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

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1   DO TESTATE AMOEBAE COMMUNITIES RECOVER IN CONCORDANCE WITH VEGETATION

2   AFTER RESTORATION OF DRAINED PEATLANDS?

3

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10

11   ABSTRACT

12   The environmental importance of peatlands has raised efforts to restore their specific ecosystem functions

13   and structure. Monitoring and assessment of peatland ecological state is fundamental in restoration programs.

14   However, most studies have focused on the responses of vegetation and, to a lesser extent, on testate

15   amoebae (TA). To our knowledge, none have addressed whether these two groups show concordance with

16   respect to drained peatland restoration. Here we assessed community concordance between TA and

17   vegetation among boreal peatlands of four different landuse management classes (natural, drained, restored

18   3–7 and 9–12 years ago). TA and vegetation communities were concordant when comparing all sites studied.

19   However, there was no concordance within management classes except for the sites restored 3–7 years ago.

20   We found that TA and vegetation communities are not surrogates of each other when measuring restoration

21   success and that a holistic understanding of the changes during restoration from an ecosystem perspective

22   requires thorough studies of both communities. TA seemed to respond faster to changes caused by

23   restoration hence, could be a better early indicator of restoration success than plants. Further, studies of TA

24   and plant communities' relationships could provide important insights into understanding the link between

25   the recovery of ecosystem structures and functions.

26   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. 500Gt 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 to central and southern Finland where pristine peatlands now correspond to less than 25% of their original area (Aapala *et al.* 1996). The increasing threat of environmental degradation has raised awareness of ecological restoration as part of conservation programs (Dobson *et al.* 1997). The environmental importance of peatlands has led to a growing number of attempts to restore or partially rehabilitate the surface water retention, 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 programs (Trepel 2007). Studies based on the assessment of the plant community composition after restoration practices 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 peatland 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 compared to vegetation, and knowing all the TA taxa is not necessary to obtain valuable ecological information. Thus, TA communities have been proposed as a tool for monitoring and assessment of peatland

58 conditions, but to date TA have been employed in relatively few studies (e.g. Jauhiainen 2002, Davis &

59 Wilkinson 2004, Raabe & Lamentowicz 2012, Turner & Swindles 2012, Koenig *et al.* 2015).

60 Well-known taxonomic groups are usually those used as biological indicators in assessment and

61 monitoring of ecosystem health, i.e. the ecosystem's ability to maintain its structure and function when

62 facing external stress (Costanza & Mageau 1999). However, the degree to which certain taxonomic groups

63 actually mirror trends among other groups and can be used as surrogates is still unknown, and studies based

64 on the surrogate-taxa approach have repeatedly been questioned (e.g. Paavola *et al.* 2003, Bilton *et al.* 2006).

65 Most bioassessment studies focus on single taxonomic group responses to environmental factors while few

66 have addressed parallel group responses (i.e. concordance). Community concordance describes the degree of

67 similarity in distributions and abundances of different taxonomic groups across a region and emerges when

68 different communities show similar responses to environmental changes (Infante *et al.* 2009). Studies that

69 have investigated concordance have mostly focused on lakes and fluvial systems (e.g. Heino 2002, Mykrä *et*

70 *al.* 2008, Infante *et al.* 2009, Jyväsjärvi *et al.* 2014) and very few have examined such patterns for peatland

71 ecosystems (Mitchell *et al.* 2000a, Lamentowicz *et al.* 2010, Hájek *et al.* 2014, Koenig *et al.* 2015, Hunter Jr

72 *et al.* 2016).

73 Aspects driving community concordance include strong species interactions within and between

74 communities (Heino 2002) and co-losses of species in response to environmental stress, including

75 anthropogenic stressors (Mykrä *et al.* 2008, Yates & Bailey 2010). Life histories and reproductive and

76 dispersal capabilities of taxa could influence the extent to which different environmental factors and biotic

77 interactions drive spatial patterns of community composition and subsequently, community concordance

78 (Shurin *et al.* 2009). Being based on species identities instead of only number of species, community

79 concordance provides a wider understanding of similarities between communities than richness measures

80 alone (Pawar *et al.* 2007). Further, when concordance does not occur among taxonomic groups at a specific

81 geographical scale, the use of a single group as an indicator for the state of the ecosystem may not be

82 appropriate (Paavola *et al.* 2006).

83 Studies examining peatland restoration efforts generally focus on the recovery of vegetation, but whether

84 important microorganisms such as TA are concordant in their responses to restoration and how these

85 responses are linked to general ecosystem functions remains an open question. Because TA are especially

86 common in *Sphagnum* and other mosses, they may potentially be concordant with peatland vegetation. We

87 therefore assessed concordance of the changes in TA and plant community structures among natural, ditched,

88 and restored boreal peatlands. We specifically aimed i) to analyse changes and concordance between TA and

89 plant communities in response to restoration processes, and ii) to identify which environmental variables

90 drive the changes in these two communities.

