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Consistent centennial-scale change in European sub-Arctic peatland vegetation toward *Sphagnum* dominance—Implications for carbon sink capacity

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Abstract

Climate warming is leading to permafrost thaw in northern peatlands, and current predictions suggest that thawing will drive greater surface wetness and an increase in methane emissions. Hydrology largely drives peatland vegetation composition, which is a key element in peatland functioning and thus in carbon dynamics. These processes are expected to change. Peatland carbon accumulation is determined by the balance between plant production and peat decomposition. But both processes are expected to accelerate in northern peatlands due to warming, leading to uncertainty in future peatland carbon budgets. Here, we compile a dataset of vegetation changes and apparent carbon accumulation data reconstructed from 33 peat cores collected from 16 sub-arctic peatlands in Fennoscandia and European Russia. The data cover the past two millennia that has undergone prominent changes in climate and a notable increase in annual temperatures toward present times. We show a pattern where European sub-Arctic peatland microhabitats have undergone a habitat change where

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currently drier habitats dominated by *Sphagnum* mosses replaced wetter sedge-dominated vegetation and these new habitats have remained relatively stable over the recent decades. Our results suggest an alternative future pathway where sub-arctic peatlands may at least partly sustain dry vegetation and enhance the carbon sink capacity of northern peatlands.

KEYWORDS
carbon dynamics, high-latitudes, northern peatlands, paleoecology, plant macrofossils, vegetation change

1 | INTRODUCTION

Arctic regions are warming at twice the rate of the global average (Post et al., 2019), and annual precipitation has increased more than 6% in the past ca. 50 years (Box et al., 2019). Warming that generally increases evapotranspiration has been predicted to result in drying of northern peatlands (Helbig et al., 2020; Swindles et al., 2019), and studies suggest that northern peatlands especially respond to changes in moisture conditions quicker and more prominently than more southern peatland types (Gong et al., 2013; Kokkonen et al., 2019; Tahvanainen, 2011). A new data compilation based on hydrologically sensitive organisms, testate amoebae, indicates a large-scale change of high-latitude Eurasian peatlands toward drier conditions, while in North American continent, the signal is weaker (Zhang et al., 2022). However, in permafrost peatlands, warming may lead to abrupt or more gradual thawing and consequent wetting (Hugelius et al., 2020; Turetsky et al., 2020). Global warming and associated changes in hydrology are altering functioning of peatlands, and understanding these processes is essential as hydrology and associated plant community response ultimately drive peatland carbon (C) dynamics (Laine et al., 2019; Maanavilja et al., 2011; Waddington & Roulet, 2000). It has been suggested that particularly the southern permafrost region is vulnerable for thawing leading to large C emissions in the form of methane (CH_4) driven by increased surface wetness and following change in vegetation, and carbon dioxide (CO_2) arising from increased decay rates and deepening of the active layer (Hugelius et al., 2020; Jones et al., 2017; Turetsky et al., 2020). Both of these processes act as positive warming feedbacks. However, warmer climate and longer growing season is also predicted to increase plant productivity of high-latitude peatlands enhancing their C sink capacity (Gallego-Sala et al., 2018; Loisel et al., 2020). These to some extent contrary processes and the related uncertainties call for better understanding of peatland vegetation changes and responses to environmental changes.

Peatlands are important C stores, currently containing 530 ± 160 Pg C (Hugelius et al., 2020), which is about 25% of the global soil C stock (Yu et al., 2010) even though peatlands only cover ca. 3% of the global land area (Xu et al., 2018). Northern peatlands, of which almost half is permafrost affected, account for ca. 80% of the total peatland C storage (Hugelius et al., 2020). Permafrost peatlands are particularly complex systems and their response

to environmental changes is variable (Sim et al., 2021; Swindles et al., 2015; Zhang, Gallego-Sala, et al., 2018) due to the spatial heterogeneity of ground ice and the physical processes associated with ice formation and melt. To date, a number of vegetation and peat property data from the high-latitudes covering the past centuries has been published (e.g., Kjellman et al., 2018; Oksanen, 2006; Oksanen et al., 2001; Sannel et al., 2018; Swindles et al., 2015), but detailed studies combining these variables with high-resolution chronologies applying both ^{14}C and ^{210}Pb age-depth data remain scarce for North American continent (Magnan et al., 2022; Piilo et al., 2019) and, for European arctic (Sim et al., 2021; Zhang, Gallego-Sala, et al., 2018). Here we address the question of how high-latitude peatland vegetation has responded to climate variations in the past considering the warm Medieval Climate Anomaly (MCA), cool Little Ice Age (LIA) and the post LIA recent warming (RW). We investigate past hydrological changes using peat forming vegetation. We discuss the analog of past changes for the on-going climate changes. Our study sites are high-latitude fens and permafrost peatlands, located in the European sub-arctic: Sweden, Finland and Russia. Most of our samples are from intermediate hydrological microhabitats (lawns) that are considered to readily reflect hydrological changes (De Vleeschouwer et al., 2010). Our high-resolution well-constrained data and robust chronologies allow us to evaluate climate–vegetation linkages through time and discuss the effects on carbon dynamics and regional differences.

