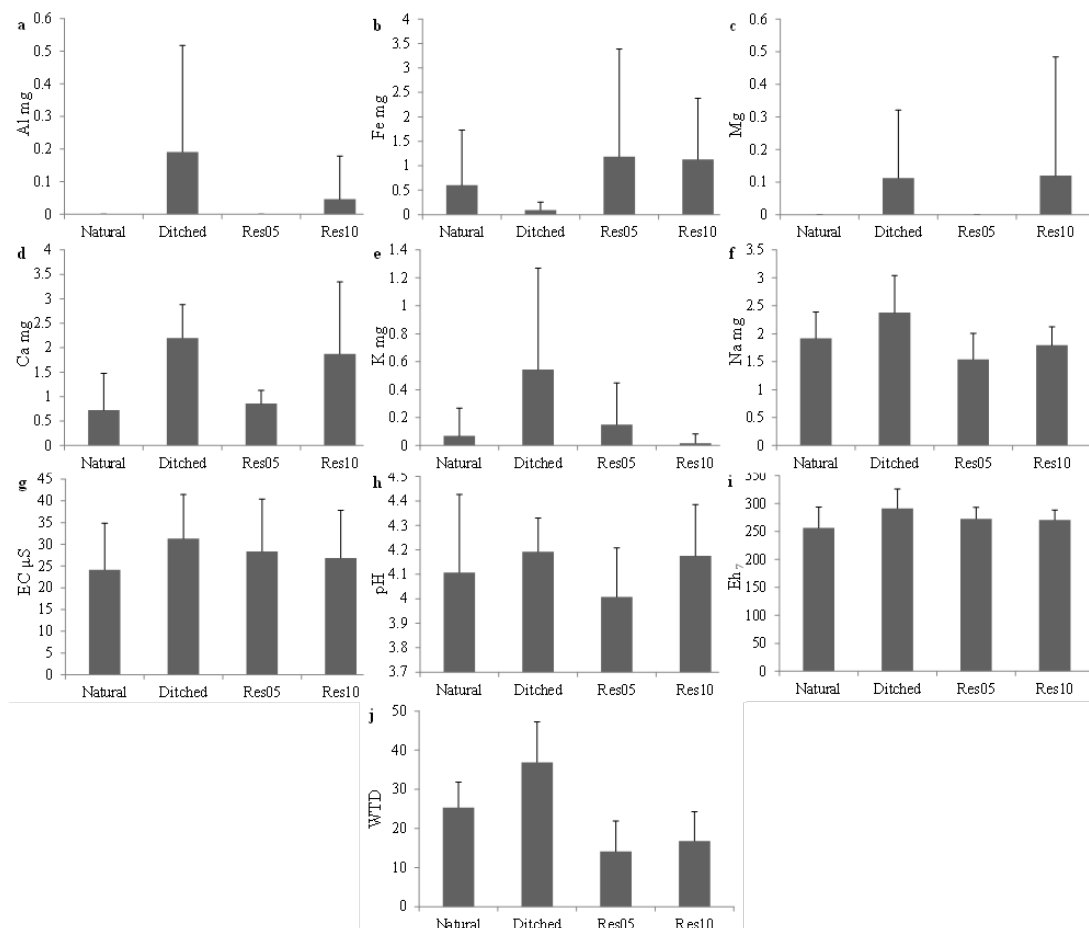|	df	x^2/F	p
*Al	3	2.47	0.481
*Fe	3	2.97	0.397
*Mg	3	4.72	0.194
*Ca	3	7.30	0.063
*K	3	5.14	0.162
**Na	3	2.75	0.079
**EC	3	0.27	0.843
**pH	3	0.89	0.470
**Eh_7	3	2.06	0.148
**WTD	3	4.16	0.025

