

1 The role of climate change in regulating Arctic permafrost peatland
2 hydrological and vegetation change over the last millennium

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9

10 **Abstract**

11 Climate warming has inevitable impacts on the vegetation and hydrological dynamics of high-latitude
12 permafrost peatlands. These impacts in turn determine the role of these peatlands in the global
13 biogeochemical cycle. Here, we used six active layer peat cores from four permafrost peatlands in
14 Northeast European Russia and Finnish Lapland to investigate permafrost peatland dynamics over the
15 last millennium. Testate amoeba and plant macrofossils were used as proxies for hydrological and
16 vegetation changes. Our results show that during the Medieval Climate Anomaly (MCA), Russian sites
17 experienced short-term permafrost thawing and this induced alternating dry-wet habitat changes
18 eventually followed by desiccation. During the Little Ice Age (LIA) both sites generally supported dry-
19 hummock habitats, at least partly driven by permafrost aggradation. However, proxy data suggest that
20 occasionally, MCA habitat conditions were drier than during the LIA, implying that evapotranspiration
21 may create important additional eco-hydrological feedback mechanisms under warm conditions. All sites
22 showed a tendency towards dry conditions as inferred from both proxies starting either from *ca.* 100
23 years ago or in the past few decades after slight permafrost thawing, suggesting that recent warming has
24 stimulated surface desiccation rather than deeper permafrost thawing. This study shows links between
25 two important controls over hydrology and vegetation changes in high-latitude peatlands: direct
26 temperature-induced surface layer response and deeper permafrost layer-related dynamics. These data
27 provide important backgrounds for predictions of Arctic permafrost peatlands and related feedback
28 mechanisms. Our results highlight the importance of increased evapotranspiration and thus provide an
29 additional perspective to understanding of peatland-climate feedback mechanisms.

30

31 **Keywords**

32 Testate amoeba, plant macrofossil, hydrology, vegetation, permafrost peatlands, last millennium, MCA,
33 LIA, recent warming

34

35 **Introduction**

36 High-latitude peatlands play a critical role in the global biogeochemical cycle, through which they also
37 contribute to climate dynamics (Frolking and Roulet, 2007). Temperature and moisture balance are key
38 factors modulating peat accumulation (Carroll and Crill, 1997; Davidson and Janssens, 2006; Ovenden,
39 1990). Global warming, especially amplified warming in high-latitude regions (IPCC, 2013), is expected
40 to directly stimulate photosynthesis and net primary productivity (NPP) in high-latitude ecosystems
41 because of increased growing season length (Charman et al., 2013). Thus, peat accumulation is expected
42 to accelerate too (Loisel and Yu, 2013). However, higher temperatures also increase peat decomposition
43 rates through accelerated microbial activity (Dorrepaal et al., 2009; Ise et al., 2008), yet there is evidence
44 from the past that during warm periods the increase in NPP exceeded the potential increase in
45 decomposition (Charman et al., 2013). Climate scenarios for high latitudes predict that mean summer
46 precipitation will increase in the future (Collins et al., 2013), which could be beneficial for peat
47 accumulation. However, increases in precipitation may be offset by increases in evapotranspiration under
48 higher temperatures (Yu et al., 2009). Also, seasonal droughts may reduce NPP and increase
49 decomposition (Yu et al., 2009). Moreover, habitat-specific plant functional types (PFTs) that
50 characterise different peatlands (fens and bogs) have different NPP dynamics and the distribution of
51 these communities can exert a control on peat accumulation patterns (Tuittila et al., 2012). While climate
52 may directly affect plant productivity and decomposition, it may also have larger-scale impacts on the
53 geographical distribution of peatland types (Väliranta et al., 2015).

