



1 Mire edge is not a marginal thing: Assessing the factors behind the
2 formation, vegetation succession, and carbon balance of a subarctic fen
3 margin.

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14 **Abstract.** Peatlands are the most dense terrestrial carbon storage and recent studies have shown that the northern
15 peatlands have continued to expand to new areas to this day. However, depending on the vegetation and hydrological
16 regime in the newly initiated areas, the climate forcing may vary. If these new areas develop as wet, fen-type peatlands
17 with high methane emissions they would initially have a warming effect on the climate. On the other hand, if the
18 development starts as dry bog-type peatlands, these new peatland areas would likely act as a strong carbon sink from
19 early on. However, although some research has concentrated on the expansion of the new northern peatland areas,
20 there remains a significant lack of studies on the successional development of the newly initiated peatland frontiers.
21 In this research, we combined palaeoecological, remote sensing and hydrological modeling methods to study the
22 expansion and successional pathway dynamics in a subarctic fen margin in Finnish Lapland and discussed possible
23 implications for carbon balance of these margin peatland areas. Our results showed that the studied peatland margins
24 had started to develop ca. 2000 years ago and have continued to expand thereafter, and this expansion has occurred in
25 non-linear fashion. In addition, the wet fen-type vegetation persisted in the studied margin for majority of the
26 development history and only the dryer conditions after the Little Ice Age instigated the fen-to-bog transition.
27 However, a notable part of the fen margins in the Lompoluovuoma and Lompolojänkkä basins has remained as a wet
28 fen-types, and their persistence was likely caused by the hydrological conditions in the peatland and in the surrounding
29 catchment. Our findings show a large variation in the peatland expansion and succession dynamics even within a
30 single peatland basin. Although changes in climate conditions had initiated the fen-to-bog process in some margins,
31 some had remained in the wet, fen stage showing resilience to allogenic forcings. Thus, when estimating the peatland



32 carbon stocks, and predicting the future trajectories for peatland development, this heterogeneity should be taken into
33 account to avoid errors caused by over-simplification of peatland lateral expansion dynamics.

34 **1 Introduction**

35 After the peatland initiation through a primary peat formation, infilling (terrestrialization), or paludification, peatland
36 area is increased by lateral expansion – the most important process of forming new peatland areas in modern climate
37 (Ruppel et al., 2013). In raised mires, these new peatland margin areas have been generally described as moist
38 minerotrophic fens and spruce swamps (Howie & Meerveld, 2011; Rydin & Jeglum, 2013), while in aapa mires
39 (patterned fens) the margins vary from dry ombrotrophic bogs to wetter lush swamps (Laitinen et al., 2005, 2007).
40 However, although the current vegetation in aapa mire margins has been described in a standard peatland literature,
41 there is an obvious lack of studies on the long-term successional development of these transitional ecotones between
42 peatlands and the surrounding mineral land. A recent study with main focus on aapa mire region of Finland showed
43 that the northern peatlands are still expanding (Juselius-Rajamäki et al., 2023), and whether these newly forming
44 peatland areas initiate and develop as moist fens or dryer bog-types can markedly affect the climate forcing of this
45 recent lateral expansion.

46

47 Lateral expansion process is driven by both allogenic and autogenic factors. For instance, forest fire or other
48 disturbance in area adjacent to a peatland decreases the evapotranspiration and causes rising water table that enables
49 peatland expansion (Kuhry & Turunen, 2006). Similarly, waterlogging may be caused by autogenic development of
50 adjacent peatland. As the peat accumulates vertically, the surface and groundwater flow pathways are directed towards
51 the margins of peat mound (Autio et al., 2023), creating suitable conditions for new peat formation (Korhola, 1996;
52 Rydin & Jeglum, 2013). On the other hand, drainage ditches located in the mire margins can prevent natural discharge
53 to peatlands blocking the lateral expansion (Sallinen et al., 2019), while high-intensity fires can destroy peat layers
54 setting back the advance of peatland margins (Kuhry, 1994; Simard et al., 2007). Also, climate affects the lateral
55 expansion of peatlands, and for example, during warm and dry climate phase between 8000 – 5000 Before Present
56 (BP) expansion of peatlands slowed down, while wet and humid climate from 5000 to 3000 BP promoted lateral
57 peatland expansion (Korhola, 1994, 1995; Ruppel et al., 2013).

58

59 The development of vegetation communities in the newly initiated peatland margins vary according to the non-linear
60 successional trajectory and is driven, particularly by seasonal water availability, and consequently transportation of
61 essential ions (Goud et al., 2018). Depending on topography, surface flow may control the first appearance of
62 vegetation communities. Later groundwater seepage, point-scale or as wider seepage front, transports moisture and
63 dissolved elements for established plants. Compared to raised mires that have grown vertically above the surrounding
64 marginal areas, and often the entire landscape (Howie & Meerveld, 2011; Rydin & Jeglum, 2013), the secondary
65 peatland development pattern over the margins is more complex for aapa mires, because the shape of the peatland



66 varies from flat to concave (Seppä, 2002) and formation of new peatland habitats is dependent of water supplies from
67 snowmelt (Sallinen et al., 2023) and dilution of ion concentrations (pH-levels). Newly established habitat types may
68 range from ombrotrophic bog-types to minerotrophic swamps and fens (Foster & King, 1984; Laitinen et al., 2005,
69 2007; Mäkilä & Moisanen, 2007; Ruuhijärvi, 1983). However, mechanisms, such as surface water hydraulic forcing,
70 which create different types of margins, are currently poorly understood.

71

72 Differences in local hydrology mirrored in the current vegetation communities suggest opposite climatic feedback
73 mechanisms for the peatland centers and marginal areas. The overall climatic effect of peatlands is and has been
74 strongly controlled by the balance between sequestration of carbon dioxide (CO₂), and release of methane (CH₄)
75 (Frolking & Roulet, 2007). Methane is produced in anoxic conditions and released into the atmosphere via vegetation,
76 ebullition or by diffusion (Lai, 2009; Rydin & Jeglum, 2013). However, in areas where the acrotelm i.e., the oxic and
77 biologically active layer of the peat, is thick most of the methane is oxidated to carbon dioxide (Lai, 2009). Thus, in
78 the peatland margins where dry bog-type vegetation communities dominate, the climate forcing is most likely
79 negative, i.e, cooling impact on climate, due to the continuous uptake of CO₂ and low CH₄ emissions. On the other
80 hand, in wet fen-type margins high methane emissions have an opposite effect on short timescales, further amplified
81 by graminoid vegetation communities (Bubier et al., 1993; Juutinen et al., 2013; Kou et al., 2022; Ward et al., 2013).

82

83 Often, the interest of (palaeo)peatland researchers has been in the deepest and oldest part of a peatland while the
84 development of peatland margins, i.e., young areas, has deserved less consideration (Korhola et al., 2010; Ruppel et
85 al., 2013). Only recently the focus has turned to peatland margins and peat profile sampling has been extended to the
86 peatland-upland ecotones (Juselius-Rajamäki et al., 2023; Lacourse et al., 2019; Le Stum-Boivin et al., 2019;
87 Mathijssen et al., 2014, 2016, 2017; Peregón et al., 2009; Schaffhauser et al., 2017). Even these studies have focused
88 more on the expansion dynamics of the peatlands, while the vegetation succession of the marginal areas has deserved
89 lesser consideration. As the past vegetation communities can be used to ascertain climate feedback, the knowledge of
90 vegetation succession in peatland margins can be used to better understand how lateral expansion has affected the past
91 climates and helps us to predict the effects of lateral expansion for future climate change.

92

93 Here, we studied the expansion and successions pathways of peatland margins in a subarctic fen, Lompolovuoma,
94 located in Finnish Lapland using a novel approach combining palaeoecological, remote sensing and hydrological
95 modeling methods. The study was conducted across three transects, from the edges towards the center of the peatland,
96 with each transect having three peat profiles. The vegetation succession was studied by a high-resolution plant
97 macrofossil analysis, and AMS (¹⁴C) radiocarbon dating was carried out to date the basal peat layers and the major
98 plant compositional shifts, respectively. To have a wider understanding of development and diversity of plant
99 communities in aapa mire margins, we used additional comparable peat profile data from three peatlands from northern
100 Finland as well as detailed remote sensing-based vegetation and land-cover classification (Räsänen et al., 2021) from



101 Lompolovuoma fen margins. Finally, water table depth and groundwater-surface water interaction fluxes derived from
102 the fully integrated hydrological model (Autio et al., 2023) were used to demonstrate the connections between altered
103 drier and wetter climatic conditions and peatland vegetation succession. The results of our study give an insight into
104 aapa mire margin succession patterns, their relation to hydrology, and a basic understanding of the peatland climate
105 feedback and carbon balance related to peatland lateral expansion in subarctic areas.

106

107 **2 Methods and materials**

108 **2.1 Study sites**

109 The Lompolovuoma study site is a subarctic fen located in the municipality of Muonio in Finnish Lapland (67° 59'
110 42" N, 24° 12' E, Fig. 1a). The site belongs to the northern aapa mire zone with more continental climate, shorter
111 growing season, and more profound frost effects than on the aapa mires located further south (Ruuhijärvi, 1983). The
112 mean annual temperature in the study site is 0.4 °C (2003-2019) and the mean annual precipitation 647 mm (2008-
113 2019) (Marttila et al., 2021).

114

115 We studied the margins of a sub-basin in a larger fen complex that comprises of several elongated, north-south aligned
116 fen areas. The vegetation in the central areas of the study site is dominated by typical wet fen taxa, such as various
117 *Carex* species and flark *Sphagnum* species. Strings are mainly occurring in the southern parts of the basin. A stream
118 runs across the peatland basin from south to north towards Lake Pallasjärvi.

119

120 Vegetation communities in the studied peatland margins resemble raised pine bog habitats in the south with low
121 hummocks and narrow lawn areas (Laine et al., 2018). The ground layer consists of *Sphagnum fuscum* and *Sphagnum*
122 *angustifolium*, and *Cladonia* sp. lichens also occurred. In the field layer *Eriophorum vaginatum*, *Rubus chamaemorus*
123 and various dwarf shrubs such as *Empetrum nigrum*, *Andromeda polifolia* and *Vaccinium vitis-idaea* was found. In
124 addition, stunted *Pinus sylvestris* grow on the hummocks.