Figure 3. Average values and standard deviations of the environmental variables measured for each land use management class: (a) aluminum, (b) iron, (c) magnesium, (d) calcium, (f) potassium, (g) conductivity, (h) pH, (i) redox potential, (j) water table depth. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.
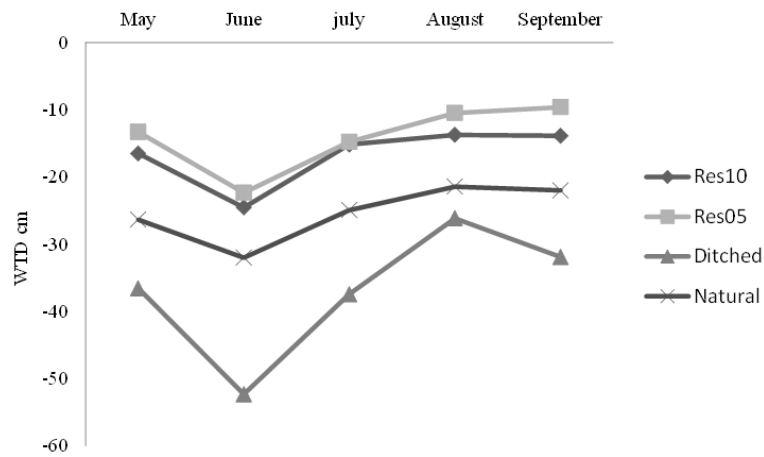
Figure 4. Monthly water table depth variation in 2007. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.
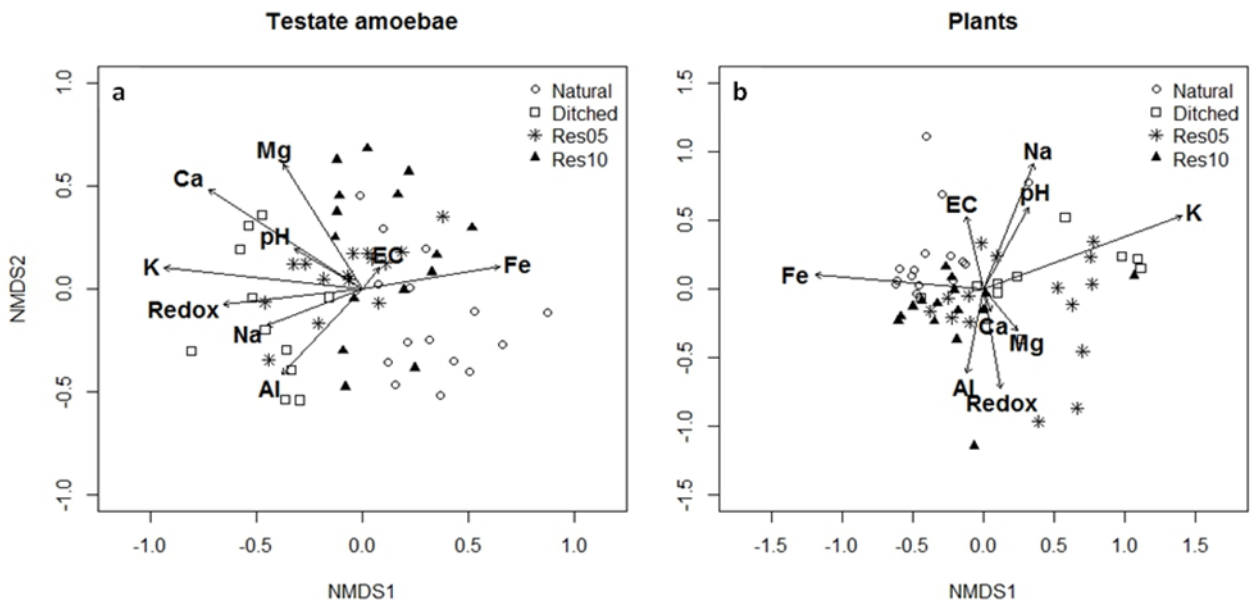

Figure 5. NMDS ordinations of testate amoebae (a) and plant community (b) relationships among management classes. Distance measure: Sørensen (Bray-Curtis). Arrow lengths represent the vector loadings of environmental variables. Res05: peatlands restored 3–7 years ago; Res10: peatlands restored 9–12 years ago.

NMDS plots grouped TA communities by management classes. A separation for communities between the Ditched and Natural sites was observed on NMDS1. Res05 sites were mainly grouped in the centre of the ordination and overlapped with all other management classes, while Res10 sites were fully separated from Ditched sites and more closely grouped to Natural sites (Figure 5a). Ordination of plant communities showed greater variation compared to TA and less clear separation along

NMDS1; however, group separation was observed for Natural and Ditched sites (upper left and centre right in the ordination, respectively). Res05 was mostly grouped closer to Ditched sites overlapping only partly with Res10, whereas Res10 sites clustered closer to Natural sites (Figure 5b).

To look for concordance between plant and TA communities we first ran separate analyses to compare TA with moss species and TA with vascular plant species (results not shown). However,

as no differences were found, both moss and vascular plants were grouped to form a plant community in all subsequent analyses. We found a significant but weak concordance between TA and plant communities (PROTEST $r = 0.44$, $m^2 = 0.79$, $p = 0.001$). To assess whether TA and plant communities were concordant within classes, we ran PROTEST separately for each. Results indicated that only communities at Res05 sites were concordant, but even this relationship was weak (PROTEST $r = 0.54$, $m^2 = 0.70$, $p = 0.01$).