2 | MATERIALS AND METHODS

2.1 | Study sites and peat sampling

We present data of 24 unpublished and 9 published (Piilo et al., 2020; Zhang, Gallego-Sala, et al., 2018; Zhang, Piilo, et al., 2018) peat records from high-latitude fens and permafrost peatlands located in the subarctic climate zone (Figure 1 and Table 1). Here we refer to fens as sites where the vegetation is composed of sedges sl. and minerotrophic/oligotrophic *Sphagnum* and brown mosses. In fens, water table is close to surface and in our sites there was conspicuous microtopography with strings or permafrost formations present. Vegetation on string and habitats overlying permafrost resembles to those of ombrotrophic dry bog
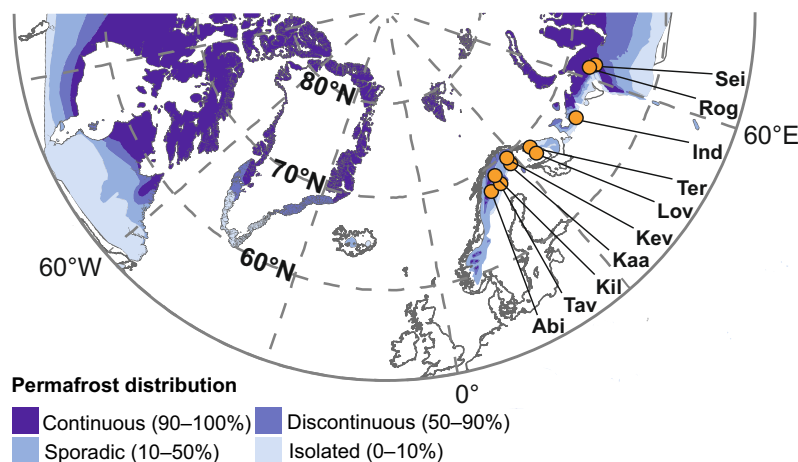
FIGURE 1 The study site locations (orange dots) in northern Fennoscandia: Abisko (Abi), Tavvavuoma (Tav), Kilpisjärvi (Kil), Kaamanen (Kaa), Kevo (Kev), Lovozero (Lov), Teriberka (Ter), and northeast European Russia: Indico (Ind), Rogovaya (Rog) and Seida (Sei). Permafrost distribution (blue shading) is based on Brown et al. (1998).

surfaces, which are dry and nutrient poor. Our study time window is two millennia, including the warm Medieval Climate Anomaly phase (MCA; 950–1250 CE) (Mann et al., 2009) and the cool Little Ice Age (LIA; 1450–1850 CE) (Wilson et al., 2016). The changes in moisture conditions are regionally less well known with higher regional variability for these periods (Cook et al., 2015; Linderholm et al., 2018). However, as the Northern Hemisphere has experienced profound warming since the 1980s (Huang et al., 2017), we paid special attention to very recent changes. Eight peat records were collected from currently dry palsa or string top surfaces, and 25 cores from intermediate lawns (Table 1), representing the microhabitats that are considered to readily reflect hydrological variations leading to changes in vegetation (De Vleeschouwer et al., 2010; Väliranta et al., 2007). The dry surfaces, where our sampling did not reach the surface of the peatland water table (WT) but hit permafrost, were dominated by dwarf shrubs, such as *Empetrum nigrum*, *Betula nana*, *Rubus chamaemorus*, and mosses such as *Polytrichum* spp, *Dicranum* spp, and lichens such as *Cladonia* spp. The lawn surfaces (WT depths: 12–38 cm) were mainly dominated by *Sphagnum fuscum*. Other species occurring in the lawn coring locations were *Mylia anomala*, *Rubus chamaemorus*, *Andromeda polifolia*, *Betula nana*, *Vaccinium uliginosum*, *V. oxycoccos*, *V. myrtillus*, *V. vitis-ideaea*, *Rhododendron tomentosum*, and *Eriophorum* spp. Prevailing vegetation and microtopographical features were considered while selecting the exact coring locations. Species or species groups such as *Carex* spp, *Eriophorum* spp, *Salix* spp, hollow *Sphagnum* species and other depression habiting bryophytes such as *Warnstorfia* spp and *Scorpidium scorpioides* dominated the wet areas of the study peatlands, but those were not sampled for this study.