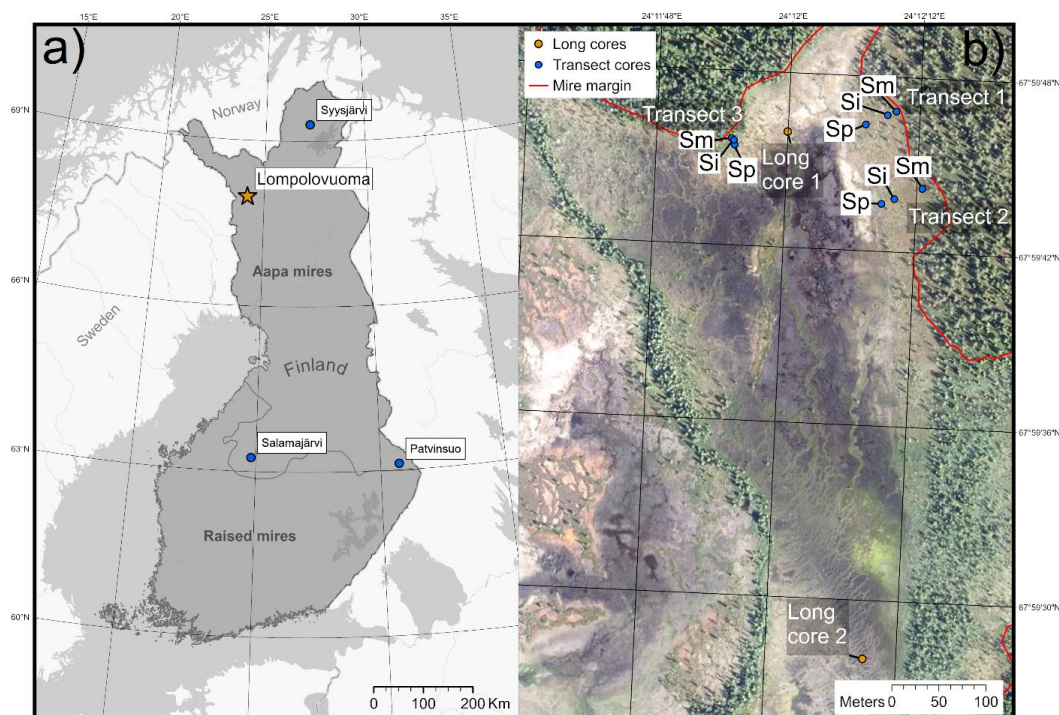
125

126 To expand our understanding of vegetation succession in aapa mire margins, we used additional three short profiles
127 collected from aapa mires elsewhere in Finland: Syysjärvi, Salamajärvi and Patvinsuo (Fig. 1a). These profiles enabled



128 comparison between different local and geographic settings across Finland. For a full description of the study sites,
129 field sampling, and laboratory analysis for supplementary sites, see Juselius-Rajamäki et al. (2023).

130



131

132 **Figure 1. a) Location of the main study site Lompolovuoma marked with an orange star while locations of the comparison**
133 **sites are marked with blue circles. Borderline separating aapa and raised mire complex areas in Finland is presented. 1. b)**
134 **The study location within Lompolovuoma basin shows the study transect samples in blue circles, and the long cores in**
135 **orange circles. For the transect samples the sample code indicates the sample location within the transect: and Sm for the**
136 **sample closest to the mire margin, Si for the sample in the middle of the transect and Sp for the sample closest to the**
137 **peatland center. Mire margins are shown with a red line. Aerial image from National Land Survey of Finland, taken in**
138 **2023.**

139

140 2.2 Field sampling

141 The field sampling for the study was conducted during the summer and the autumn of 2022. To study the lateral
142 expansion dynamics, we sampled a total of three transects coded as T followed by transect number with three peat
143 core samples coded as S followed by core location indicator: p for sample located closest to the peatland center, i for
144 the intermediate sample, and m for the sample located closest to the margin. Each transect ran from the edge of the
145 peatland towards the center. We established two transects from the east edge and one transect from the north edge of
146 the fen sub-basin (Fig. 1b). The peat cores were taken with a box corer (7 × 4 × 65 cm) down to mineral subsoil. To



147 reconstruct Holocene peatland initiation, in addition to the peat cores sampled from the mire margin, four long cores
148 were collected from two different locations of the central part of the study basin: two of the long cores, a and b, were
149 respectively located close to each other and are representing replicates (Fig. 1b). These samples were collected using
150 a Russian peat corer (3 × 50 cm). The profiles were described and classified in the field, and the length of the profile
151 was measured. The location of each sampling point was recorded using Trimble R8 GPS device with ± 0.05 m
152 accuracy and the distance between each transect sampling point was measured using a tape measurer. After sampling,
153 the peat cores were carefully wrapped in plastic to avoid any contamination and transported to University of Helsinki
154 premises. The samples were stored in a cold room prior to further analysis.

155

156 **2.3 Laboratory analysis**

157 The short profiles were cut into 1-cm subsamples and from these subsamples, dry bulk density (BD, g/cm³) and
158 sediment organic matter (OM) based on the loss on ignition method (LOI) were determined. We used LOI values to
159 differentiate between the mineral subsoil and the peat. We defined peat initiation depth based on the first layer where
160 LOI ≥ 70 % (Korhola, 1994). In addition, we analyzed the C/N-content as following: 4 cm interval (transect 1 and 3)
161 and 5 cm interval (transect 2) using LECO TruSpec micro-Elemental Determinator. For the long profiles, contact layer
162 between limnotelmatic *Equisetum* peat and fen peat, without visible *Equisetum* remains, was first determined in the
163 field and then confirmed using a stereomicroscope.

164

165 To reconstruct past changes in vegetation, plant sub-macrofossil analysis for each short peat profile was conducted at
166 4 cm intervals and when prominent changes occurred the interval was increased to every second cm. The percentage
167 proportion of each peat forming vegetation type of a total sample volume (100 %) was analyzed from 5 cm³ peat
168 samples that were gently rinsed under running water in a 100 µm sieve. The residue was analyzed under a
169 stereomicroscope following Väiliranta et al. (2007) and Mauquoy et al. (2014). For example, seeds and leaves were
170 counted in exact numbers and the percentage of unidentified organic material (UOM) estimated for highly decomposed
171 organic remains that had lost their microscopical characteristics. A compound light microscope was used for higher
172 taxonomic level identification. Software Tilia (Grimm, 1991) and C2 (Juggins, 2007) were used to create diagrams.

173

174 To study the lateral expansion and succession dynamics of the fen margins, we applied AMS radiocarbon (¹⁴C)
175 determinations to date the basal peat of each short profile and the depths corresponding to the major regime shifts in
176 vegetation e.g., first occurrence of the *Sphagnum* mosses overlying sedge-dominated peat and the shift to *Sphagnum*
177 dominance. For the long profiles we dated the shift from limnotelmatic *Equisetum* peat to fen peat to gain
178 understanding of long-term development of the Lompolovuoma fen. Terrestrial plant remains and/or charcoal were
179 prioritized for ¹⁴C analyses over bulk peat samples (Quik et al., 2022). However, in three cases regarding the short
180 cores, the peat was highly decomposed and bulk peat had to be used (Table 1). In addition, bulk peat was used as
181 material for the AMS dating of the long cores. Rootlets were carefully removed from the bulk peat samples. Samples



182 were dated in Poznan Radiocarbon laboratory (Poznan, Poland). We calibrated ^{14}C BP ages against the INTCAL 20
183 NH calibration curve (Reimer et al., 2020) and modern dates (pMC % modern carbon) by using the Bomb21 NH1
184 calibration curve (Hua et al., 2022). Finally, calibrated ages were rounded to the nearest 5 years.

185

186 For the comparison profiles, radiocarbon dating results were acquired from Juselius-Rajamäki et al. (2023). In
187 addition, radiolead (^{210}Pb) dating was performed for the comparison profiles at the Department of Chemistry,
188 University of Helsinki. The separation method used for ^{210}Po was a combination of several previously published
189 methods (Ali et al., 2008; Flynn, 1968; Kauranen & Miettinen, 1966; Sanderson, 2016). Dried peat samples were
190 digested with concentrated acids HNO_3 and HCl . ^{209}Po tracer spike was added to the samples at the beginning of the
191 analysis to monitor the yield loss. After digestion, the samples were evaporated to dryness, dissolved into a dilute HCl
192 solution, filtered, and transferred into deposition vessels made from PTFE. Ascorbic acid was added to reduce
193 interfering impurities, e.g. Fe, in the samples. ^{210}Po was deposited spontaneously onto a silver disc in the deposition
194 vessel using a heated water bath (65-75 °C) with constant stirring for 2.5-3 hours. The activity concentration of ^{210}Po
195 was measured from the silver disc with a PIPS (passivated implanted planar silicon) detector. The activity
196 concentration of ^{210}Pb in the samples was obtained via equilibrium of ^{210}Po and ^{210}Pb in the samples.

197

198 **2.4 Age-depth models**

199 Age-depth models with ^{14}C ages were done using Bacon package ver. 3.2.0 (Blaauw & Christen, 2011) in R software
200 ver. 4.3.1 (R Core Team, 2023). We assumed different peat accumulation rates for different vegetation community
201 stages, and these were acquired from the literature representing similar vegetation communities and geographic
202 locations (Granlund et al., 2022; Mäkilä et al., 2001; Mathijssen et al., 2014; Rydin & Jeglum, 2013; Zhang et al.,
203 2020). After an initial model run, these prior values were modified based on individual peat profile characteristics to
204 ensure age-depth model fit. Boundaries were set for the profiles based on vegetation community shifts, and different
205 accumulation rates were calculated for different plant communities. For the profiles with both ^{14}C and ^{210}Pb ages, e.g.,
206 (SyJ T1Sm, SJ T3Sm, and PS T1Sm), we used Plum package ver. 0.4.0 (Aquino-López et al., 2018) in R software
207 ver. 4.3.1 (R Core Team, 2023). For the comparison peat profiles, the same prior accumulation rates were used as for
208 the Lompolovuoma study site. Again, to accommodate for the individual peat profile characteristics, the rates were
209 modified to ensure age-depth model fit. The individual age-depth models containing the accumulation rates and used
210 boundaries are presented in supplementary figures 2A-2L.

211

212 **2.5 Lateral expansion rate and vertical peat increment calculations**

213 Lateral expansion rates (cm/year) were calculated between adjacent peat sections in each transect. The rates were
214 calculated by dividing the horizontal distance between adjacent dated profiles (cm) with the difference of the basal
215 ages, respectively (years). Vertical peat increment (mm/year) was calculated for different vegetation community
216 stages separately. We divided the thickness (mm) of the corresponding vegetation community stage in the section by



217 the duration (years) of the corresponding vegetation community stage. Mean calibrated ages from the age-depth model
218 were used.

219

220 **2.6 Current vegetation community coverage analysis**

221 We used field and remote sensing-based land cover type data presented in (Räsänen et al., 2021), where also
222 methodology is described in detail, to estimate the proportion of vegetation communities in the peatland margins.
223 Here, we use simplified classification based on ombrotrophic – minerotrophic gradient to describe habitat conditions
224 and related vegetation community. In addition, tree-covered fens were separated from open fens. Applied vegetation
225 communities are: “bog”-type (referring to dry conditions), “fen”-type (referring to wet conditions), and tree-covered
226 fens (referring to forested peatland) and these enable comparison with the remote sensing data. These were combined
227 from the land cover type classes with similar ecological characteristics: dwarf shrub pine bogs and dwarf shrub bogs
228 as the bogs, tall sedge fens and flarks as the fens and paludified spruce, birch, and mixed forests as the tree-covered
229 fens. We delineated our study basin Lompolovuoma and adjacent Lompolojänkkä basin based on the land cover
230 dataset in ArcGis Pro ver. 3.1.0 (ESRI, 2023) and calculated the proportion of each land cover type for the whole
231 peatland area and for the peatland margins. For the peatland margins, we chose a 25-meter distance from the peatland-
232 forest border to represent the marginal peatland area. This distance prevented any overlap of the marginal areas even
233 in the narrowest parts of the peatland and allowed non-biased analysis of the marginal peatland types irrelevant to the
234 topography or vegetation on site.