91

92 METHODS

93 Study sites

94 Study sites were located in the south-boreal climatic-phytogeographical zone of Southern Finland between

95 61° 53´–62°51´N and 22°53´–25°26´E. In this region, the larger peatland formations are mainly raised bogs,

96 while small weakly minerotrophic *Sphagnum*-dominated mires are typically found in a mosaic landscape

97 pattern with coniferous forests. Sampling sites are located ca. 150m above sea level with a mean annual

98 temperature of +4°C and precipitation ca. 650mm. We selected 19 study sites divided in four land use

99 management classes: i) natural (n=5), ii) drained (n=4), iii) drained and restored 3–7 years before the

100 sampling (n=5), and iv) drained and restored 9–12 years before the sampling (n= 5). For brevity,

101 management classes will hereafter be referred to as Natural, Ditched, Res05, and Res10.
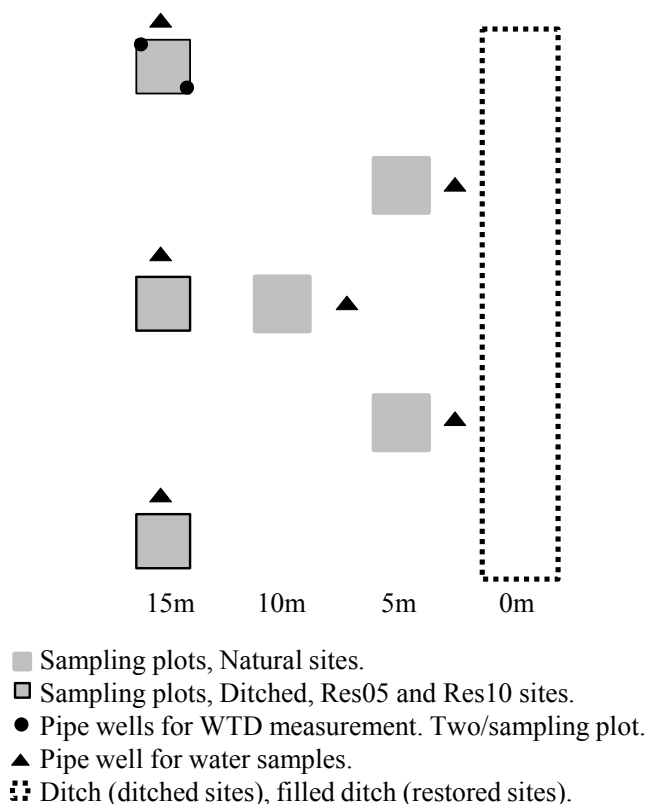
102   Selection of pine fen sites of low minerotrophy was based on field observations and historic aerial

103 photographs ensured that original tree stands of the drained and restored sites were similar. Sites consisting

104 of naturally similar type of vegetation were located in a mosaic of ombro-mesotrophic peatland vegetation,

105 where *Sphagnum* was the main peat-forming plant genus. Based on topographic data and field observations,

106 surface water flow was considered independent for each management class. Peat depth ranged from 95cm to

107 more than 200cm with underlying soil of till or sand.

108   Sites without altered hydrology by ditches or other direct measures represent the least impacted

109 management class and are subsequently referred to as ''Natural''. Even though we acknowledge that forestry

110 measures in distant parts of Natural site catchments may have slight impacts on their hydrology

111 (Tahvanainen 2011), such effects were not obvious. Ditched and Restored sites were drained for forestry

112 purposes during the 1960s and 1970s. During the 1980s, peatlands were restored by filling in the ditches and

113 by removing trees in areas where drainage had significantly increased tree growth. More detailed information

114 about the studied peatlands is given in Haapalehto *et al.* (2014).

115

116 Field sampling and sample processing

117 A grid of 20 1m^2 plots was established at each site (Figure 1). At the Ditched and Restored sites, the plots

118 were situated in five parallel transects, spaced four meters apart and running perpendicular to the ditch. At

119 each transect, there was a plot at 5, 10 and 15 meters distance from the ditch. A 15m x 20m grid of plots was

120 used at the Natural reference sites. Within each of the study sites, the location of the first plot was

121 randomised.

15m   10m   5m   0m

▨ 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).

122

123 Figure 1. Study sampling design for: testate amoebae, plants and environmental variables. Distances (m)

124 refer to distance of the 1m² plots to the ditches at the Ditched and Restored sites. At Natural sites, a similar

125 arrangement of plots was used. Res05: peatlands restored 3-7 years ago; Res10: peatlands restored 9-12

126 years ago.

127   For water chemistry analyses at the Natural sites, three 32mm diameter polypropylene pipe wells with

128 2mm slits spaced at 2–3cm intervals and polypropylene filter gauges were distributed in the central part of

129 the sampling grid. At the Ditched and Restored sites filter gauges were set at a distance of 15m to the ditch

130 and 10m apart (Figure 1). Samples were collected in August 2007. Redox potential (Eh$_7$), electrical

131 conductivity (EC) and pH were measured between two to five hours after sample collection using a Consort

132 SP50X meter with SP50X, SK10T and SP10B electrodes, respectively. Samples were then stored in darkness

133 at +4°C before further analysis. Cation concentrations (Al, Ca, Fe, K, Mg, Na) were obtained after filtration

134 with 0.45 μm pore size filters and analysed with a PerkinElmer Optima 4300 DV inductively coupled plasma

135 optical emission spectrometer. Water table depth (WTD) was measured five times (May, June, July, August,

136 and September) in 2008 in selected plots from two permanent polypropylene pipe wells. WTD values were

137 corrected for the natural slope (see Haapalehto *et al.* 2014) and averaged to absolute levels throughout the

138 site. WTD data are usually recorded as negative values, but to facilitate the readability, inverse, positive

139 values are used here throughout the text.