54 Arctic permafrost peatlands are sensitive to climatic changes (Gałka et al., 2017a; Lamarre et al., 2012;
55 Swindles et al., 2015a; Teltewskoi et al., 2016; Tremblay et al., 2014) and at the same time, they affect
56 local microclimate, hydrology, vegetation, peat and carbon accumulation and these non-climatic factors
57 again influence the degradation and aggradation of permafrost (Zuidhoff and Kolstrup, 2000). Due to
58 pronounced microtopography and persisting ice, eco-hydrological processes and therefore peat
59 accumulation patterns in permafrost peatlands are very complex (Oksanen, 2006; Oksanen et al., 2001),
60 making the evaluation of climate change impacts on these environments challenging. Northern
61 Hemisphere mean annual temperature for the last 30- and 50-year periods is likely higher than any other
62 preceding equally long measurement period during the past 800 years (Masson-Delmotte et al., 2013).
63 Permafrost ground temperature monitoring studies have documented a rising trend over the last 20-30
64 years and observations suggest permafrost thaw in the southern margins of the permafrost area (Brown
65 and Romanovsky, 2008; Johansson et al., 2011; Sannel et al., 2016). Even though these observations are
66 not ubiquitous (Brown and Romanovsky, 2008), a widespread permafrost thaw can be expected as a

67 consequence of global warming. It may be speculated that Arctic permafrost peatlands are on the edge
68 of their climatological niche and have low potential to remain stable under future climate changes (Bosio
69 et al., 2012). One presumption is that when permafrost thaws or if the active layer deepens considerably,
70 permafrost areas become large CO₂ sources due to accelerated decomposition rates (Abbot et al., 2016;
71 Koven et al., 2011; Schadel et al., 2016). It is suggested that these dynamics may be one of the most
72 significant potential feedbacks from terrestrial ecosystems to the atmosphere in the future (Schuur et al.,
73 2008). However, because of the scarcity of information and data, disentangling the links between
74 permafrost peatland vegetation, hydrology and climate, the future balance of NPP and decomposition
75 processes in permafrost peatlands has remained uncertain. These coupled dynamics can be investigated
76 by comparing palaeoecological data to documented climate epochs such as the Medieval Climate
77 Anomaly (MCA) from *ca.* AD 950-1200, the Little Ice Age (LIA) from *ca.* AD 1400-1850, and recent
78 warming since the late 19th century (e.g., Cook et al., 2004; Esper et al., 2002; Hanhijärvi et al., 2013;
79 Wilson et al., 2016).

80 In this study we investigated past hydrological changes and associated variations in vegetation
81 composition during the last millennium in four permafrost peatlands. We used two different proxies;
82 testate amoebae (Amesbury et al., 2016; Charman et al., 2007; Swindles et al., 2015b) and plant
83 macrofossils (Väliranta et al., 2007; 2012) to reconstruct past moisture conditions and vegetation history,
84 which enabled cross validation of results and therefore more dependable data interpretation (Loisel and
85 Garneau, 2010; Väliranta et al., 2012). Using ¹⁴C and ²¹⁰Pb dating, we linked detected changes to known
86 climate periods. Replicate records from the same peatland and/or close-by regions allowed us to evaluate
87 whether detected changes were climate-driven and regional or forced by autogenic factors (Mathijssen
88 et al., 2016; 2017; Swindles et al., 2012). Our hypotheses were 1) that permafrost thawing triggered by
89 warm climate conditions (e.g., MCA and recent warming), is reflected in proxy records as a change
90 towards wetter plant communities and more hydrophilic testate amoeba assemblages, and that 2)
91 permafrost aggradation under colder climate conditions such as LIA results in dry conditions through
92 raising of the peat surface. Furthermore, we evaluate whether and how the peatland response to MCA
93 warming differs from the on-going recent warming.

94

95 **Study sites**

96 Our four study sites are located in two regions: two sites (Indico and Seida) are located in the
97 discontinuous permafrost zone of Russia whereas the other two (Kevo and Kilpisjärvi) are in the sporadic
98 permafrost zone of the Finnish Lapland (Fig. 1 and Table 1).

99 Indico and Seida are located in the Arctic Northeast European Russian tundra. The peat plateaus in these

100 two peatlands are elevated a few metres from the surrounding mineral soil and the vegetation is
101 dominated by shrub-lichen-moss communities, such as *Betula nana*, *Rhododendron tomentosum*,
102 *Empetrum nigrum*, *Sphagnum fuscum*, *Polytrichum strictum*, *S. lindbergii* and sedges *Eriophorum* spp.
103 Compared to Seida, Indico presents extensive areas covered by lichens and mosses with a lower shrub
104 layer. Large bare peat surfaces occur on both sites (Repo et al. 2009).