235

236 **2.7 Hydrological analyses**

237 To study the hydrological drivers behind the development of divergent peatland types at the fen margins detected in
238 vegetation coverage analysis, we used the fully integrated physically based-hydrogeological model HydroGeoSphere
239 (Aquanty, 2015). The model allows explicit simulation of water exchange between groundwater and surface water
240 and can be parameterized using physical properties of peat and mineral soils. The high spatial resolution of the model
241 makes it suitable to estimate water fluxes at the scale of vegetation inventories and remote sensing data. This model
242 has been previously implemented for the Pallaslompolo catchment, and the full methodology for this hydrogeological
243 model is described in Autio et al. (2023). Due to the original study boundaries, this model only covers Lompolojänkkä
244 sub-basin. In this study, we (1) investigated the resulting hydrological conditions in terms of groundwater-surface
245 water exchange flux and (2) compared the impact of the current (baseline) and the drier climate in terms of water table
246 elevation (Helama et al., 2017) .

247

248 In (1), we investigated the prevailing groundwater-surface water exchange fluxes of the transient model run averaged
249 over the summer of 2017 within each peatland type. For (2), we studied the effect of drier climate conditions by
250 comparing the outputs of the steady-state simulations for the current climate with the effective rainfall P_{eff} equal to
251 385 mm (average for 2016-2018) and the drier climate of P_{eff} equal to 250 mm. The value of 250 mm is within the



252 measured range that varied between 170 mm and 574 mm in 2008-2018 but represents a significantly lower value
253 than the measured long-term mean of 358 mm for the years (2008-2018). Due to the variable density of the model
254 computing mesh, the model output was first plotted in the postprocessing visualisation software Tecplot 360 EX 2022
255 R2, which accommodates value interpolation over element size. The variables were divided into separate bins
256 according to magnitude, hereafter referred to as contour groups showing spatial variation in model output. The
257 resulting raster image was imported to GIS mapping software (ESRI, 2023), georeferenced and clipped according to
258 the defined peatland margins for each peatland type. The areas of each contour group were then calculated respectively
259 for each peatland type.

260

261 **3 Results**

262 **3.1 Peat initiation and spatial development of the peatland margins**

263 In transect 1, the oldest basal date ca. 2230 cal BP was dated from the peat profile closest to the mire center (T1Sp)
264 (Table 1). For the intermediate profile (T1Si) the basal age was ca. 1185 cal BP and for the profile next to the forest
265 (T1Sm) basal age was ca. 990 cal BP. In transect 2, the oldest basal age found in the intermediate profile (T2Si) was
266 1930 cal BP while younger basal ages of 1025 cal BP and 390 cal BP were found for the T3Sp and T3Sm, respectively
267 (Table 1) Oldest basal age in transect 3 was 1390 cal BP in the intermediate sample T2Si (Table 1) while the basal
268 age in the sample closest to the mire center (T3Sp) was 1225 cal BP and in the peatland margin (T3Sm) 765 cal BP.

269

270 Long core (LC) dating results suggest that a shift from limnetic peat to fen peat occurred ca. 6300 cal BP at
271 earliest and around 4000 cal BP at latest (Table 1). This change occurred earlier in the northern part of the sub-basin
272 (LC1a ca. 6290 cal BP and LC1b ca. 6360 cal BP). In the southern part, this shift occurred ca. 4865 cal BP for LC2a
273 and ca. 4365 cal BP for LC2b.

274



275 Table 1. Peat profile description. Coring location describes the location of the sampling across the transects with “Margin” being located closest to the mire-forest
 276 boundary, and “Peatland” closest to the mire center. Sample type describes the location within the profile with “Basal” representing the contact layer between peat and
 277 mineral subsoil, “Sphagnum occurrence” indicating the first occurrence of Sphagnum mosses and “Sphagnum dominance” the first layer with clear Sphagnum-
 278 dominance. Sample description indicates material used in ¹⁴C analyses. Age (cal BP) with 95 % confidence interval show calibrated median age with 95.4 % confidence
 279 intervals.

Laboratory code	Core code	Sample location	Sample type	Depth (cm)	Dated material	¹⁴ C Age (BP)	±	pMC	±2	Age (cal BP) with 95.4 % confidence interval
Poz-162912	T1Sm	Margin	Sphagnum occurrence	7-8	Sphagnum and feather moss leaves and stems			103.46	0.33	-60 (-5 – -65)
Poz-162911	T1Sm	Margin	Basal	19-20	Bulk	1085	30			990 (1060 – 930)
Poz-162914	T1Si	Intermediate	Sphagnum dominance	27-28	Sphagnum moss leaves and stems, woody	315	30			390 (460 – 305)
Poz-162913	T1Si	Intermediate	Basal	30-31	Woody	1250	50			1185 (1285 – 1065)
Poz-165854	T1Sp	Peatland	Sphagnum dominance	21-22	Sphagnum moss leaves and stems			121.63	0.35	-35 (-5 – -35)
Poz-162924	T1Sp	Peatland	Sphagnum occurrence	36-37	Sphagnum moss leaves and stems, woody	845	30			740 (790 – 685)
Poz-162925	T1Sp	Peatland	Basal	40-41	Woody, charred wood	2210	30			2230 (2325 – 2125)
Poz-162917	T2Sm	Margin	Sphagnum dominance	25-26	Sphagnum moss leaves and stems, woody	85	30			115 (260 – 25)
Poz-162916	T2Sm	Margin	Basal	29-30	Shrub leaves, woody, bulk	320	35			390 (470 – 305)
Poz-165855	T2Si	Intermediate	Sphagnum dominance	32-33	Sphagnum moss leaves and stems	75	30			115 (260 – 30)
Poz-162920	T2Si	Intermediate	Sphagnum occurrence	41-42	Sphagnum and feather moss leaves and stems	570	70			590 (665 – 505)
Poz-162918	T2Si	Intermediate	Basal	48-49	Woody	1995	30			1930 (1995 – 1835)
Poz-162922	T2Sp	Peatland	Sphagnum dominance	35-36	Sphagnum and feather moss leaves and stems	150	30			145 (285 – 50...)
Poz-162921	T2Sp	Peatland	Basal	46-47	Woody	1140	30			1025 (1175 – 960)
Poz-165856	T3Sm	Margin	Sphagnum dominance	8-9	Sphagnum moss leaves and stems, woody			107.25	0.33	-55 (-5 – -60)
Poz-162880	T3Sm	Margin	Basal and Sphagnum occurrence	19-20	Woody, charred wood	870	30			765 (905 – 690)
Poz-165857	T3Si	Intermediate	Sphagnum dominance	14-15	Bulk with majority (>95%) of Sphagnum, woody			109.35	0.34	-50 (-5 – -55)



Poz-162619	T3Si	Intermediate	Basal and <i>Sphagnum</i> occurrence	32-33	Woody	1520	30			1390 (1515 – 1315)
Poz-165859	T3Sp	Peatland	<i>Sphagnum</i> dominance	13-14	Bulk with majority (>95 %) of <i>Sphagnum</i>			135.14	0.35	-25 (-25 – -30)
Poz-162923	T3Sp	Peatland	<i>Sphagnum</i> occurrence	21-22	Woody	105	30			110 (270 – 15)
Poz-162882	T3Sp	Peatland	Basal	40-41	Woody	1290	30			1225 (1290 – 1175)
Poz-165876	LC1a	Fen lawn	Fen peat	127-129	Bulk peat with roots removed	5490	40			6290 (6395 – 6200)
Poz-165959	LC1b	Fen lawn	Fen peat	123-124	Bulk peat with roots removed	5595	35			6360 (6445 – 6300)
Poz-165085	LC2a	Fen lawn	Fen peat	180-181	Bulk peat with roots removed	4305	35			4865 (4965 – 4830)
Poz-165086	LC2b	Fen lawn	Fen peat	189-191	Bulk peat with roots removed	3930	35			4365 (4515 – 4245)



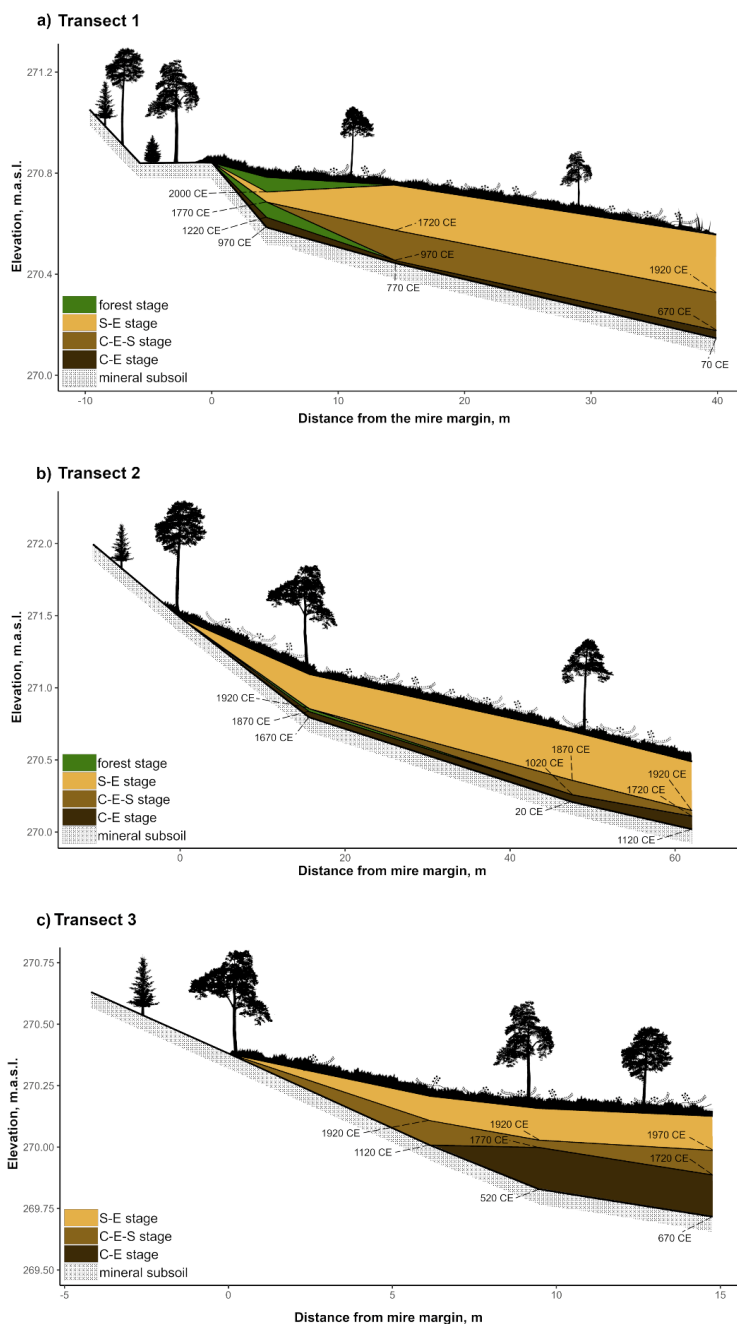
281 **3.2 Peat properties**

282 A shift from mineral layer to organic layer was sharp in all profiles and in the upper parts of the profiles, the loss on
283 ignition (LOI, %) values varied only slightly (Fig. 3, 4, 5). In transect 3, the mineral material has intruded into the
284 peat at depths of 14 cm (T3Sp) and 23 cm (T3Si). Compared to LOI (%), more fluctuations were visible in bulk density
285 (BD, g/cm³) values (Fig. 3, 4, 5). Above the sharp mineral subsoil – peat contact, the BD decreased towards the surface
286 with the lowest values found at the top of peat profiles. A stepwise decrease in BD occurred in peat profiles T1Sp,
287 T2Si, T2Sp and T3Sm while a gradual decrease in BD values was observed in other profiles. Carbon content (%)
288 above the mineral subsoil contact varied only slightly along the peat profiles (Fig. 3, 4, 5) and highest nitrogen contents
289 along the peat profiles were found in the layers closest to the mineral subsoil and the surface (Fig. 3, 4, 5).