140   Plants and TA were sampled from the plots located next to the polypropylene pipe wells (three plots at

141 each site). We estimated the relative abundance (percentage of coverage) of each taxon of vascular plants,

142 bryophytes, and some lichens for each sampled plot. Sampling was done during July and August 2007. To

143 obtain TA, approximately 10cm³ of bryophyte mass was extracted (see also Booth *et al.* 2010). Samples

144 were stored in plastic Ziploc bags, frozen, defrosted and oven dried, stored in paper bags and analysed in

145 2013 using the protocol proposed by Booth *et al.* (2010). To retain TA, each sample was boiled for 10

146 minutes in distilled water with one tablet of *Lycopodium clavatum* spores (batch 1031) standard preparation

147 from Lund University (Sweden), and sieved it through a 300μm mesh to remove coarse materials and onto a

148 7μm mesh. Retained TA were centrifuged at 3000 rpm for five minutes and stored in distilled water. A

149 minimum of 150 TA was counted and identified using 40X magnification (Olympus BX41 microscope). As

150 the standing plant community is the result of several years of development, non-living TA were also included

151 in the analysis to integrate the accumulation of tests over the entire time period. TA identification was based

152 on characteristics of the shell following a number of different taxonomic keys (e.g. Charman *et al.* 2000 with

153 modifications by Booth 2008, Meisterfeld 2002, Clark 2003, Mitchell 2003a, Mitchell 2003b, Mazei &

154 Tsyganov 2006).

155

156 Data analysis

157 We calculated species richness, Shannon diversity index, and relative abundances of TA and vegetation

158 communities for each site (using plot averages), and averaged by management classes. For TA communities,

159 density was estimated using the *Lycopodium* counts as an external marker (see Stockmarr 1971 for details)

160 and relative abundances were calculated as a percentage of the total counted. ANOVA and Tukey's (HSD)

161 post hoc test were performed to assess differences in species richness and Shannon diversity indices between

162 management classes. Due to the unbalanced design, permutational MANOVA (PerMANOVA) was used to

163 test the significance of the differences in structure and composition among the communities in the four

164 management classes. Differences in water chemistry and WTD were analysed using ANOVA or Kruskal-

165 Wallis depending on whether the data met the normality and homoscedasticity assumptions. To summarise

166 variability in the communities, a Non-metric Multidimensional Scaling (NMDS) based on Sørensen's (Bray-

167 Curtis) distance was performed. We used NMDS to examine the degree of concordance of water chemistry

168 variables with community ordinations. WTD was not included in the community ordinations, as these data

169 were not taken at exactly the same time as the biological samples. A two dimensional NMDS solution

170 achieved a moderate stress level for plant communities but not for TA communities; however, for simplicity

171 of comparison we retained the two dimensional TA solution. Concordance between TA and plant

172 communities was tested using the PROTEST analysis (Peres-Neto & Jackson 2001). All calculations were

173 done using R (version 3.0.2) and the vegan package for NMDS and PROTEST analyses (Oksanen *et al.*

174 2015).

175

176 RESULTS

177 Community data

178 Altogether 44 TA and 45 plant taxa were found in our study. TA taxon richness at Natural sites ($\bar{X}$= 17.7

179 range 14–24, SE= 0.71) was higher than at Ditched, Res05, and Res10 sites (ANOVA $F_{[1,3]}$= 15.79, $p<$

180 0.001) whereas no differences were found among Ditched, Res05, and Res10 sites (Table 1; Figure 2a). TA

181 Shannon diversity index was generally higher at Natural sites, where the highest value was 2.56, while the

182 lowest values were found at Res05 sites (Figure 2c). We observed differences in TA diversity only between

183 Natural-Res05 and Natural-Res10 sites (Table 1). The highest cell density was found at Res10 sites ($\bar{X}$=

184 24953 cells/10cm³) and the lowest at Ditched sites ($\bar{X}$= 6767 cells/10cm³).