105 At the two sites in Finnish Lapland, Kevo and Kilpisjärvi, the peatlands are characterised by separate
106 permafrost mounds a few metres high and surrounding wet flarks. The mound vegetation is dominated
107 by dwarf shrubs, such as *Betula nana*, *Empetrum nigrum*, *Rubus chamaemorus* and bryophytes
108 *Polytrichum strictum* and *Dicranum* spp. Different *Sphagnum* species such as *S. fuscum*, *S. balticum*, *S.*
109 *majus* and *S. riparium* occur along a hydrological gradient from dry hummock to wet hollow and
110 *Eriophorum* spp. are also present.

111

112 **Materials and methods**

113 *Sampling*

114 In total, six active layer peat cores (Table 1) were collected from the four permafrost peatland sites using
115 a Russian peat corer with a diameter of 5 cm. In Indico, three replicate peat cores (Ind1-3) were collected
116 along a transect from the centre to the margins of the site to assess potential differences in sensitivity
117 across the peatland surface. A single core was collected from each of the other sites. Individual cores
118 were wrapped in plastic and transported to the laboratory in sealed PVC tubes and stored in a freezer.
119 The cores were later defrosted and sub-sampled in 1-cm or 2-cm thick slices for further analyses. In some
120 cases, analysis of both proxies from the same sample was not possible due to a lack of material. When
121 this occurred, analysis was carried out using stratigraphically adjacent samples. In core ‘Sei’ from Seida
122 the limited amount of material meant that only testate amoeba analysis was possible.

123

124 *Chronology*

125 Eighteen bulk peat samples were sent to the Finnish Museum of Natural History (LUOMUS, Helsinki,
126 Finland) and the Poznan Radiocarbon Laboratory (Poznan, Poland) for accelerator mass spectrometry
127 (AMS) ¹⁴C dating (Table 1). Bulk peat samples were used because of high decomposition of some peat
128 sections, which made picking out known macrofossils very difficult or impossible. Additionally, a recent
129 study suggested that there is no significant difference between ages derived from bulk material and plant
130 macrofossils in these settings (Holmquist et al., 2016). The chronology of the top parts of three peat cores
131 were determined using ²¹⁰Pb dating (Table 1). The samples were processed at the University of Exeter,
132 UK. A dry ca. 0.2-0.5 g subsample from each 1-cm interval was analyzed for ²¹⁰Pb activity after spiking

133 with a ^{209}Po yield tracer. The procedure followed a modified version of Ali et al. (2008).
134 An age-depth model for each core was developed using CLAM 2.2 (Blaauw, 2010) in R version 3.2.4 (R
135 Core Team, 2014), with ^{14}C ages internally calibrated using the INTCAL 13 calibration curve (Reimer
136 et al., 2013). ^{210}Pb ages were obtained through the Constant Rate of Supply model (CRS) (Appleby and
137 Oldfield, 1978), which was chosen over the Constant Initial Composition model because there was a
138 subsurface maximum in ^{210}Pb activity in these three cores, suggesting that the peat accumulation rate has
139 not been constant over time. Both ^{14}C and ^{210}Pb dates were included in the final age-depth models (Fig.
140 2). A smooth spline method was selected to develop the age-depth models with the exception of core Kev
141 BS, which yielded age reversals when the default smoothing parameter 0.3 of CLAM model was
142 employed and relatively large deviations of the calibrated ^{14}C dates to the age-depth model curve when
143 changing this parameter, so a linear interpolation method was used instead for that core. Calibrated
144 radiocarbon ages were rounded to the nearest 5 years. Negative ages indicate post-bomb ages (i.e. -50
145 cal. BP = AD 2000). In this study we focused solely on the time period of the last millennium.