290

291 **3.3 Fossil plant communities and succession of the peatland margins**

292 Three main vegetation stages were identified in the Lompolovuoma margin peat profiles (Fig 2a-c, Fig 3-5). The first
293 and oldest stage consisted of the remnants of *Cyperaceous* and *Ericaceous* vegetation (C-E), but lacked brown mosses
294 usually associated with calcareous fens. This phase was characterized by a high proportion of unidentified organic
295 matter (UOM), indicating a high level of humidification. The second stage contained remains of mixed *Cyperaceous*-
296 *Ericaceous-Sphagnum* (C-E-S) vegetation. The transition from stage 1 to 2 occurred gradually in some peat profiles
297 while sometimes shift was abrupt. In this transition *Sphagnum* sect. *Acutifolia* started to replace *Cyperaceous*
298 vegetation. In the transects 1 and 3 the high level of decomposition prevented species-level identification of *Sphagnum*
299 mosses in early C-E-S stage. However, in transect 2, the C-E stage was directly overlain by *Sphagnum fuscum*. In the
300 final *Sphagnum – Ericaceous* stage (S-E), the plant community is dominated by *Sphagnum* mosses, and the
301 *Cyperaceous* vegetation is nearly or completely missing. *Sphagnum* species consists of *Sphagnum fuscum*, *S.*
302 *capillifolium*, *S. russowii*, and *S. angustifolium*. A varying degree of *Ericaceous* vegetation is usually mixed with the
303 *Sphagna*. Varying amounts of forest bryophytes, such as *Pleurozium schreberi* is also detected through the peat layers.
304 In addition, in the marginal profiles of transect 1, the mire vegetation was replaced twice by forest vegetation, and
305 similar replacement occurred once in the margin of transect 2. Macrofossil data is presented in supplementary figures
306 3A-3C.



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Figure 2a-c. Transect profiles. The figures show the vegetation community stages: C-E (Carex – Ericaceous), C-E-S (Carex – Ericaceous – Sphagnum), and S-E (Sphagnum – Ericaceous) as well as the forest community stages in the margins of T1 and T2. In addition, the onset of each stage at the location peat profiles is shown with ages (CE = Common Era) derived from the age-depth model. The ratios between the x and y axes varies between the illustrations. The vegetation is presented to give a rough impression of real-life conditions in the study transects locations and is not in the true scale.



313 At the onset of peat development in the mire margins, the C-E vegetation community dominated (Fig. 2a-c, Fig. 3-5).
314 In transects 1 and 2 this layer was thin, only up to 4 cm in transect 1 and from 5 cm to 9 cm in transect 2. In the transect
315 3 the C-E layer was markedly thicker, 16 cm in T3Si and 18 cm in T3Sp. Duration of the C-E stage was highly
316 variable: in transect 1 the C-E stage lasted between ca. 250 (T1Sm) and 600 years (T1Sp). In transect 2 C-E stage
317 lasted between ca. 200 (T2Sm) and 1000 (T2Si) years. In transect 3 the C-E stage was missing from the profile closest
318 to the mire margin (T3Sm), and *Sphagnum* mosses established directly on top of the mineral subsoil. The duration of
319 the C-E stage in T3Si was ca. 1250 years and in T3Sp ca. 1050 years.

320

321 The C-E stage ended asynchronously across Lompolovuoma mire margin and in most of the cases the C-E stage was
322 followed by the mixed C-E-S stage where *Sphagna* started to colonize the margins. The establishment of *Sphagna*
323 marking the start of the C-E-S occurred between ca. 670 and 970 CE in transect 1, between ca. 1020 and 1720 CE in
324 transect 2, and between ca. 1720 and 1770 CE in transect 3. No C-E-S stage was detected in samples T1Sm and T2Sm.
325 Instead, the vegetation shifted towards a mix of *Ericaceous* vegetation, *Pleurozium schreberi* and *Dicranum* sp.
326 Suggesting turn to dryer conditions. In T3Sm, the C-E-S stage occurred directly over the mineral subsoil.

327

328 On contrary to asynchronous shift from C-E stage to C-E-S stage, the change to ombrotrophic vegetation community
329 (S-E) with high proportion of *Sphagna* appeared nearly simultaneously across all studied margins. This stage started
330 between ca. 1870 and 1970 in all peat sections in transects 2 and 3 and similarly also in T1Sp. Only in T1Sm (1770
331 CE) and T1Si (1720 CE) the shift to S-E vegetation community stage occurred earlier. Currently S-E vegetation type
332 is predominant across the transects.

333

334 A comparable successional pathway as in Lompolovuoma was detected from Syysjärvi study site in eastern Lapland
335 (Supp. fig. 1). A 1-cm thick *Ericaceous* vegetation layer overlaid mineral soil, and this community was shortly replaced
336 by a 2-cm thick C-E layer similar to the results found in Lompolovuoma. These stages lasted only ca. 15 years,
337 respectively, after which C-E-S stage with some *Sphagna* took over ca. 1970 CE. Above 3-cm thick C-E-S stage, the
338 S-E stage mostly comprised by *Sphagnum capillifolium* that took over in ca. 1980 and has persisted ever since.

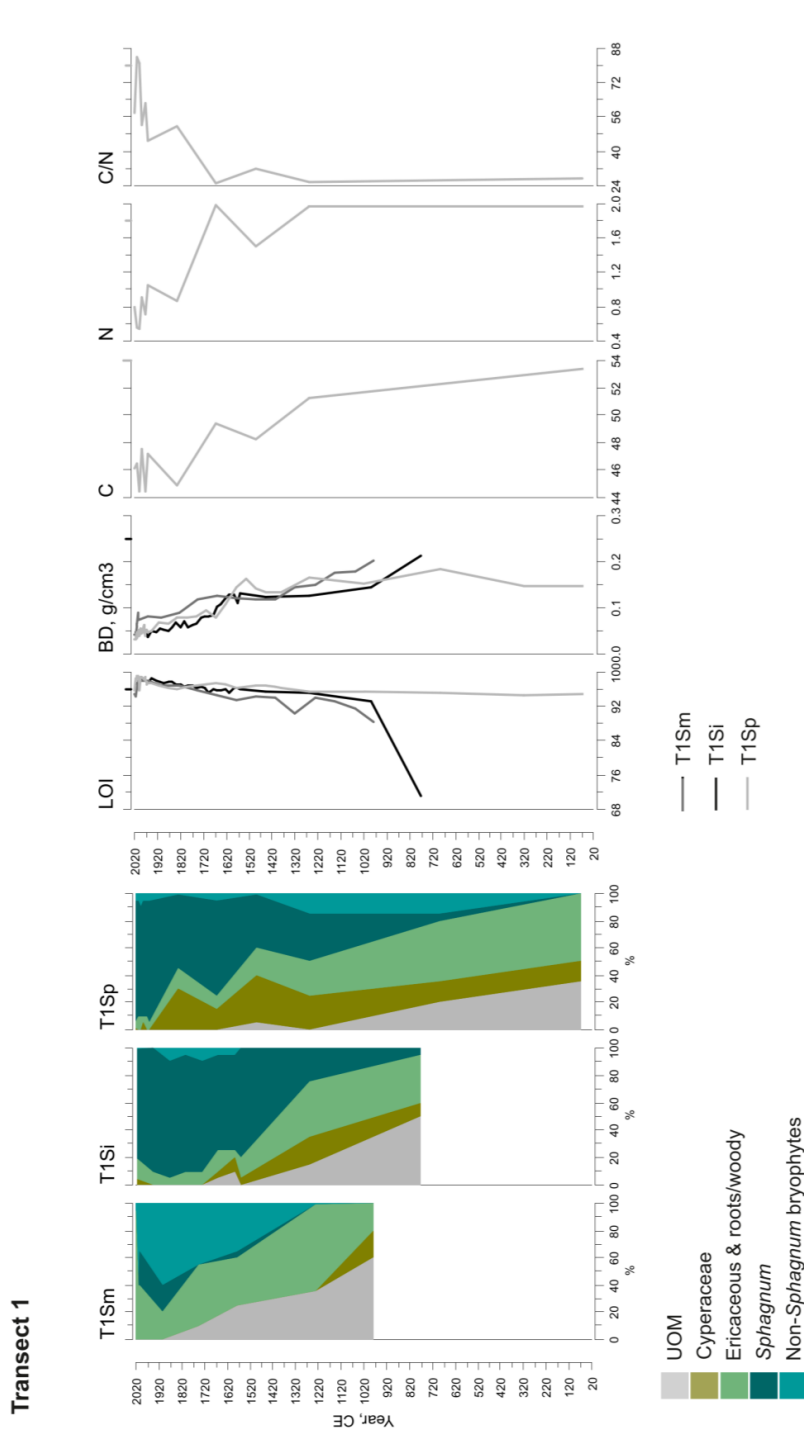
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340 Different successional pathways were found from Salamajärvi and Patvinsuo peatland sites (Supp. Fig. 1). In
341 Salamajärvi, there was no evidence of *Cyperaceous* vegetation. Rather, the peat layers comprising of *Ericaceous*
342 vegetation with a small amount of *Sphagnum* mosses initiated directly on mineral subsoil in ca. 1830 CE in the margin
343 of the Salamajärvi peatland. Afterwards, proportion of *Sphagna* gradually started to increase and *Sphagnum* mosses
344 became dominant ca. 1950 CE. Currently, *Sphagnum capillifolium* is the dominating moss species.