185

186 Table 1. Tukey's (HDS) results for TA taxon richness and Shannon diversity. Res05: peatlands restored 3-7

187 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
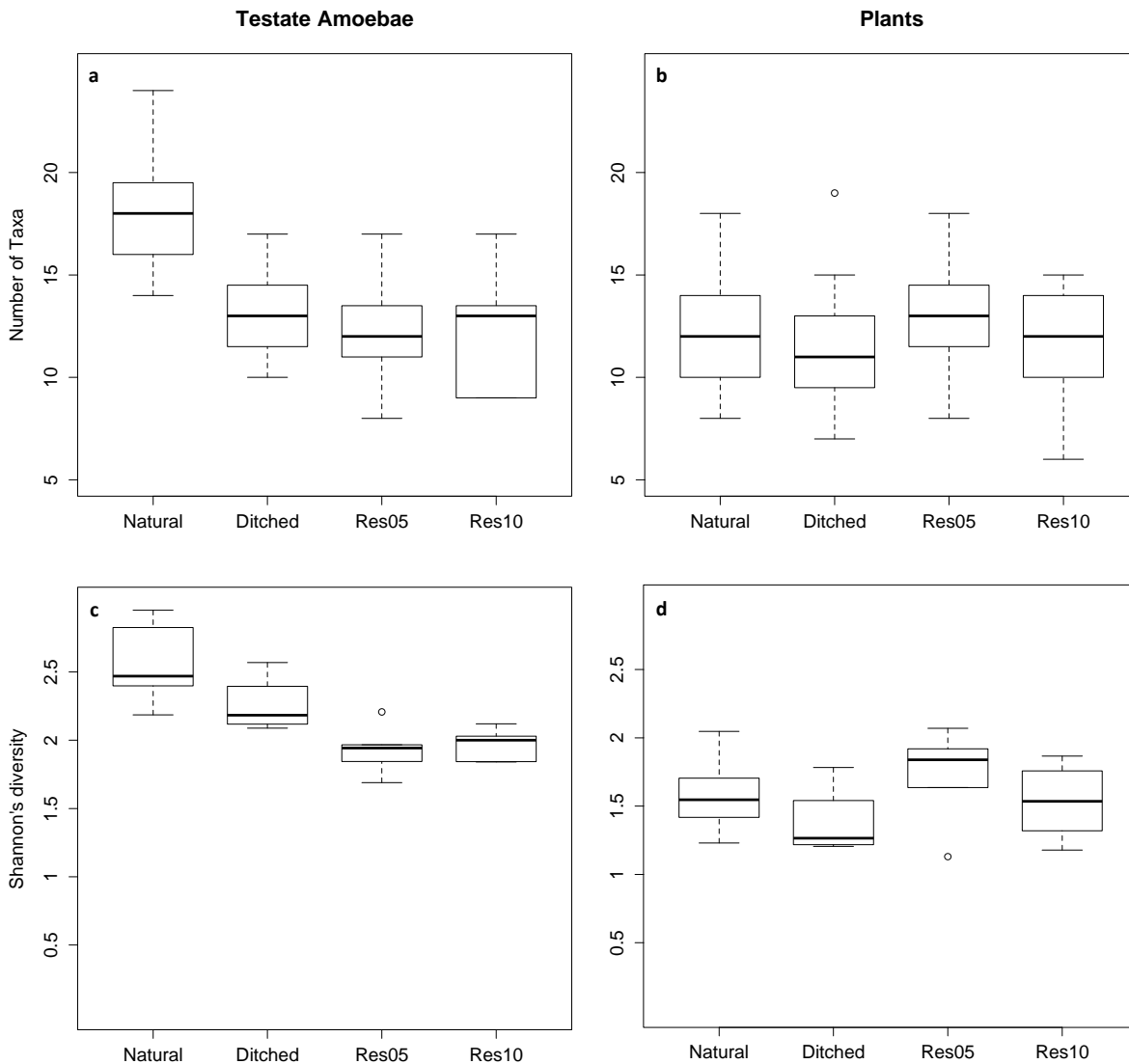
Figure 2. Taxon richness boxplots for testate amoebae (a) and vegetation (b). Shannon's diversity boxplots for testate amoebae (c) and vegetation (d) for each management class. Circles: outliers, upper whisker: maximum value excluding outliers, upper box line: upper quartile, middle line inside box: 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.

196   No differences in the mean number of plant taxa were found between management classes (Figure 2b). In

197   general, plant diversity tended to be higher at Res05 sites but, overall, there were no significant differences

198   between classes (F= 0.9, p= 0.46; Table 1; Figure 2d). TA community structure and composition differed

199   between classes except between Res05 and Res10 (Table 2). For vegetation communities, only Natural sites

200   differed from all other classes (Table 2, see also Haapalehto 2014).

201

202   Table 2. PerMANOVA pairwise comparisons for TA and plant community structure and composition.

203   Res05: peatlands restored 3-7 years ago; Res10: peatlands restored 9-12 years ago.

				TA							Plants			
		df	*SS*	*MS*	*Pseudo*-F	r^2	*p*	*df*	*SS*	*MS*	*Pseudo*-F	r^2	*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

204

205   On average, TA communities in Natural, Res05, and Res10 sites were mainly dominated by *Arcella*

206   *catinus* and *Bullinularia indica.* At Ditched sites, *Trigonopyxis arcula* was the most widely dominant taxon

207   followed by *A. catinus*. More than 50% of the TA species were found over all sites regardless of

208   management class, but some species displayed a more restricted distribution. For example, *Arcella artocrea,*

209   *Centropyxis ecornis, Difflugia leidyi, Difflugia lithophila, Hyalosphenia minuta* and *Pseudodifflugia*

210   *fascicularis* were present just at Natural sites while *Hyalosphenia elegans* and *Physochila griseola* were

211   absent from Ditched and Res05 sites (Table 3). Vegetation communities were dominated by *Sphagnum*

212   *angustifolium* at all sites regardless of management class. However, densities were highly variable.