The study sites represent permafrost peatlands (26 peat records) or high-latitude fens (7 peat records: Kaamanen (*n* = 4), Lovozero: Lov1.3, Lov2.2 (*n* = 2), and Teriberka (*n* = 1)) (Figures 1 and 2). The sites in Fennoscandia are within the sporadic permafrost zone and in Russia within the discontinuous permafrost zone. Indico, Seida,

and Rogovaya are located in the northeast European Russian tundra (study sites described e.g., in Oksanen et al., 2001; Ronkainen et al., 2015; Zhang, Gallego-Sala, et al., 2018). For further details of the study sites see for Tavvavuoma (Sannel et al., 2018), for Abisko (Malmer et al., 2005), for Kaamanen (Aurela et al., 1998; Piilo et al., 2020), for Kevo (Oksanen, 2006), and for Kilpisjärvi (Zhang, Piilo, et al., 2018).

To address the vegetation and apparent C accumulation patterns of high-latitude peatlands, a total of 33 short (24–60 cm) surface peat profiles were collected. A Russian peat corer (3 × 50 cm) and a box corer (7 × 4 × 65 cm) were used to collect the topmost peat overlying the seasonal frost, permafrost, mineral ground or if the aforementioned conditions were not met the maximum length of the collected peat record was limited to the length of the corer. Peat records were wrapped in plastic and, avoiding compaction, transported to the University of Helsinki, where they were cut into 1 cm subsamples and stored in resealable plastic bags at 6°C.

2.2 | Chronology

To establish chronologies, we combined radiocarbon (^{14}C) and lead-210 (^{210}Pb) dating methods. In total, 94 samples were ^{14}C dated with accelerator mass spectrometry (AMS). Each peat profile has two to five ^{14}C dates and all of the 33 peat profiles are dated with ^{210}Pb and the data are available in this publication or through Zenodo (https://doi.org/10.5281/zenodo.7415020). The samples for ^{14}C and ^{210}Pb analysis were selected to overlap, in order to cross-validate and the reliability of the dating results. Samples for ^{14}C analysis were cleaned: roots and rootlets were removed (Holmquist et al., 2016). A subset of 52 samples were sent for ^{14}C analysis to the Finnish Museum of Natural History (LUOMUS, Helsinki, Finland), 36 samples to Poznan Radiocarbon Laboratory (Poznan, Poland), and 5 samples were

TABLE 1 Study site information. Elevation meters above the sea level (m a.s.l.), mean annual temperature (MAT, °C), mean annual precipitation rounded to the nearest 10 (MAP, mm). The weather data for Abisko are from ca. 10km distance from the studied sites and cover 1989–2018. Naimakka weather station is about 35km northeast from Tavvavuoma and about 10 km southeast from Kilpisjärvi, litto study sites, and covers the period 1995–2019 (Swedish Meteorological and Hydrological Institute, http://opendata-catalog.smhi.se/explore/). For Kilpisjärvi, Peera, site the weather data are from Enontekiö Kilpisjärvi Kyläkeskus meteorological station ca. 15km southeast from the site, for Kevo site; from Utsjoki Kevo meteorological station ca. 10km southwest from the sites and for Kaamanen; from Inari Ivalo airport station 60km south of the site for the period 1981–2010 (Pirinen et al., 2012). Weather data for Lovozero (Lovozero weather station ca. 10–15km northwest from the sites) and Teriberka (Murmansk weather station located ca. 60km west of the site) cover the period 1966–2015 (Marshall et al., 2016). The weather data for Indico are from Indiga meteorological station, ca. 60km northwest of the site, covering the period 1981–2010 ("Weather and Climate", http://www.pogodaiklimat.ru/history/22292.htm). For Seida and Rogovaya, the weather data are from Vorkuta meteorological station ca. 60–70km northeast from the sites, covering the period 1977–2006 (Marushchak et al., 2011). *Published cores (Piilo et al., 2020; Zhang, Gallego-Sala, et al., 2018; Zhang, Piilo, et al., 2018). Active layer thickness (the seasonally thaw peat layer on top of permafrost) and water table depths (WTD) are single point measurements measured between August and September from the coring holes. NA indicates the lack of permafrost or dry conditions with no water table at the exact collection location of the peat record at the time of sampling