146

147 *Testate amoeba and plant macrofossil analysis*

148 Testate amoeba sample preparation procedure followed a modified version of Booth et al. (2010).
149 Samples were boiled in distilled water for 15 minutes. Samples were sieved using a 180- μm mesh
150 instead of the standard 300- μm mesh as some materials contained a large quantity of decomposed plant
151 detritus. All samples were back-sieved using a 15- μm sieve. Materials retained on the 15 μm sieve were
152 centrifuged at 3000 rpm for 5 minutes. 50-100 individual testate amoeba shells for each sample were
153 counted and identified to species level or 'type' under a light microscope with 200-400 \times magnification.
154 Taxonomy followed Charman et al. (2000), but occasionally online sources were used to aid
155 identification (<http://www.arcella.nl/>; user.xmission.com/~psneeley/Personal/FwrPLA.htm).
156 Occasionally the lower parts of the peat sections were highly decomposed and decomposed plant material
157 hindered testate amoeba identification. These samples were treated with 5% KOH to disaggregate and
158 remove fine organics before sieving (Barnett et al., 2013; Charman et al., 2010). However, because the
159 test count did not reach 50 specimens in these deeper samples, they were not included in the water-table
160 depth (WTD) reconstructions.

161 For plant macrofossil analysis, volumetric samples (2-5 cm^3) were gently rinsed under running water
162 using a 140- μm sieve. No chemical treatment was necessary. Remains retained on the sieve were
163 identified and proportions of different plant types were estimated using a stereomicroscope. Further
164 identification to species level was carried out using a high-power light microscope following Väiliranta
165 et al. (2007). In addition to identifiable plant remains, the proportion of unidentified organic matter

166 (UOM) was also estimated.

167

168 *WTD reconstruction*

169 Testate amoeba WTD reconstructions were performed using the Rioja package (Juggins, 2015) in R
170 version 3.2.4 (R Core Team, 2014). The modern training set contained 59 testate amoeba taxa from 145
171 samples collected from the same study sites (Zhang et al., 2017). A tolerance-downweighted weighted
172 averaging with inverse deshrinking based model was applied and z scores of the reconstructed WTD
173 values were then calculated over the total length of all the cores to illustrate hydrological changes ($z > 0$
174 indicates drier than average conditions and $z < 0$ indicates wetter than average conditions; $\Delta z = 1$
175 represents 8.14 cm WTD range in our dataset), as the reconstructions may poorly represent actual
176 magnitude of water table changes (Swindles et al., 2015c). Model testing and validation are discussed in
177 Zhang et al. (2017).

178

179 **Results**

180 *Chronology and vertical peat growth*

181 Age-depth models show that peat accumulation rates have not been consistent between the study sites
182 over the last few millennia (Fig. 2, Table 1). The thickness of active layers in four sites ranged from 31
183 cm to 45 cm and basal ages of active layers ranged from 1485 to 7230 cal. BP. In most cases, 25-30 cm
184 peat thickness covered the last millennium, except in Seida where only 7 cm of peat has accumulated
185 during the last millennium. Mean peat accumulation rates over the last millennium ranged from 0.10 to
186 0.81 mm/year. Vertical growth has been slower at Seida and Kilpisjärvi when compared to Indico and
187 Kevo.

188

189 *Testate amoeba assemblages and reconstructed WTD*

190 In total, 35 testate amoeba taxa were found in the four study sites. The most dominant taxa for all sites
191 were *Diffflugia pristis*, *Pseudodiffflugia fulva* type, *P. fascicularis* type and *Trigonopyxis minuta* type (Fig.
192 3). In Indico *Archerella flavum*, *Cyclopyxis arcelloides* type, *D. pulex*, *Hyalosphenia minuta* and *Nebela*
193 *militaris* type were also occasionally abundant, while in Seida *Assulina muscorum*, *C. arcelloides* type
194 and *Trinema/Corythion* type were present abundantly. In Kevo *Trinema/Corythion* type was dominant in
195 the topmost samples while in Kilpisjärvi the samples were dominated by *Arcella catinus*.

196 Three cores were analysed from Indico (Ind1-3), Russia. The testate amoeba assemblages of core Ind1
197 (Fig. 3a) were first dominated by *P. fulva* type and *D. pristis* at 985 cal. BP. After that until ca. 445 cal.
198 BP *P. fulva* type was the most abundant. Between ca. 445 and -30 cal. BP, *P. fulva* type, *P. fascicularis*

199 type and *C. arcelloides* type were dominant. *A. flavum* and *A. seminulum* were frequently encountered
200 in samples before -58 cal. BP, after which the proportion of *H. minuta* increased. WTD reconstructions
201 showed that wet conditions occurred at 985 cal. BP, after which relatively dry conditions persisted, with
202 only slight fluctuations before ca. 10 cal. BP. At ca. 10 cal. BP, a change from dry to wet conditions was
203 detected. After a ca. 50-year wet phase, a gradual transition from wet to dry occurred.