DISCUSSION

Natural sites showed higher TA richness with more diverse communities than other management classes. However, we did not find similar results for plant species richness. Res10 sites showed the lowest TA richness and diversity, which could be attributed to the high dominance of *Arcella catinus* at many of the sites, where this species accounted for more than 70 % of the community. Spatial limitation is less likely to occur in soils than in above-ground environments (Wanner & Xylander 2005). Hence, TA might face less competitive pressure as different taxa may simply occupy different ecological niches, whereas plant species tend to compete for the same space and nutrients. As Natural sites have not undergone extreme environmental changes compared to the other management classes, their higher taxon richness could be attributed to a longer time for cumulative colonisation without a significant TA taxon replacement. This supports the observations by Wanner & Xylander (2005), who studied TA colonisation and successional processes and found temporal changes in TA species composition but very little or no species replacement.

Restoration efforts to rehabilitate peatlands focus mainly on raising the water table to recreate natural habitat conditions. Substratum moisture is often found to be the main factor controlling TA communities (Tolonen 1986), particularly in *Sphagnum* dominated peatlands (Booth 2001), with higher densities of TA cells usually found in soils with high water holding capacity (Fournier *et al.* 2012). Despite the lack of corresponding moisture data, we assume that restoration measures increased peat moisture due to elevated water table levels. As a consequence, increasing TA cell densities could be expected at restored sites over time. We did observe such patterns, as the highest TA densities were found at Res10 sites and the lowest at Ditched sites.

Testate amoebae communities at the wettest sites (Natural, Res10 and Res05) were mostly dominated by *A. catinus* and *B. indica*, while taxon dominance at Ditched sites shifted towards *T. arcula*. However, both *A. catinus* and *B. indica* were highly abundant across all sites suggesting that, although these species are considered indicators of dry conditions, they can display a broad moisture tolerance. Some less abundant species such as *A. artocrea, C. ecornis, D. leidyi, D. lithophila, H. minuta* and *P. fascicularis* were found exclusively at Natural sites. This suggests that not all species recolonise even within a decade after restoration. Poor recolonisation by some typical plant species after restoration (Haapalehto *et al.* 2011, Hedberg *et al.* 2012) highlights the need to avoid degradation of natural habitats, as species that disappear from a site may be very difficult to reinstate without costly and uncertain re-introduction programmes (see also Moreno-Mateos *et al.* 2015). *H. elegans* and *Ph. griseola* occurred only at Natural sites and sites restored ten years ago, suggesting either that they have a longer recolonisation time or that disturbed habitats are just not appropriate for those species. Among plant species, *S. angustifolium* remained dominant across all sites. This species has a wide ecological niche and is known to survive in drained peatlands. However, *S. angustifolium* densities increased rapidly following restoration measures (Haapalehto *et al.* 2011).

The ordinations showed significant relationships of TA communities with Ca and K. Strong relationships between Ca and TA communities have been reported before (e.g. Lamentowicz *et al.* 2010, Hájková *et al.* 2011, Raabe & Lamentowicz 2012, Jassey *et al.* 2014). These could be due to the importance of Ca for shell building in some TA species (Lamentowicz *et al.* 2011). TA relationships with other nutrients have also been observed (e.g. Mitchell *et al.* 2000b, Jauhiainen 2002, Mitchell *et al.* 2004) but their direct effects on TA are not fully understood. Such correlations could arise when water chemistry and nutrient availability indirectly affect TA communities by controlling their prey organisms such as bacteria, fungi, other Protista and micrometazoa (Mitchell *et al.* 2004).

Plants were strongly related to levels of K and Fe, indicating the vital importance of pore water chemistry. The highest K concentrations were found at Res05 sites, and the lowest in Natural and Res10. As an easily leachable cation, K may be released from dying biomass and rewetted organic material after hydrological restoration. Hence, the lower concentrations of K in pore water at Res10 sites

might indicate that K is efficiently taken up during the regrowth of *Sphagnum* and other peatland species. Additionally, after ditch filling small ponds (i.e. topographically lower areas) are formed at restored sites enabling the establishment of anaerobic and reducing conditions that could favour reduction of Fe^{3+} to Fe^{2+} (Haapalehto *et al.* 2014). The reduced form of Fe is readily available for uptake by plants and facilitates plant regrowth.