345

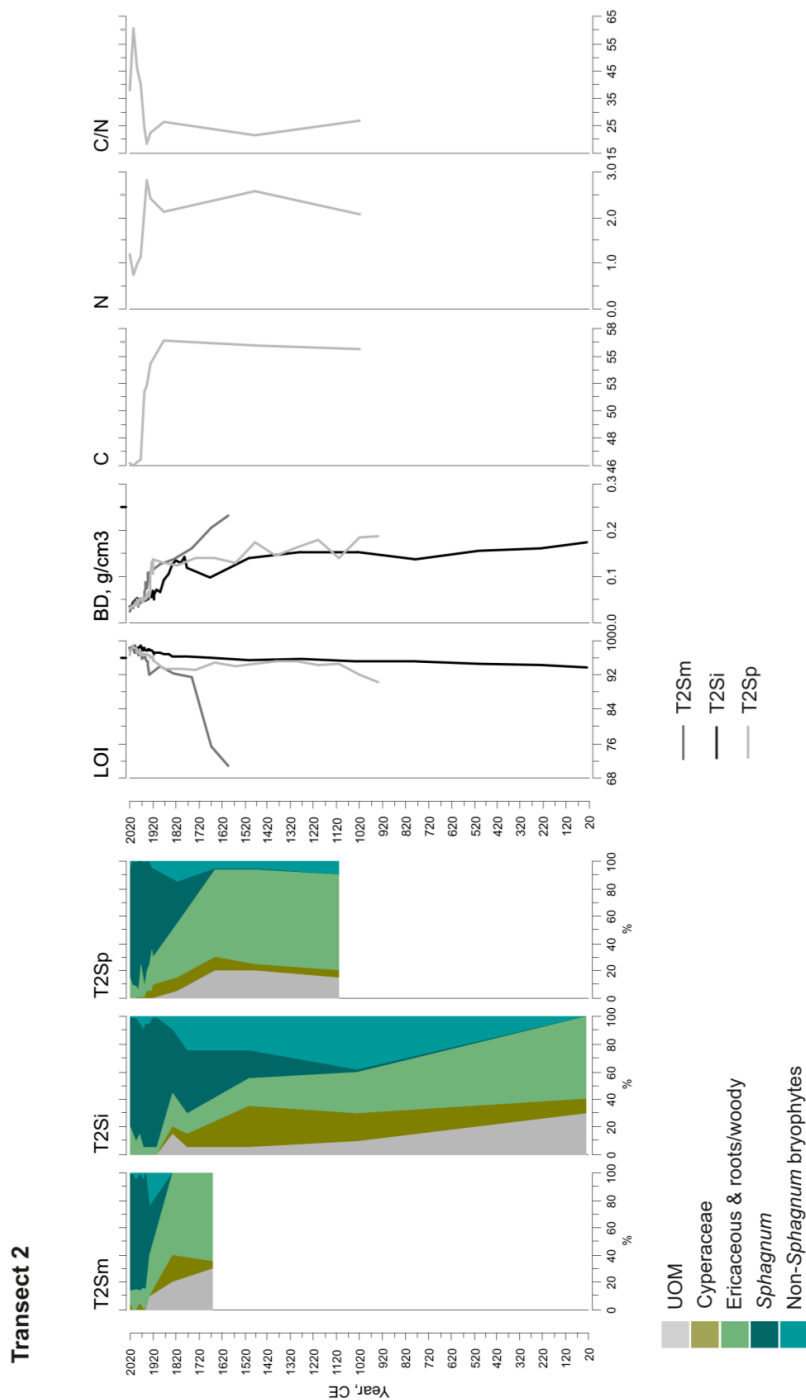


346 When peat formation started in Patvinsuo margin (Supp. fig. 1) ca. 1850 CE, the initial vegetation consisted of C-E-
347 S vegetation. At first, proportion of *Sphagnum* mosses started to increase, and ca. 1915 CE those were the dominant
348 taxa. However, between ca. 1915 and 1950 CE *Sphagnum* mosses together with remains of *Cyperaceae* nearly
349 disappeared and mostly Ericaceous vegetation remained and supplemented by the presence of *Cenococcum sclerotia*
350 that suggest dry mire margin conditions. However, towards present, the amount of *Sphagnum* mosses again increased
351 and currently they form most of the coring site vegetation, with *Sphagnum russowii* being the most common species.



352

353 **Figure 3.** Fossil plant records (left) including undetected organic matter (UOM) and loss of ignition (LOI), bulk density (BD) and carbon and nitrogen contents and C/N
 354 ratio (right) for transect 1. Proportion of vegetation type and LOI in percentages (%), unit for bulk density is g/cm³. Carbon content (%), nitrogen content (%), and C:N
 355 ratio is available for profile T1Sp only.



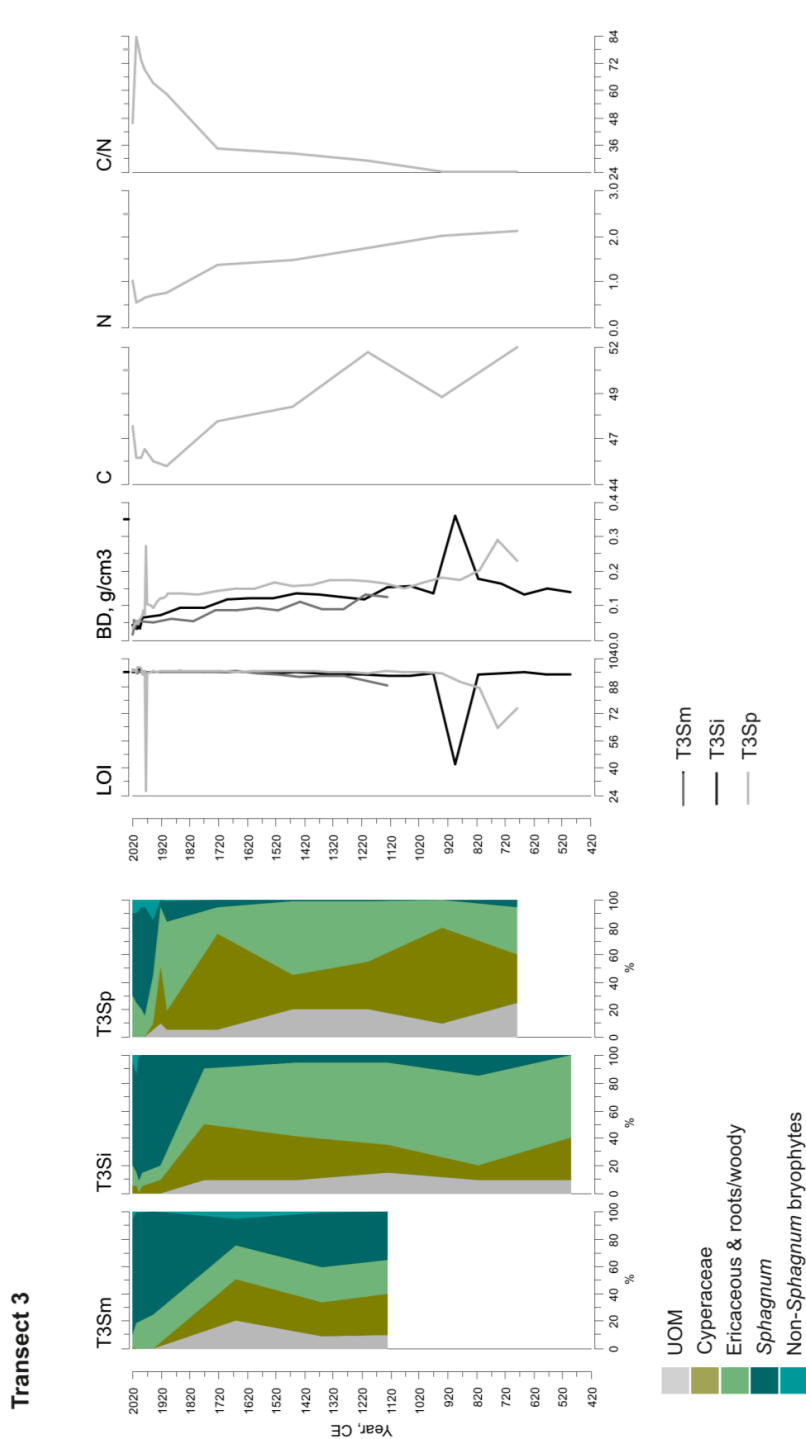
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Figure 4. Fossil plant records (left) including undetected organic matter (UOM) and loss of ignition (LOI), bulk density (BD) and carbon and nitrogen contents and C/N ratio (right) for transect 2. Proportion of vegetation type and LOI in percentages (%), unit for bulk density is g/cm³. Carbon content (%), nitrogen content (%), and C:N ratio is available for profile T2Sp only.



360
 361 **Figure 5.** Fossil plant records (left) including undetected organic matter (UOM) and loss of ignition (LOI), bulk density (BD) and carbon and nitrogen contents and C/N
 362 ratio (right) for transect 3. Proportion of vegetation type and LOI in percentages (%), unit for bulk density is g/cm³, carbon content (%), nitrogen content (%), and C:N
 363 ratio is available for profile T3Sp only.

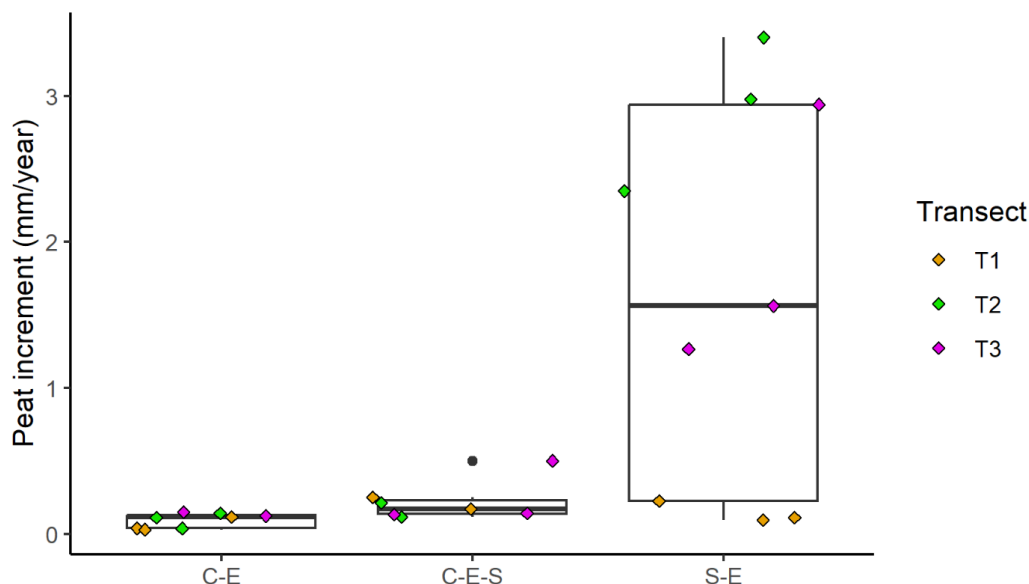


364 **3.4 Lateral expansion rates and vertical peat increment**

365 The rate of lateral expansion varied from 0.53 cm/year (T3Si to T3Sm) to 5.23 cm/year (T1Si to T1Sm). The median
366 lateral expansion rate for all transects was 2.25 cm/year with interquartile range of 1.72 – 2.90 cm/year.