204 The bottom part of core Ind2 (Fig. 3b) was a mixture of peat and sand and testate amoeba were
205 absent or scarce, so testate amoeba data were available only from ca. 430 cal. BP onwards. The
206 assemblages were dominated by *C. arcelloides* type and *P. fulva* type between ca. 430 and 10 cal. BP but
207 towards the core surface *N. militaris* type became the dominant taxon. WTD reconstructions showed a
208 dry-wet shift at ca. 175 cal. BP and a wet-dry shift at ca. 0 cal. BP. During the period 175-0 cal. BP,
209 conditions were generally wet, but fluctuating. Since ca. 0 cal. BP an obvious drying trend prevailed.

210 In core Ind3 (Fig. 3c), *D. pulex* and *P. fulva* type dominated the assemblages between ca. 1020 and
211 950 cal. BP. Then *T. minuta* type became abundant until ca. 490 cal. BP after which *D. pristis* and *A.*
212 *flavum* were the most abundant taxa until ca. 215 cal. BP. After that, *D. pristis*, *N. militaris* type and *T.*
213 *minuta* type were the most common taxa. The WTD reconstruction showed very dry conditions prevailed
214 until ca. 400 cal. BP, when an obvious dry to wet shift occurred. However, the dominance of the medium
215 wet indicator *D. pristis* (Zhang et al., 2017) suggests only relatively wet conditions. Starting from this
216 shift, a slight wet to dry trend persisted until present-day.

217 At Seida (Fig. 3d), testate amoeba assemblages around 1060 cal. BP were dominated by *P. fulva* type,
218 while between ca. 1060 and 350 cal. BP *D. pristis* and *A. muscorum* were the most abundant taxa.
219 Relatively wet conditions were inferred between ca. 650 and 350 cal. BP and after 350 cal. BP, *A.*
220 *muscorum*, *C. arcelloides* type and *Trinema/Corythion* type were the dominant taxa. WTD
221 reconstructions indicated that this site was persistently dry.

222 At Kevo (Fig. 3e), the assemblage was dominated by *P. fulva* type for the period ca. 1140-100 cal. BP,
223 then *T. minuta* type and *T. arcuata* type became abundant between ca. 100 to -20 cal. BP. Towards the
224 surface, *T. minuta* type together with *Trinema/Corythion* type were the most abundant taxa. WTD
225 reconstructions showed that dry conditions existed through the core with a relatively wet event recorded
226 at ca. 550 cal. BP. A drying trend prevailed from ca. 50 cal. BP until present.

227 At Kilpisjärvi (Fig. 3f), the assemblages generally resembled those of Kevo but the timing of comparable
228 assemblage change differed. *D. pristis*, *P. fulva* type and *P. fascicularis* type were abundant between ca.
229 1080 and 450 cal. BP. Large proportions of *D. pristis* and *T. minuta* type were recorded between ca. 450
230 and 0 cal. BP, with *A. catinus* and *T. minuta* types dominant towards recent times. Interestingly, some
231 samples (18-23 cm) contained large quantities of diatoms including taxa such as *Pinnularia major*,

232 *Cymbopleura subcuspidata*, *Eunotia praerupta*, *Eunotia serra* and *Brachysira vitrea*. The amount of
233 diatoms was so overwhelming that testate amoeba could not be reliably counted or identified, so these
234 samples were omitted from the WTD reconstruction. WTD reconstructions suggested a relatively wet
235 phase *ca.* 650–450 cal. BP after which, dry but slightly fluctuating conditions persisted until the present.