In NMDS ordination vegetation communities displayed more within-class variation than did TA communities. While TA communities differed between Ditched & Res5 (PerMANOVA), plants did not show differences. These results suggest that TA taxa may be better suited than plants as indicators of early restoration success, on account of their rapid response to hydrological change. Indeed, this was observed by Warner & Chmielewski (1992), who found changes in TA taxa composition within 2½ years of peatland drainage. Talbot *et al.* (2010), who studied peat cores from drained peatlands, also found that TA species indicative of dry conditions reached their highest percentages around the time of drainage, suggesting a very quick response potential of the TA communities to environmental disturbance. Our results highlight the severity of hydrological disturbance by drainage as TA communities still displayed clear differences from those at Natural sites even a decade after restoration. Observed long-term drainage impacts on TA are paralleled by changes in plant communities after drainage (Laine *et al.* 1995, Kareksela *et al.* 2015). From visual inspection of NMDS, plant communities ten years after restoration appeared more similar to those of Natural sites. Maanavilja *et al.* (2014) suggested that only a large rise in water table level would induce significant changes in vegetation communities. In our study plants were sampled 15 m from the ditch where water table changes due to drainage and restoration are smallest and where plant community compositions still largely overlap (Haapalehto *et al.* 2014, Kareksela *et al.* 2015). Finally, Wardle (2002) pointed out that aboveground vegetation communities and soil microorganisms differ in their resistance, resilience, adaptation strategies and dispersal abilities. These differences might also relate to the observed time lags in responses of TA and plant communities to restoration measures.

When comparing all sites, TA and vegetation communities were concordant although this relationship was weak. When each management class was separately analysed we found no community concordance within the management

classes except in the case of Res05 sites. Some studies on stream community concordance (e.g. Infante *et al.* 2009) have suggested scale dependency, which could explain the patterns observed. However, the fact that concordance between TA and plant community was found to be weak, and within-class community concordance apparently lacking, suggests that TA and vegetation community composition are determined in different ways except during the early post-restoration period. Thus, our results suggest that, overall, communities i) respond differently to the same set of environmental factors, or ii) are affected by different environmental factors over timespans exceeding five years, or iii) have different timescales of succession processes, and/or iv) display low overall interaction. Additionally, from their comparison of vascular plants, bryophytes, fungi, diatoms, desmids and TA, Hájek *et al.* (2014) suggested that body size and lifespan play key roles in determining concordance between communities.

In peatland ecosystems, microtopographical transitions can occur at scales of a few centimetres and it is important to avoid the associated ecological gradients, as far as possible, when designing sampling schemes. Gradients at sub-centimetre scales may also be relevant in the context of TA (Mitchell *et al.* 2000a). Vertical variation in habitat conditions is caused mainly by differences in chemical composition between groundwater and rainwater, and is enhanced by cation exchange in the presence of *Sphagnum*. Mitchell *et al.* (2000b) suggest that, because moss and TA species are totally dependent on microsite conditions, they might show different responses than vascular plants which access 'soil' water *via* roots at various depths. However, in separate analyses to compare TA with moss species and TA with vascular plant species, we found no differences in concordance patterns (results not shown).

Restoration strategies such as rewetting of drained peatlands aim primarily to restore vegetation cover (e.g. Similä *et al.* 2014), and this makes plant communities the obvious indicators for restoration success. Our results suggest that the effects of restoration on other components of the peatland ecosystem (e.g. TA communities) may not be properly reflected by the use of vegetation-based indicators alone. Studies of the microbial loop in peatlands by Gilbert *et al.* (1998) revealed that TA, using a wide range of organisms as prey, can account for almost half of the microbial community. Through their feeding TA regulate bacterial biomass and contribute to nutrient mineralisation, nutrition

of soil animals, and plant growth. Griffiths (1994) found that Protista (mainly TA) can account for 20–40 % of N mineralisation as they excrete bacterial N into the soil. Because the TA communities of Res05 sites were more similar than those of Ditched sites to the TA communities of the targeted original ecosystem, restoration by rewetting appears to be efficient in inducing rapid recovery of an important structural component of the ecosystem.

While the relationship is still poorly understood, previous studies suggest that recovery of some important ecosystem functions (e.g. surface peat accumulation) precedes the recovery of ecosystem structure (Kareksela *et al.* 2015). In accordance with that study, our results suggest that recovery of the community structure of TA precedes that of plants and may even be a prerequisite for the recovery of higher plants and ecosystem functions. Thus, TA could play a fundamental role in facilitating plant succession by providing nutrients and consolidating the assembly process on newly exposed land surfaces (Hodkinson *et al.* 2002).

Despite some similarities in early responses, we conclude that TA and vegetation communities cannot be used as surrogates for one another when measuring restoration success. To gain a holistic understanding of the changes in important ecosystem components during restoration from an ecosystem perspective requires the use of both vegetation and TA communities, as also suggested by Raabe *et al.* (2012). However, the shorter generation time of TA enables them to respond more rapidly to environmental changes than vegetation, which makes them better early indicators of restoration success - particularly because post-restoration successional changes in TA communities appear to be targeted towards re-establishment of the site's original community composition. Our results also suggest that further studies on the relationship between TA and plant communities could provide important insights into understanding how the crucial link between ecosystem structure and functions operates during recovery. Better assessment of the dynamics and interplay of post-restoration recolonisation processes for plant and TA communities in the boreal region will require longer-term studies than were achievable here.

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