367

368 The lowest vertical peat increment rates (mm/year) were detected for C-E stage with median of 0.12 mm/year and
369 interquartile range (IQR) of 0.04 – 0.13 mm/year (Fig. 6). For C-E-S stage the median vertical peat increment was
370 0.17 mm/year (IQR = 0.13 – 0.23 mm/year). The highest vertical peat increment rates occurred in S-E stage with
371 median value of 1.56 mm/year (IQR = 0.17 – 2.94 mm/year).



372

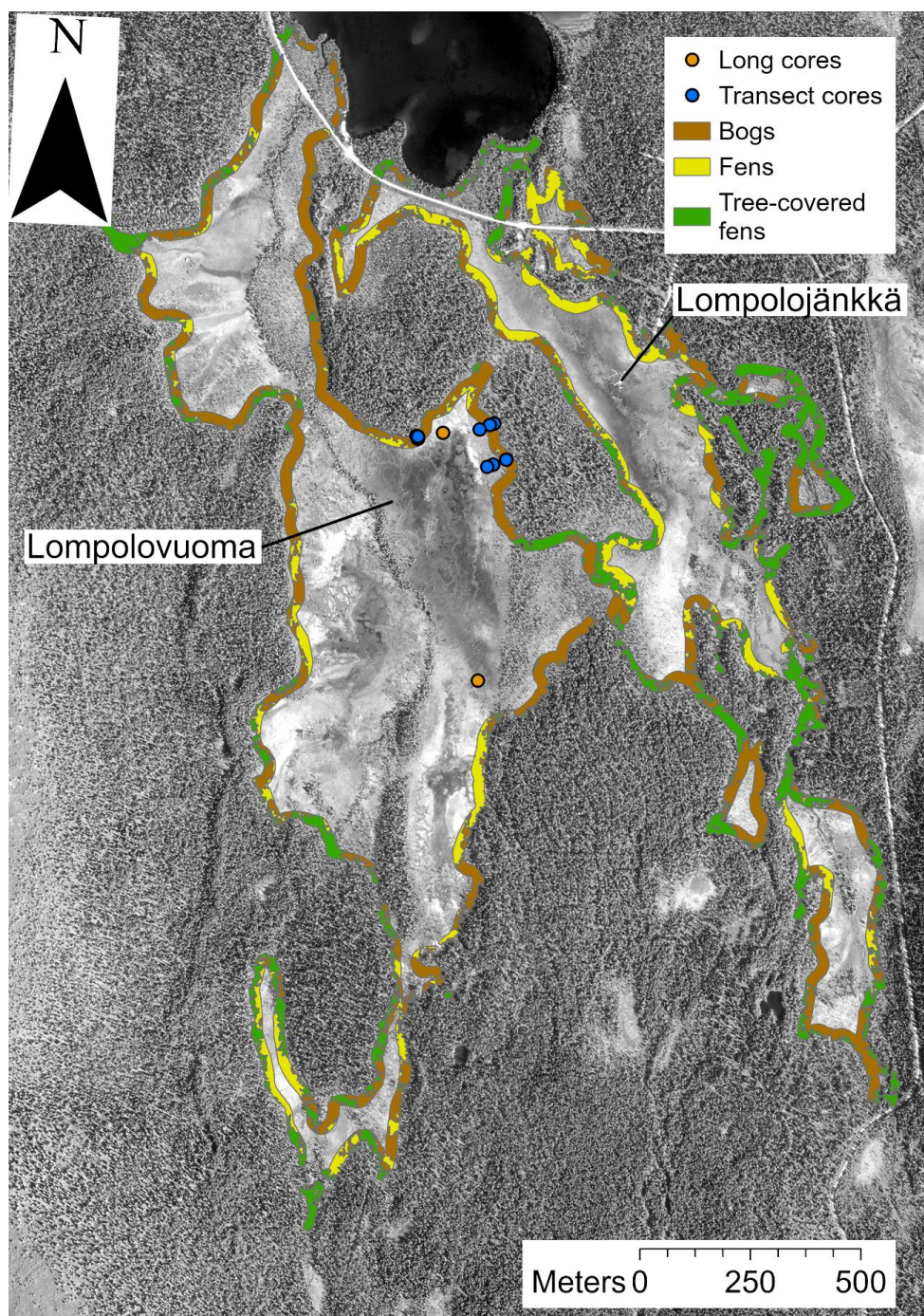
373 **Figure 6. Peat increment rates (mm/year) for different plant community stages. The black horizontal line shows the median**
374 **value, the boxplot shows interquartile range from 1st to 3rd quarter while the whiskers show minimum and maximum values.**
375 **Individual black dots show outlier values while diamonds show peat increment rates (mm/year) for each profile.**

376 **3.5 Vegetation community cover analysis**

377 The total area of Lompolovuoma and Lompolojännkä peatland basin is 141.2 ha, of which 34 % is classified as a bog-
378 type, 46 % as fen-type, and 21 % as tree-covered fen (Table 2). The area 25 meters from the peatland border is in total
379 43.9 ha and covers 31 % of the total peatland area. In these marginal areas, bog type constituted 44 %, fen-type 23 %, and
380 tree-covered fens 33 % of the mire margin area (Fig. 7, Table 2). In Lompolovuoma basin, where our study
381 transects were located, the coverage of bog-type in the peatland margin is 54 % while in adjacent peatland basin,
382 Lompolojännkä, bog-type is covering smaller area, 35 %. On the contrary, higher coverage of fen-type is found in the



383 margins of the Lompolojätkä (26 %) than in Lompolovuoma (20 %). Similarly, larger areas were covered by tree-
384 covered fens in Lompolojätkä (39 %) than in Lompolovuoma (26 %).



385

386

387

388

Figure 7. Peatland margin vegetation communities. The area 25 meters from the peatland margin is divided into bog-type (brown), fen-type (yellow), and tree-covered fen type (green) in Lompolovuoma study basin and adjacent Lompolojänkkä basin. In addition, location of the study transect peat cores (blue circles) and long cores (orange circles) are shown.



389 **Table 2. The vegetation class coverage and peatland area. Table shows the total area of the Lompolovuoma and**
 390 **Lompoljännkä peatland basins, and proportion of 3 vegetation community classes in the peatland basins: Bog-type, fen-**
 391 **type, and tree-covered fen type. In addition, the total area of the 25-meter margin, and proportions of the vegetation**
 392 **community classes is shown. In the final 2 columns, the proportion of the vegetation community classes is shown individually**
 393 **for Lompolovuoma and Lompoljännkä basins.**

Vegetation class	Peatland		Peatland margins			
	Total area, ha	Total area, %	Margin area, ha	Margin area, %	Lompolovuoma	Lompoljännkä
Bog-type	47.4	34 %	19.2	44 %	54 %	35 %
Fen-type	64.8	46 %	10.3	23 %	20 %	26 %
Tree-covered fen	29.0	21 %	14.4	33 %	26 %	39 %
Total area	141.2	100 %	43.9	100 %	100 %	100 %

394

395 3.6 Hydrological analyses

396 The simulated groundwater – surface water (GW-SW) exchange patterns for the current climatic and groundwater
 397 table (GWT) elevation change are shown in Figure 8a and 8b, respectively. The calculated areas by contour group and
 398 peatland vegetation group are presented in Table 3 for the GW-SW exchange fluxes and in Table 4 for the changes in
 399 terms of GWT elevation.

400

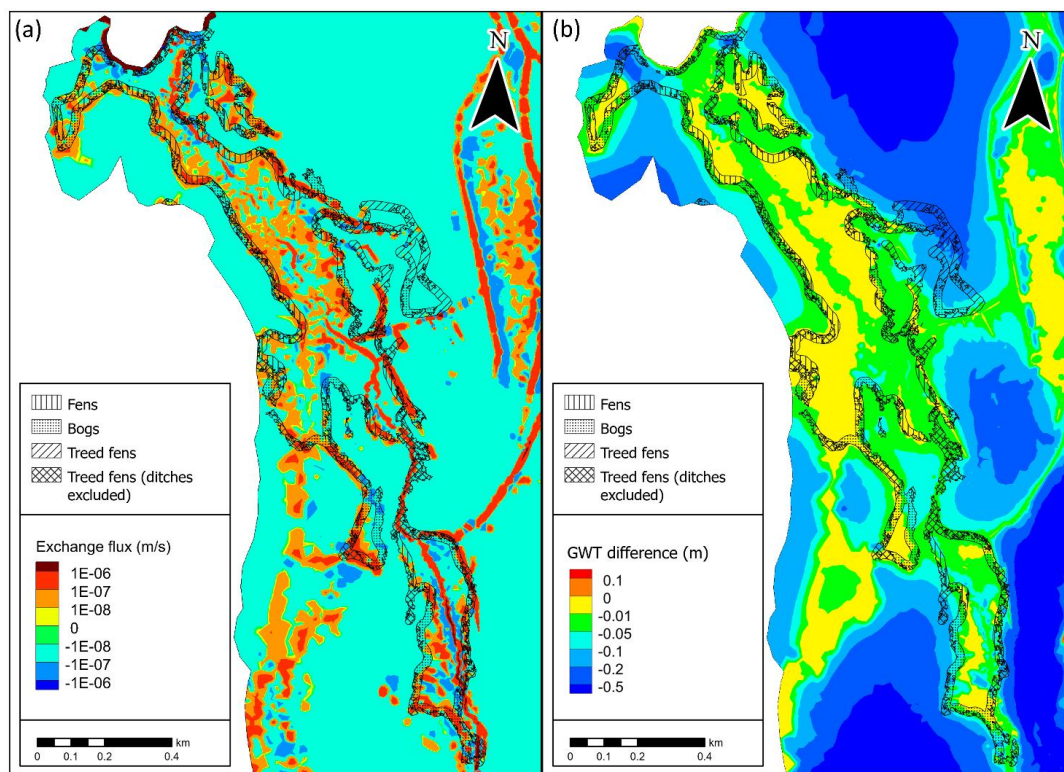
401 In terms of exchange flux, the areas classified as fens indicate the dominance of the GW exfiltration over infiltration
 402 processes in the simulations. In contrast, the bog areas indicate more balance between infiltration and exfiltration
 403 processes with a slight prevalence of the infiltration area. The areas classified as treed fens show the dominance of
 404 infiltration. However, ~30 % of the total treed fen area is in the vicinity of the ditch network (the rightmost part of the
 405 peatland system), which impacted the peatland vegetation as indicated by aerial photos (National Land Survey of
 406 Finland, 2023). After excluding the drained areas from treed fens, the GW-SW exfiltration pattern is more balanced
 407 with a slight prevalence of exfiltration.