236

237 *Vegetation, presence of permafrost and microtopographical evolutions*

238 Plant assemblages varied between the cores (Fig. 3). Plant composition data were used to classify the
239 contemporary habitat conditions and to infer the presence/absence of permafrost (e.g., Oksanen, 2006;
240 Pelletier et al., 2017). In general, we interpret that communities dominated by sedges and brown mosses
241 indicate permafrost-free/thaw habitats while highly decomposed peat with ericaceous/woody remains
242 sometimes accompanied by lichens and fungi sclerotia indicate peat accumulated on top of permafrost
243 following the up-heave of the peatland surface. Though in general *Sphagna* assemblages are used to shed
244 light on moisture conditions they can also help to identify the presence or absence of permafrost.
245 Temporal permafrost melt may create suitable conditions for wet *Sphagna* but these species may also
246 represent permafrost-free hollow conditions. Dry *Sphagna* may grow on top of permafrost hummocks,
247 but equally on permafrost-free hummocks. In addition, though sedges are considered non-permafrost
248 species, some species such as *Eriophorum* spp. can grow on peat plateaus, thus more than a single
249 indicator is usually needed to identify potential presence of permafrost.

250 At Indico, between 1300 and 985 cal. BP, hummock shrub vegetation dominated in Core Ind1 (Fig. 3a),
251 probably indicating presence of permafrost. At around 985 cal. BP abundant sedge remains indicate wet
252 conditions, which in turn suggest permafrost free conditions, i.e. permafrost melting. After this, until *ca.*
253 10 cal. BP, a mixed sedge-shrub phase, accompanied by fungi sclerotia, prevailed and peat was highly
254 decomposed. These together suggest re-establishment of permafrost. From *ca.* 10 to -40 cal. BP, a wet
255 hollow phase, dominated by *S. majus* and *Warnstorfia* spp., occurred and this might indicate temporary
256 melting of permafrost. This wet phase was followed by hummock conditions with *S. fuscum*, suggesting
257 permafrost re-aggradation.

258 Ind2 (Fig. 3b) had a similar succession history, yet the timing differed. A highly decomposed
259 Ericales stage with presence of fungi sclerotia between 1725 and 175 cal. BP was followed by
260 *Eriophorum vaginatum* dominated phase at *ca.* 175 cal. BP. After that, a wetter lawn stage dominated by
261 *S. rubellum* prevailed until *ca.* 30 cal. BP. This pattern suggests alternating permafrost aggradation and
262 melting. Similarly, the near-surface layers were dominated by *S. fuscum*, indicating permafrost re-
263 establishment.

264 Ind3 (Fig. 3c) vegetation succession differed from the other two Indico records. A highly

265 decomposed Ericales stage occupied peat layers dated to *ca.* 1020-880 cal. BP suggesting hummock
266 conditions on top of permafrost. Interestingly, after 880 cal. BP there was a community shift where
267 Ericales were replaced by other hummock communities, now dominated by *S. fuscum*. This phase lasted
268 until *ca.* 235 cal. BP. Due to a limited amount of material, we have no continuous plant macrofossil data
269 for the time-window from 215 cal. BP to present day (-52 cal. BP). Currently dwarf shrubs Ericales grow
270 at the coring location.

271 At Kevo (Fig. 3e), a mixed sedge-shrub vegetation characterised the entire peat core, suggesting that no
272 major hydrological changes have taken place in the recent past. However, after *ca.* 380 cal. BP the plant
273 mixture was accompanied by lichens probably suggesting permafrost conditions.

274 At Kilpisjärvi (Fig. 3f), before *ca.* 790 cal. BP sedges were the most dominant taxa but occasionally
275 accompanied by other taxa such as Bryophyta spp. This community suggests a typical permafrost-free
276 fen. The short period between *ca.* 790 and 550 cal. BP was dominated by hummock species *S. fuscum*.
277 The following stage, which started at *ca.* 550 cal. BP and lasted until present was dominated by Ericales
278 spp. and indicated relatively stable hummocky conditions on top of permafrost.

279

280 **Discussion**

281 *MCA-induced permafrost thaw and desiccation*

282 In NE European Russia, extensive regional-scale permafrost aggradation occurred from *ca.* 2200 cal. BP
283 onwards (Hugelius et al., 2012; Routh et al., 2014). Therefore, we should be able to detect potential
284 MCA-induced permafrost dynamics and hydrological changes in our Russian cores. Our records suggest
285 that at first, the MCA warming resulted in permafrost melting and consequent establishment of fen-type
286 communities or *Sphagnum*, which corresponds to previous European Russian studies (Routh et al., 2014).