213   *Pleurozium schreberi* was the second most dominant species at Res05 and Ditched sites, while at Res10 and

214   Natural sites *S. magellanicum* and *S. fuscum* were more abundant (see Haapalehto 2014).

215

216   Table 3. TA average relative abundances in percentage and standard deviations for each management class.

217   (*) Taxa found just at natural sites; (**) taxa found at Natural and in sites restored 10 years ago; (***) taxa

218   found at all but Ditched sites; (****) taxa found just at Ditched sites. Res05: peatlands restored 3-7 years

219   ago; Res10: peatlands restored 9-12 years ago.

Taxa	Natural X̄	Natural SD	Ditched X̄	Ditched SD	Res05 X̄	Res05 SD	Res10 X̄	Res10 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 were recorded at Ditched sites except for Fe (Figure 3). WTD varied between the management classes (Table 4) and between months, with the lowest depths recorded at the Ditched sites (Figure 4).

228

229 Table 4. ANOVA (*) and Kruskal-Wallis (**) for water chemistry variables. Calculations are based on

230 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

231
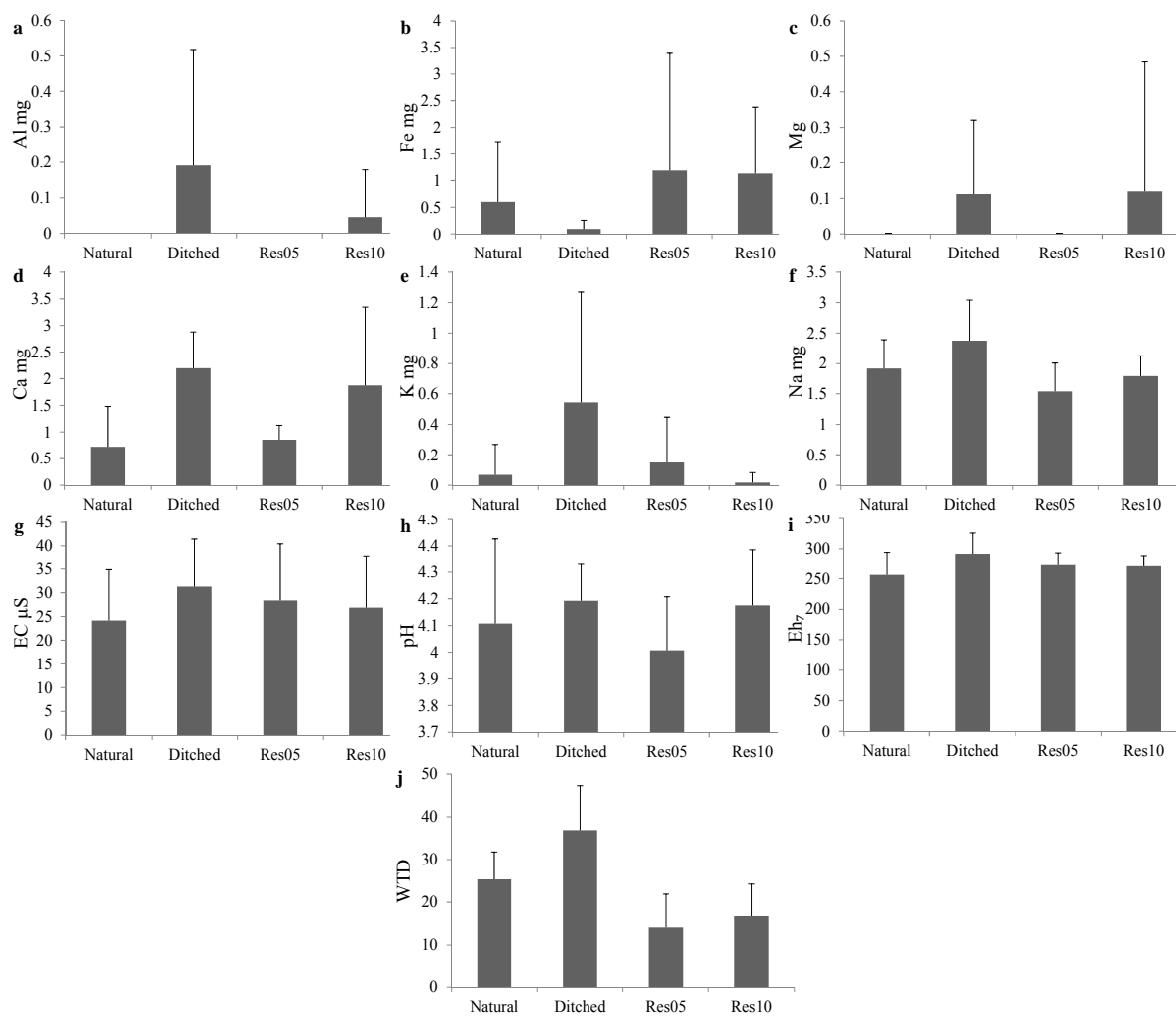
232

233 Figure 3. Average values and standard deviations of the environmental parameters measured for each land

234 use management class. (a) aluminum, (b) iron, (c) magnesium, (d) calcium, (f) potassium, (g) conductivity,