408

409 In terms of groundwater table elevation changes, the simulated drier climatic conditions have a mild impact on the
 410 areas classified as fens, with 59 % of the water table decreasing by less than 1cm and 89 % by less than 5 cm. In
 411 contrast, the areas classified as bog are more susceptible to GWT changes. They are characterised by significantly less
 412 extent of the areas with mild (less than 1 cm and 5 cm) table decrease (only 28 % and 70 % respectively) and a
 413 significant portion (30 %) with a substantial decline (more than 5 cm). The treed fen areas, excluding ditches, suggest
 414 that the water table decrease would be variable, with more GWT reduction than in the case of open fens but lower
 415 than in the case of bogs.



416



417

418 **Figure 8a.** The GW-SW exchange flux patterns from Lompolojännkä sub-basin averaged for summer 2017 representing
 419 the current climate conditions. Positive flux values indicate the locations of groundwater exfiltration and infiltration
 420 towards groundwater. **8b.** The groundwater table elevation changes result from the drier climate conditions. Negative
 421 values indicate the groundwater level decrease and positive increase.

422

Table 3. Exchange flux contour areas by vegetation type. Treed fens (ditches excluded) exclude the open drainage areas.

Exchange flux (m/s)		Area (m ² / %)			
Min value	Max value	Fen	Bog	Treed fens	Treed fen (ditches excluded)
	<-1E-6	0 / 0 %	18 / 0 %	0 / 0 %	0 / 0 %
-1E-06	-1E-07	1471 / 2 %	2818 / 4 %	3130 / 4 %	2360 / 4 %
-1E-07	-1E-08	18822 / 30 %	34813 / 47 %	46693 / 55 %	26342 / 45 %
-1E-08	0.00	2936 / 5 %	3662 / 5 %	2549 / 3 %	2256 / 4 %
0.00	1E-08	3067 / 5 %	3603 / 5 %	2661 / 3 %	2388 / 4 %
1E-08	1E-07	23583 / 38 %	19196 / 26 %	12452 / 15 %	10989 / 19 %
1E-07	1E-06	12529 / 20 %	9859 / 13 %	16696 / 20 %	14106 / 24 %
1E-6>		83 / 0 %	85 / 0 %	555 / 1 %	552 / 1 %
Total negative flux		23229 / 37 %	41311 / 56 %	52373 / 62 %	30957 / 52 %
Total positive flux		39262 / 63 %	32743 / 44 %	32363 / 38 %	28035 / 48 %
Total flux		62491	74053	84736	58993



423

424 **Table 4. Water table difference between baseline and drier climates by contour areas and vegetation type. Treed (ditches**
 425 **excluded) exclude the open drainage areas.**

Water table decrease from the baseline model (m)		Area (m ² / %)			
Min value	Max value	Fen	Bog	Treed fens	Treed fen (ditches excluded)
-0.2	-0.5	15 / 0 %	642 / 1 %	8084 / 10 %	921 / 2 %
-0.1	-0.2	1496 / 2 %	7855 / 11 %	11539 / 14 %	4043 / 7 %
-0.05	-0.1	5531 / 9 %	13195 / 18 %	11111 / 13 %	6479 / 11 %
-0.01	-0.05	18608 / 30 %	31348 / 42 %	35656 / 42 %	31314 / 53 %
0	-0.01	36846 / 59 %	21040 / 28 %	18428 / 22 %	16317 / 28 %
Total		62495	74080	84818	59074

426

427 **4 Discussion**

428 We studied lateral expansion and vegetation succession of peatland margins in a subarctic Lompolovuoma fen in
 429 Finnish Lapland. Our results show that the studied margins in Lompolovuoma started to develop ca. 2000 years ago
 430 and the youngest basal age of 390 cal BP was located still a few meters from the current forest edge. Peat initiation in
 431 the margins occurred in several independent loci that only later coalesced into a continuous peatland. The initial wet
 432 *Cyperaceous – Ericaceous* marginal communities inhabited the fen margins over the time periods reaching from a
 433 few centuries to a millennium and the following establishment of *Sphagnum* moss dominated communities was
 434 asynchronous. Starting from the end of the 1800th century, these margins shifted to a climax bog plant community
 435 characterized by hummock *Sphagna* and *Ericaceous* vegetation. This change occurred mostly over a remarkably short
 436 time, in a few decades. However, our data also showed that forest vegetation had on several occasions intruded to the
 437 already established peatland, suggesting an on-going “power-struggle” between peatland and forest ecosystems. The
 438 marginal “bog-type” vegetation currently covers roughly 50 % of the margins in the Lompolovuoma sub-basin, while
 439 in the adjacent sub-basin of Lompolojänkkä, only 35 % have reached the ombrotrophic stage. Our hydrological GW-
 440 SW model indicates that in the “fen-type” margins high water-tables are sustained even during dry climatic conditions,
 441 showing a resistance-potential to fen-to-bog transition.

442

443 **4.1 Non-linear development of peatland margins in Lompolovuoma fen**

444 The formation of Lompolovuoma peat margins investigated here began ca. 2200 years ago. Similar to the results by
 445 Juselius-Rajamäki et al. (2023), these data contradict the traditional perception that peatland expansion has ceased or
 446 markedly slowed down during the last 2000 years in Fennoscandia (Ruuhijärvi, 1983; Sjörs, 1983). Rather, the current
 447 finds suggest this presumption is due to under-representation of studies and sample collection from the mire marginal
 448 areas rather than an actual ceasing of lateral expansion (Kuhry & Turunen, 2006; Ruppel et al., 2013). In transects 2
 449 and 3, the expansion of new peat surfaces occurred from individual miniature loci evidenced by the oldest basal ages
 450 found from the middle of the profiles, while in transect 1 the oldest basal age was acquired for the profile closest to



451 the main mire (Fig. 2a-c). However, the basal age and the basal elevation of the T1Sp matches closely to the age and
452 elevation of the oldest bottom age of transect 2, suggesting a relatively simultaneous initiation process.

453

454 The basal ages from the studied transects show that after the initial peat formation, the individually formed peat patches
455 spread both downhill towards the main mire area, and uphill towards the adjacent forest. Only later, separate peat
456 patches were connected to main mire basin. Such convergence of the multiple smaller loci to a single peatland mass
457 has been reported both during the early Holocene (Almquist-Jacobson & Foster, 1995; Korhola, 1992, 1994;
458 Mathijssen et al., 2014, 2017) and for more recently developed mire margins (Juselius-Rajamäki et al., 2023).
459 However, the mechanisms behind the development of individual peat patches and the later convergence have received
460 only little attention and remain unresolved (Noble et al., 1984).

461

462 In Lompolovuoma, the peat initiation occurred in steep slopes on average exceeding 0.5° , a threshold known to restrict
463 peat formation (Almquist-Jacobson & Foster, 1995; Loisel et al., 2013; Zhao et al., 2014). Thus, in the past, suitable
464 conditions promoting the initiation of individual peat patches must have existed. The peat patches may have started to
465 form in small topographical depressions that, although initially well-drained, may become impervious due to
466 deposition of organic or fine inorganic matter, formation of hardpans in the Spodosol layer, or deposition of ash due
467 to forest fires, creating favourable conditions for peat formation (Klinger, 1996; Le Stum-Boivin et al., 2019; Mallik
468 et al., 1984; Noble et al., 1984; Rydin & Jeglum, 2013). No full-scale subsoil topography measurements were
469 conducted, but field survey data did not reveal any clear depressions underlying any of the oldest peat profiles. Another
470 scenario is, that under sufficiently humid conditions the peat formation began directly on the steep slopes, as suggested
471 for southern Finland peatlands (Korhola, 1996). Climate reconstructions suggest wet climate phase prevailed in
472 Lapland between 2500 and 2000 BP (Eronen et al., 1999; Luoto & Nevalainen, 2015), which may have promoted peat
473 formation even in a relative steep slope, such as presented here.

474

475 The vertical growth of peat as a driving mechanism for lateral expansion has been traditionally linked to raised mires
476 (Foster & Wright, 1990). However, although the shape of the Lompolovuoma surface has remained concave, the low
477 hydraulic conductivity of saturated peat (Ingram, 1978; Rydin & Jeglum, 2013) combined with the large amounts of
478 waters flowing from surrounding uphill areas, especially during the snow-melt period (Autio et al., 2023) could
479 nevertheless cause flooding in suitable locations even if these locations were separated from the main mire body.
480 Similarly, previous studies have shown that although no elevated mire centre exists, significant lateral expansion of
481 peatland has occurred (Almquist-Jacobson & Foster, 1995; Korhola, 1994, 1996; Korhola et al., 2010; Mathijssen et
482 al., 2017), suggesting that even on flat or concave shaped peatland basins peat accumulation can lead to redistribution
483 of waters towards mire margins. Low-severity fires in adjacent forests are also known to promote peatland lateral
484 expansion, as the reduced tree-cover decreases evapotranspiration and promotes colonization of *Sphagnum* due to
485 increased light availability (Le Stum-Boivin et al., 2019; Novenko et al., 2021). However, in our basal layers, no
486 charcoal was found, so forest fire likely did not play an important role in the peat initiation in question.

487



488 4.2 Autogenic and allogenic drivers behind the plant community succession

489 The initial *Cyperaceous* – *Ericaceous* stage found in our study site is commonly present in the basal layers of the
490 peatland margins in Finland (Juselius-Rajamäki et al., 2023; Mathijssen et al., 2017). On the other hand, many studies
491 have shown that *Sphagna* is frequently found in the first stages of the paludification process (Le Stum-Boivin et al.,
492 2019; Noble et al., 1984; Rydin & Jeglum, 2013). This variation can also be seen in our comparison profiles, as the
493 margin of Syysjärvi site shows similar development as in Lompolovuoma, while in the more southern Salamajärvi
494 and Patvinsuo *Sphagnum* mosses were already present during the initial paludification (Supp. fig. 1). The lack of
495 *Sphagnum* mosses in Lompolovuoma margin during the peatland initiation is likely explained by the hydrological
496 conditions. At the onset of the peatland expansion, the water table was likely fluctuating, as shown by the presence of
497 both forest mosses and mycorrhizal fungi *Cenococcum geophilum* (van Geel, 1978) linked to dry conditions, and
498 discovered *Cyperaceous* vegetation usually referring to relatively wet hydrological regime. *Sphagnum* mosses require
499 constantly humid conditions for colonization (Fenton et al., 2007; Sundberg & Rydin, 2002), and even though they
500 can tolerate limited periods of desiccation (Hájek & Vicheroová, 2014), the prolonged fluctuating water sources in
501 margins likely prevented early colonization by *Sphagnum* mosses. Only after the gradual development of mire
502 conditions proper in the margins, was the spread of the peat mosses possible.