287 At Indico (Ind1) there was a vegetation change from shrub vegetation to sedges, corresponding with the
288 wet conditions reconstructed from testate amoebae (Figs. 3a and 4). Core Ind3 shows a transition from
289 shrub community to *S. fuscum* at *ca.* 900 cal. BP. (Figs. 3c and 4). This kind of *Sphagnum* establishment
290 has been proposed to be a result of warming and altered peatland hydrology and chemistry (Loisel and
291 Yu, 2013). However, here the relatively dry conditions implied by *S. fuscum* contrasts our first hypothesis,
292 possibly due to only partial permafrost thaw. Wet communities were replaced by shrub communities and
293 supported by testate amoeba reconstructed dry conditions which prevailed for the latter part of the MCA
294 (Figs. 3a and 3c). This phenomenon may either result from melt water drainage (Wilson et al., 2017), or
295 be caused by increased evaporation (Swindles et al., 2015a).

296 In Fennoscandia, our results suggest that Kevo and Kilpisjärvi peatlands stayed permafrost free until *ca.*
297 600 cal. BP (see also Oksanen 2006). During the MCA, a relatively dry habitat prevailed at Kevo, while

298 at Kilpisjärvi a wet fen prevailed (Figs. 3e and 3f). Interestingly, the samples from Kilpisjärvi dated *ca.*
299 970-630 cal. BP contained large amounts of diatoms and chronologically this clearly wet phase
300 corresponds to a diatom bloom event reported from a northern Swedish peatland (Kokfelt et al., 2009;
301 2016). Kokfelt et al. (2016) suggested that this wet phase was likely due to the Samalas volcanic eruption
302 in AD 1257 (693 cal. BP) and consequent acid deposition, which resulted in changes in vegetation. At
303 around 790 cal. BP, *S. fuscum* established at the expense of previous rich fen plant communities and this
304 was possibly triggered by volcanic impact rather than permafrost aggradation. However, none of the
305 other peat sections analyzed for this study have diatom-rich layers or conspicuous plant community or
306 moisture shifts dated to around the time of the eruption. During this time period typically dry shrubby
307 conditions prevailed in the other sites, which may have been less sensitive to acid deposition.

308

309 *LIA-induced permafrost aggradation and drying*

310 In NE European Russia, in line with our second hypothesis, plant data suggest relatively stable dry
311 hummocky habitats during the LIA, whereas testate amoeba data mainly indicate dry conditions, with
312 occasional wet phases (Figs. 3 and 4). The discrepancies between the two proxies suggest testate amoeba
313 are more sensitive to environmental changes than plant communities (Gałka et al., 2017b; Loisel and
314 Garneau, 2010; Väiliranta et al., 2012). These synchronous wet shifts in testate amoeba records at around
315 450-400 and 175 cal. BP (Fig. 4) contradict our second hypothesis of dry LIA conditions. However, the
316 timing of wet phases corresponds to many other wet records registered, for example, in parts of northwest
317 and central Europe (Charman et al., 2006; Gałka et al., 2014; Väiliranta et al., 2007). These climate-
318 caused wet interruptions failed to trigger vegetation changes with the exception of the Ind2 record, which
319 showed a plant community change from shrubs to sedges dated to c. 175 cal. BP. This possibly suggests
320 a greater sensitivity of peatland margins to environmental changes, as core Ind2 was collected from a
321 more marginal location than Ind1 and 3.

322 Unlike at Indico and Seida, the beginning of LIA at Kilpisjärvi and Kevo seems to have been wet, which
323 corresponds to the humid climate recorded in other parts of Finland (Väiliranta et al. 2007 and references
324 therein). Consistent with our second hypothesis, conditions subsequently shift and remain dry for the rest
325 of the LIA *ca.* 550-100 cal. BP, most evident in testate amoeba records. Plant macrofossil data from
326 Kilpisjärvi also support this shift by showing a vegetation change from *Sphagnum* domination to a dwarf
327 shrub community, whilst at Kevo the drying reflected by testate amoeba data failed to cause clear
328 vegetation changes (Figs. 3e and 3f). In contrast, according to previous studies from Kevo (e.g., Oksanen
329 2006), LIA triggered permafrost initiation led to dry elevated peat surfaces and vegetation changes,
330 highlighting that one single peat core sometimes cannot capture a comprehensive regional story

331 (University of Leeds Peat Club 2017). At Kilpisjärvi, a marked change to dry conditions indicated by
332 testate amoeba records happened around 175 cal. BP but this is absent at Kevo. This dry phase contrasts
333 the wet shifts at Indico and Seida, suggesting that the drivers of these changes were more regional in
334 scale.