235 (h) pH, (i) redox potential, (j) water table depth. Res05: peatlands restored 3-7 years ago; Res10: peatlands

236 restored 9-12 years ago.
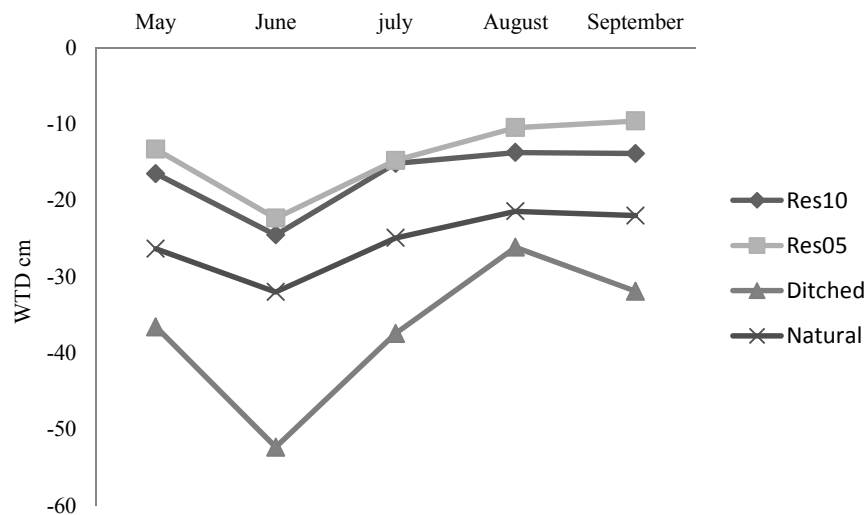
237

238 Figure 4. Monthly water table depth variation in 2007. Res05: peatlands restored 3-7 years ago; Res10:

239 peatlands restored 9-12 years ago.

240   A two-dimensional solution NMDS ordination of the TA communities produced the lowest stress at=

241 0.207. Ca and K were significantly correlated with TA community variability ($p= 0.02$ and $p= 0.01$,

242 respectively; Figure 5a). The ordination of the plant community resulted in a two-dimensional solution (final

243 stress= 0.168) with significant relation to Fe ($p<0.01$), K ($p<0.01$) and Na ($p= 0.04$; Figure 5b).

244   NMDS plots grouped TA communities by management classes. A separation for the communities

245 between the Ditched and Natural sites was observed on NMDS1. Res05 sites were mainly grouped in the

246 centre of the ordination and overlapped with all other management classes, while Res10 sites were fully

247 separated from Ditched sites, and more closely grouped to Natural sites (Figure 5a). Ordination of plant

248 communities showed higher variations compared to TA and less clear separation along NMDS1; however,

249 group separation was observed for Natural and Ditched sites (upper left and central right in the ordination,

250 respectively). Res05 was mostly grouped closer to Ditched sites overlapping only partly with Res10, whereas

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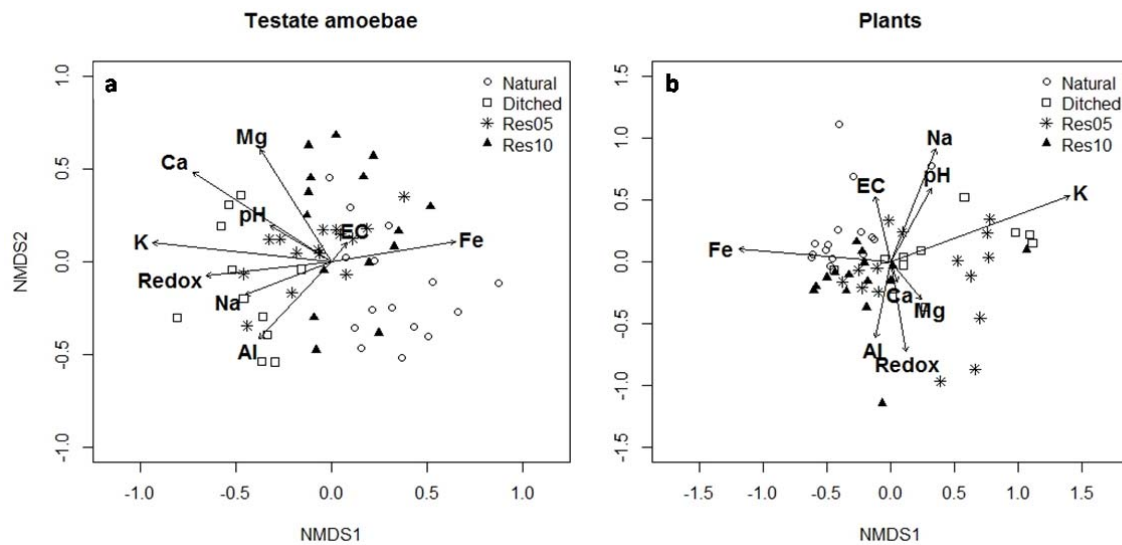
Figure 5. NMDS ordinations of testate amoebae (a) and plant community (a) relationships among management classes. Distance measure: Sørensen (Bray-Curtis). Arrow lengths represent the vector loadings of environmental variables. Res05: peatlands restored 3-7 years ago; Res10: peatlands restored 9-12 years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

To look for concordance between plant and TA communities we first ran separate analyses to compare TA to moss species and TA to 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 relation 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 compared to aboveground environments (Wanner & Xylander 2005). Hence, TA might face less competitive pressure as different taxa may simply occupy different ecological niches, whereas plant

272   species tend to compete for the same space and nutrients. As Natural sites have not undergone extreme

273   environmental changes compared to the other management classes, their higher taxon richness could be

274   attributed to a longer time for cumulative colonisation without a significant TA taxon replacement. This

275   supports the observations by Wanner & Xylander (2005) who studied TA colonisation and successional

276   processes, and found temporal changes in TA species composition but no or very little species replacement.