503

504 After the initial C-E stage, colonization of *Sphagna* occurred asynchronously between 670 and 1770 CE. This gradual
505 transition towards mixed *Cyperaceous* – *Ericaceous* – *Sphagnum* vegetation was likely moulded by autogenic
506 development as changes driven by allogenic forcing would occur over large areas within a relatively short time span
507 rather than over a millennium, as discussed in Väiliranta et al. (2017). This conclusion is supported by the fact that no
508 evidence of forest fires was found in the peat profiles. Similarly, no such contemporary climate event has been detected
509 which could promote large scale changes in vegetation and simultaneous spatial colonization of *Sphagna* (Hanhijärvi
510 et al., 2013; Linderholm et al., 2018; Luoto & Nevalainen, 2015). The comparison profiles from Patvinsuo and
511 Salamajärvi also show gradual increase in the *Sphagnum* mosses, albeit at much shorter time scale than witnessed in
512 Lompolovuoma, while in Syysjärvi the shift to *Sphagnum* moss dominance was extremely rapid (Supp. fig 1).

513

514 Although the decomposition of the bottom-most layers of peat prevented complete species-level identification of
515 *Cyperaceous* vegetation, increasing number of *Eriophorum vaginatum* remains were found in layers preceding the
516 *Sphagnum* colonization (Supp. fig. 3A-3C). Like *Sphagnum* mosses, tussock-forming *Cyperaceous* vegetation may
517 act as ‘ecosystem engineers’ (Palozzi & Lindo, 2017; Väiliranta et al., 2017) and the importance of *Eriophorum*
518 *vaginatum* facilitating the fen-to-bog transition has been recognized in various studies (Hughes, 2000; Hughes &
519 Dumayne-Peaty, 2002; Väiliranta et al., 2017). These species can alter local conditions, such as hydrology and acidity
520 (Hughes, 2000; Hughes & Dumayne-Peaty, 2002) and produce litter highly resistant to decay, thus promoting peat
521 accumulation (Wein, 1973). This accumulation process can be further amplified by presence of *Ericaceous* vegetation
522 (Hughes, 2000). Although in the studied margins the accumulation of the peat during C-E stage was modest, elevated
523 surface combined with increased acidity seems to have been sufficient to create conditions suitable for establishment



524 of *Sphagnum* species found in the studied margins, likely protecting them from alkaline waters and complete
525 inundation known to impede colonization *Sphagna* (Granath et al., 2010; Ruuhijärvi, 1983; Sallantausta, 2006).

526

527 After the colonization, *Sphagnum* mosses accelerate the change in local conditions (Rydin & Jeglum, 2013), increasing
528 their competitiveness against other mire vegetation and leading to ombrotrophication. In some cases, this change can
529 occur rapidly (Tahvanainen, 2011) and synchronously over wide area (Loisel & Bunsen, 2020), while also more
530 gradual changes have been observed (Väliranta et al., 2017). In Lompolovuoma, initially, the abundance of *Sphagna*
531 remained low after the first establishment, but a more dramatic change occurred towards the end of the 19th century,
532 when *Sphagnum* mosses started dominating the margin plant communities, and most of the Cyperaceous vegetation
533 disappeared, leading to the current S-E vegetation stage. This change coincided with the end of the ‘Little Ice Age’
534 (LIA), when humid and cool climate conditions were followed by increasingly warm temperatures (Hanhijärvi et al.,
535 2013). Similar post-LIA fen to bog shifts have been reported in previous studies where data is captured from central
536 parts of the peatland (Granlund et al., 2022; Kolari et al., 2022; Loisel & Yu, 2013; Magnan et al., 2018; Piilo et al.,
537 2019; Primeau & Garneau, 2021; Robitaille et al., 2021), while our results show similar recent changes occurring in
538 the margins. Current results are supported by a study from adjacent Lompolojätkä basin showing a similar kind of
539 recent vegetation shift in the margins (Kuuri-Riutta et al., 2024) and those of our comparison profile from Syysjärvi
540 (Supp. fig. 1). Thus, although aapa mires are generally described as having wet central parts and dryer margins, our
541 results show that dryer margins supporting *Sphagna* may have formed rather recently.

542

543 Although these recent fen-to-bog transitions have occurred during dry climatic conditions post-LIA, similar shift has
544 also occurred during wet climate phases (Väliranta et al., 2017), as the only requirement for the process is the
545 separation of the peat surface from the groundwater supply (Hughes, 2000; Hughes & Barber, 2003). During wet
546 climatic conditions, the accumulation of peat is promoted, rather high water-table levels are maintained, and the fen-
547 to-bog transition leads to a bog pool and lawn communities (Hughes & Barber, 2003). On the other hand, dry climate
548 conditions decrease the water-table, that enables the species with tolerance towards drought or fluctuating water-tables
549 to out-compete other species (Hughes & Barber, 2004). In Lompolovuoma margins, hummock-forming *Sphagnum*
550 species, especially *Sphagnum fuscum*, increased markedly during the ultimate shift to ombrotrophic bog conditions.
551 The final fen-to-bog transition in the studied mire margins appears to be caused by the drier and warmer climate, as
552 only sporadic presence of non-hummock *Sphagna* was detected in the peat profiles (Supp. fig. 3A-3C). Moreover, the
553 most marginal peat profiles in transect 1 and transect 2, as well as in comparison profile from Patvinsuo, show that
554 the peatland vegetation has been replaced completely by forest vegetation on several occasions. This suggests that
555 peatland expansion may be reversed at least temporary.

556

557 However, based on the remote sensing data, similar ombrotrophication has not occurred across all margins in
558 Lompolovuoma and adjacent Lompolojätkä basins. The ombrotrophic S-E stage can currently be found roughly in
559 50 % of the margins of the Lompolovuoma basin while this stage has been reached only in ca. 35 % in adjacent
560 Lompolojätkä. Similarly, the central part of adjacent Lompolojätkä basin has shown no evidence of fen-to-bog



561 transition (Mathijssen et al., 2014), but transition is ongoing in the margins (Kuuri-Riutta et al., 2024). Thus, it appears
562 that for the transition from fen to bog to occur, certain prerequisites and conditions must be met. Our hydrological
563 model, based on the Lompolojänkää basin, showed that while marginal fens were generally ground-water recipients,
564 the bog-type vegetation acted preferentially as surface water infiltration areas. By decreasing the effective precipitation
565 in the hydrological model to mimic dryer conditions, the highest levels of water table drawdown were found in the
566 current “bog-type” margins, marking these locations more likely to suffer drying conditions. Although both the
567 analysis of vegetation cover (Räsänen et al., 2021) and hydrological model (Autio et al., 2023) contain some degree
568 of uncertainty, the application of the hydrological model over the marginal peatland types supports our hypothesis of
569 drop in ground-water levels as a likely cause for the final shift towards ombrotrophic climax stage.

570

571 4.3 Implication for carbon balance and future trajectories of vegetation succession in aapa mire margins

572

573 The wet C-E stage lasting between 150 and 1250 years in the studied margins has likely had a climate warming effect.
574 Although the net peat accumulation rates presented in our study do not consider the decomposition process (Piilo et
575 al., 2020; Young et al., 2019), the peat increment rates seem to have been low during this period (Fig. 6), likely not
576 compensating for the methane emissions generally associated with similar fen-type conditions (Juutinen et al., 2013;
577 Kou et al., 2022). It has been shown that in fen conditions climate forcing from peatland complex can remain positive
578 (e.g., climate warming effect) for most of the development history and only after continuous carbon uptake and
579 expansion of bog vegetation the climate forcing turns negative (Korhola et al., 1996; Mathijssen et al., 2017, 2022).
580 Thus, in the studied margin, a shift to decay-resistant *Sphagnum* vegetation and lower water table leading to reduced
581 methane emissions would likely have the same effect. Decrease of the Cyperaceous vegetation especially during the
582 last ca. 100 years would have reduced the methane emissions even further (Bubier et al., 1993; Ward et al., 2013).
583 Although our study did not include carbon balance calculations, the shift towards bog community on the studied
584 margins suggest that under current conditions, the margins would likely proceed to have a climate cooling effect.

585

586 As this study and studies by Juselius-Rajamäki et al. (2023) and Kuuri-Riutta et al. (2024) show, new peatland areas
587 are currently widely being formed in the mire margins all over subarctic and boreal zone under natural conditions.
588 However, in many places this development has been blocked by the ditching of mire margins (Sallinen et al., 2019),
589 while the widespread drying of peatland surfaces during the last ca. 300 years may suggest that detrimental climatic
590 conditions for lateral expansion are forming (Swindles et al., 2019). In addition, as revealed by this study, the
591 succession of mire margins even in the same peatland can differ, with some margins retaining their initial wet
592 minerotrophic characteristics, while others develop to ombrotrophic bogs. Due to the opposite climate forcing, the
593 effect of this recent mire expansion on the climate depends on the scope of different peatland types across new mire
594 margins and their later development. The knowledge on the developing peatland margins and their plant community
595 succession still remains scarce. As the lateral expansion of peatlands has had a significant effect on atmospheric
596 greenhouse gas concentrations in the past (Korhola et al., 2010; Peng et al., 2024), we suggest that more studies across



597 the northern peatland margins are needed to reveal the wider effect of this recent lateral peatland expansion on the
598 global carbon budgets.

599

600 **5 Conclusions**

601 Our research shows that the studied mire margin in Lompolovuoma basin has continued to increase in area since ca.
602 2000 cal BP, but this development has not progressed linearly. Rather, the current mire margin has formed from
603 several individual loci and via patches that have merged as the local hydrology has transformed suitable for peat
604 formation. After the initial wet “fen-type” conditions, that persisted for markedly long period, colonization by
605 *Sphagnum* mosses, the change to current “bog-type” conditions represents a remarkable swift shift. This change was
606 driven by dryer climatic conditions following the LIA as shown by our hydrological model. However, not all margins
607 in Lompolovuoma and Lompolojänkää basins have shifted to “bog-type” communities suggesting that wetter “fen-
608 types” are at least partially resistant to hydrologically driven regime shifts. This study shows that even on the basin-
609 scale, peatland margins are highly heterogeneous systems, and this should be taken into account when assessing the
610 effects of past and future lateral expansion trend on the peatland area and peatland carbon dynamics.

611

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618 **Author contributions**

619 T.-J.-R. and M.V. conceived the idea for the article. T.J.-R., E.T., M.V., A.A., H.M., and P.A.-A. collected the field
620 data. T.-J.-R. and S.P. performed the macrofossil analysis. T.J.-R. and S.S.-P. conducted the ²¹⁰Pb-analysis. T.J.-R.
621 conducted the spatial analysis. A.A., H.M., and P.A.-A. conducted hydrological modelling. T.-J.-R. created the initial
622 draft for the manuscript. All authors contributed to the drafts and gave the final approval for publication.

623 **Data availability statement**

624 The data for peat properties, peat core locations and age-depth models is available on the figshare:
625 <https://doi.org/10.6084/m9.figshare.25941493.v1>

626 **Conflict of interest statement**

627 The authors declare that the research was conducted in the absence of any commercial or financial relationships that
628 could be construed as a potential conflict of interest.



629

630 **References**

631

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