335

336 *Implications of recent warming*

337 Interestingly, our data consistently suggest a habitat change towards drier communities in recent decades,
338 contradicting our first hypothesis that warming results in wetting. The drying is reflected as a change
339 from wet *Sphagna* to dry *Sphagna* (Ind1 and 2), from *Sphagnum* spp. to Ericales shrubs (Ind3) or by an
340 appearance of lichens and dry bryophyte taxa (Kev BS; Fig. 3). Additional testate amoeba data from
341 Seida, Russia also repeat this pattern (Fig. S1). Chronologically, this habitat change corresponds to
342 extensive permafrost degradation reported for the last *ca.* 50 years elsewhere (Sannel and Kuhry, 2011;
343 Swindles et al., 2015a). Local instrumental temperature data from both regions show increasing mean
344 annual temperatures in recent decades (Bekryaev et al., 2010; Bulygina and Razuvaev, 2012; Mikkonen
345 et al., 2015) and warming is projected to continue (Collins et al., 2013). This may have two-fold
346 consequences for permafrost peatlands: accelerated wetting due to thawing of permafrost but followed
347 by desiccation afterwards due to draining and/or an increase in evapotranspiration. Such dynamics were
348 recorded in Ind1 and Ind2 for the recent period, where permafrost thawing caused wet *S. majus* and *S.*
349 *rubellum* establishment, which were later replaced by dry *S. fuscum*. The final permafrost degradation
350 could lead to a formation of a northern fen-type environment (Swindles et al. 2015a), but only of the
351 surface falls in surface height further as a result of loss of ice.

352

353 **Conclusions**

354 Our study emphasises the complex nature and variable sensitivity of permafrost peatlands even within a
355 single site, and highlights the need for a multiproxy approach to environmental change reconstructions.
356 Although hydrological and vegetation reconstructions of six cores showed some core-specific dynamics,
357 when put together our data suggest that in general, LIA conditions were dry, supporting hummocky
358 conditions on top of permafrost. Furthermore, we infer that conspicuous short wet events occurred as a
359 result of the MCA and recent warming, which triggered permafrost thawing. However, some of the
360 hydrological conditions during the MCA were drier than those of during the LIA and recent warming is
361 associated with drier conditions across all sites even where thawing initially led to wetter conditions. The
362 changes towards drier conditions during both the MCA and over the last 150 years suggest that
363 evapotranspiration is an important factor in regulating surface peatland moisture conditions during warm

364 periods in the subarctic.
365 The hydrological changes during the most recent warming led to especially pronounced drying of the
366 peat surfaces following thawing, even where initial thaw caused temporarily wetter surfaces. We suggest
367 that drying is more likely to occur where limited permafrost is present, because initial increased surface
368 wetness caused by thawing and surface collapse will be relatively minor, and can revert to drier
369 conditions driven by increased evapotranspiration. Whilst it is likely that continued future warming will
370 result in extensive permafrost degradation and subsequent increased surface wetness and Arctic fen
371 development at the landscape-level, our data show that permafrost peatland ecosystems may also respond
372 in more complex ways, including drying. Future changes in precipitation and evapotranspiration are more
373 uncertain than temperature rise, but may be critical in determining future hydrology and vegetation shifts
374 in permafrost peatlands.

375

376 **Acknowledgements**

377 HZ acknowledges the support of the China Scholarship Council for her PhD study (grant no.
378 201404910499) at the University of Helsinki. Further funding was provided by the Academy of Finland,
379 the University of Helsinki and the Natural Environment Research Council, UK (NERC Standard grant
380 NE/I012915/1) Nicole Sanderson helped with ²¹⁰Pb analyses, Jaakko Leppänen provided cartographical
381 help, Paul Mathijssen, Tiina Ronkainen and Pirita Oksanen assisted with fieldwork, and Jan Weckström
382 identified the diatoms. We thank Tiina Ronkainen for her comments on the early version of the
383 manuscript.

384

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