277   Restoration efforts to rehabilitate peatlands focus mainly on raising the water table to recreate natural

278   habitat conditions. Substratum moisture is often found to be the main factor controlling TA communities

279   (Tolonen 1986) particularly in *Sphagnum* dominated peatlands (Booth 2001) with higher densities of TA

280   cells usually found in soils with a high water holding capacity (Fournier *et al.* 2012). Despite the lack of

281   corresponding moisture data, we assume that restoration measures increased peat moisture due to elevated

282   water table levels. As a consequence, increasing TA cell densities should be expected at restored sites over

283   time. We did observe such patterns, as the highest TA densities were found at Res10 sites and the lowest at

284   Ditched sites.

285   Testate amoebae communities at the wettest sites (Natural, Res10, and Res05) were mostly dominated by

286   *A. catinus* and *B. indica* while at Ditched sites, taxon dominance shifted towards *T. arcula*. However, both *A.*

287   *catinus* and *B. indica* were highly abundant across all sites suggesting that despite these species are

288   considered indicators of dry conditions, they can display a broad moisture tolerance. Some less abundant

289   species, such as *A. artocrea, C. ecornis, D. leidyi, D. lithophila, H. minuta,* and *P. fascicularis,* were found

290   exclusively at Natural sites. This suggests that not all species recolonize even within a decade after

291   restoration. Poor re-colonization of some typical plant species after restoration (Haapalehto *et al.* 2011,

292   Hedberg *et al.* 2012) highlights the need to avoid degradation of natural habitats, as species that disappear

293   from a site may be very difficult to reinstate without costly and uncertain re-introduction programs (see also

294   Moreno-Mateos *et al.* 2015). *H. elegans* and *Ph. griseola* only occurred at Natural sites and sites restored 10

295   years ago, suggesting that they either have a longer recolonization time, or that disturbed habitats are just not

296   appropriate for those species. Among plant species, *S. angustifolium* remained dominant across all sites. This

297   species has a wide ecological niche, and is known to survive in drained peatlands. However, *S. angustifolium*

298   densities increased rapidly following restoration measures (Haapalehto *et al.* 2011).

299   Ordinations showed significant relationship of TA communities with Ca and K. Strong relationships

300   between Ca and TA communities have been reported before (e.g. Lamentowicz *et al.* 2010, Hájková *et al.*

301   2011, Raabe & Lamentowicz 2012, Jassey *et al.* 2014). These could be due to the importance of Ca for the

302   shell building process of some TA species (Lamentowicz *et al.* 2011). TA relationships with other nutrients

303   have also been observed (e.g. Mitchell *et al.* 2000a, Jauhiainen 2002, Mitchell *et al.* 2004) but their direct

304   effects on TA are not fully understood. Such correlations could arise when water chemistry and nutrient

305   availability indirectly affect TA communities by controlling their prey organisms such as bacteria, fungi,

306   other Protista, and micrometazoa (Mitchell *et al.* 2004).

307   Plants were strongly related to levels of K and Fe, indicating the vital importance of pore water chemistry.

308   The highest K concentrations were found at Res05 sites, and the lowest in Natural and Res10. As an easily

309   leachable cation, K may be released from dying biomass and rewetted organic material after hydrological

310   restoration. Hence the lower concentrations of K in pore water at Res10 sites might indicate that K is

311   efficiently taken up during the regrowth of *Sphagnum* and other peatland species. Additionally, after ditch

312   filling small ponds, topographically lower areas are formed at restored sites enabling the establishment of

313   anaerobic and reducing conditions that could favour reduction of Fe^{3+} to Fe^{2+} (Haapalehto *et al.* 2014). This

314   reduced form of Fe is readily available for uptake by plants and facilitates plant regrowth.

315   In NMDS ordination vegetation communities displayed more within-class variation compared to TA.

316   While TA communities differed between Ditched & Res5 (PerMANOVA) plants did not show differences.

317   These results suggest that TA taxa might be better suited than plants as indicators of early restoration success

318   thanks to their rapid response to hydrological variations. This indeed was observed by Warner &

319   Chmielewski (1992) who found changes in TA taxa composition within 2½ years of peatland drainage.

320   Further, also Talbot *et al.* (2010) who studied peat cores of drained peatlands found that TA species

321   indicative of dry conditions reached their highest percentages around the time of drainage, suggesting a very

322   quick response potential of the TA communities to environmental disturbance. Our results highlight the

323   severity of hydrological disturbance by drainage as TA communities still displayed clear differences from

324   those at Natural sites even a decade after restoration. Observed long-term drainage impacts on TA are

325   paralleled by changes in plant communities after drainage (Laine *et al.* 1995, Kareksela *et al.* 2015). From

326   visual inspection of NMDS, vegetation communities 10 years after restoration appeared more similar to

327   Natural sites. Further, Maanavilja *et al.* (2014) suggested that only a large rise in the water table level would

328   induce significant changes in vegetation communities. Indeed, in our study plants were sampled 15m from

329   the ditch where water table changes to drainage and restoration are smallest and where plant community

330 compositions still largely overlap (Haapalehto *et al.* 2015, Kareksela *et al.* 2015). Finally, Wardle (2002)

331 pointed out that aboveground vegetation communities and soil microorganisms differ in their resistance,

332 resilience, adaptation strategies, and dispersal abilities. These differences might also relate to the observed

333 time lags in responses of TA and plant communities to restoration measures.

334   When comparing all sites, TA and vegetation communities were concordant although this relationship

335 was weak. When each management class was separately analysed we found no within management class

336 community concordance except for Res05 sites. Some studies on stream community concordance (e.g.

337 Infante *et al.* 2009) have suggested a scale dependency, which could explain the observed patterns. However,

338 the fact that TA and vegetation community concordance was found to be weak, and the apparent lack of

339 within-class community concordance suggest that TA and vegetation community composition are

340 determined in different ways except during early post-restoration. Our results thus suggest that either overall

341 communities i) respond differently to the same set of environmental factors, or ii) are affected by different

342 environmental factors over timespans exceeding 5 years, or iii) have different time scales of succession

343 processes, and/or iv) display low overall interaction. Additionally, Hájek *et al.* (2014) from their comparison

344 of vascular plants, bryophytes, fungi, diatoms, desmids, and TA suggested that body size and life span play a

345 key role when determining concordance between communities.

346   In peatland ecosystems, microtopographic transitions can occur at scales of a few centimetres reducing

347 the ability to avoid ecological gradients when sampling. Even though microtopographic transitions at the

348 centimetre scale are specifically important when designing the sampling, even smaller gradients may still

349 exist at the scale of TA (Mitchell *et al.* 2000b). This vertical variation is mainly caused by differences in the

350 chemical composition of ground water and rainwater and is enhanced by *Sphagnum* cation exchange

351 (Mitchell *et al.* 2000a). As moss species and TA are dependent on microsite conditions, they might reflect

352 different conditions than vascular plants, which are rooted at different depths (Mitchell *et al.* 2000a).

353 However in separate analyses to compare TA to moss species and TA to vascular plant species we found no

354 differences in concordance patterns (results not shown). Restoration strategies such as rewetting of drained

355 peatlands aim mainly at restoring the vegetation coverage of sites (e.g. Similä *et al.* 2014). To this end, plant

356 communities are obvious indicators of restoration success. However, our results suggest that restoration

357 effects on other components (e.g. TA communities) in peatlands might not be reflected properly by the use of

358 vegetation-based indicators alone. Gilbert *et al.* (1998) studied the microbial loop in peatlands and revealed

359   that TA can account for almost half of the microbial community using a wide range of organisms as prey.

360   Through their feeding TA regulate bacterial biomass, contribute to nutrient mineralisation, nutrition of soil

361   animals, and plant growth. Griffiths (1994) found that, in general, Protista and mainly TA can account for

362   20–40% of N mineralisation as they excrete bacterial N into the soil. As the TA communities of Res05 sites

363   were more similar to the targeted original ecosystem than Ditched ones, restoration by rewetting appears to

364   be efficient in inducing a rapid recovery of an important structural ecosystem component. While the

365   relationship is still poorly understood, previous studies suggest that recovery of some important ecosystem

366   functions like surface peat accumulation precedes the recovery of ecosystem structure (Kareksela *et al.*

367   2015). In accordance with that study, our results suggest that the recovery of TA community structure

368   precedes that of plants and in fact may even be a prerequisite for the recovery of higher plants and ecosystem

369   functions. Thus, TA might play a fundamental role in the facilitation of plant succession by providing

370   nutrients and consolidating the assembly process on newly exposed land surfaces (Hodkinson *et al.* 2002).

371   In conclusion, despite some similarities in early responses, TA and vegetation communities cannot be

372   used as surrogates of each other when measuring restoration success. To gain a holistic understanding of the

373   changes in important ecosystem components during restoration from an ecosystem perspective requires the

374   use of both vegetation and TA communities as also suggested by Raabe and Lamentowicz (2012). However,

375   the shorter generation time of TA compared to vegetation enable them to respond faster to environmental

376   changes making them better suited as early indicators of restoration success particularly because post-

377   restoration successional changes in TA communities appear to be targeted towards the re-establishment of

378   the site's original community composition. Our results also suggest that further studies on the relationship

379   between TA and plant communities could provide important insights into understanding the crucial link

380   between the recovery of ecosystem structure and functions. Better assessment of the dynamics and interplay

381   of the post-restoration re-colonisation processes of the two communities in the boreal region will require

382   studies spanning longer time scales than were studied here.

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