Site	Core codes	Microhabitat	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l)	MAT (°C)	MAP (mm)	Active layer thickness (cm)	WTD (cm)	pH
Abisko	Abi1.2, Abi1.3	Lawn	68°21'27.0000"	019°03'12.3000"	350	0.3	345	40–45	20	4–4.5
	Abi2.2	Lawn	68°21'01.8600"	018°52'22.6200"	350			45	13	
Tavvavuoma	Tav1.1, Tav1.2, Tav1.3	Lawn	68°27'51.9600"	020°54'26.6400"	550	−1.7	455	NA	17–20	5–5.5
	Tav2.1, Tav2.2	Lawn	68°28'38.1000"	021°01'06.6600"	610			55/NA	22–24	4.5–5
Kilpisjärvi, litto	I1V, I1M, I2V, I2M	Dry palsa (I1M, I2M), Lawn (I1V, I2V)	68°43'25.6800"	021°25'19.6200"	400	−1.7	455	55–60/NA	14–25/NA	4.5–5
Kilpisjärvi, Peera	Kil2*	Dry palsa	68°53'04.3700"	021°03'10.3100"	460	−1.9	490	36	NA	4.5
Kevo	Kevo2*	Dry palsa	69°48'35.2200"	027°11'48.2100"	280	−1.3	430	35	NA	4.5
	Kevo2P2	Dry palsa	69°49'26.1012"	027°10'20.7012"	290			35	NA	4.5
Kaamanen	K1EP*, K1BS*, K3EP*, K3BS*	Dry string (K1EP, K3EP), Lawn (K1BS, K3BS)	69°08'22.9200"	027°16'17.8800"	140	−0.4	470	NA	16–20/NA	4.5–5.5
Lovozero	Lov1.3	Lawn	67°58'45.8400"	035°03'49.5600"	160	−1.2	480	NA	35	4
	Lov2.2	Lawn	68°01'10.4400"	034°58'15.6000"	180			NA	30	4
	Lov3.1, Lov3.2, Lov3.3	Lawn	67°59'38.4600"	035°01'06.3000"	160			NA	32–38	4
Teriberka	Ter2.1	Lawn	68°52'27.1200"	034°28'48.9600"	220	0.4	490	NA	17	5
Indico	Ind4*, Ind5*	Lawn	67°16'01.0000"	049°52'59.9000"	50	−2.3	420	50	20	4
Rogovaya	Rog2, Rog4, Rog8, Rog11, Rog14	Lawn	67°19'39.7200"	062°36'28.2600"	120	−5.6	500	35–50/NA	12–27	4
Seida	Sei2*	Dry palsa	67°07'00.1200"	062°57'00.0000"	100	−5.6	500	40	NA	5

dated in A. E. Lalonde AMS Laboratory (University of Ottawa, Canada). Dried and ground subsamples of ca. 0.1–0.6 g were ^{210}Pb dated at every cm (12M, K3M, Sei2, Kev2 and Kil2) and every other cm for the rest of the cores at the University of Exeter, United Kingdom. The subsamples were spiked with a ^{209}Po yield tracer and after analyzed with alpha spectrometry for ^{210}Pb activity (for detailed procedure see Estop-Aragonés et al., 2018; Kelly et al., 2017).

To create age-depth models, ^{14}C results and ^{210}Pb data (Bq/kg) were integrated into a single chronology using Plum (Aquino-López et al., 2018), which is Bayesian methodology for ^{210}Pb dating. Plum allows the integration of other dating, in this case ^{14}C dates, into a single age-depth model without the need to remodel the ^{210}Pb dates. This transparent integration allows for a more realistic measurement of the uncertainty (Aquino-López et al., 2018), and the practice is further described in Zhang et al. (2020). The models were created using the rplum package for R version 3.6.0 (R Core Team, 2014). For the 9 previously published records, new age-depth models were created using Plum. Weighted mean ages of each age-depth model were used in this study. Peat growth rates (mm year^{-1}) were calculated based on the age-depth model results.

2.3 | Plant macrofossil analysis

To reconstruct the changes in vegetation, plant macrofossils were examined following Mauquoy et al. (2010) and Väliranta et al. (2007). From each of the peat profiles, plant macrofossils were studied on 1 or 2 cm interval and when prominent changes in the plant assemblages were recorded, the resolution was increased to 1 cm interval. Volumetric subsamples (2–5 ml) were rinsed under running water in a 140-μm sieve, the residue was analyzed with a stereomicroscope for percentage proportions of main peat components of a total sample volume (100%) and for example seeds and leaves were counted as exact numbers, these data are available through Zenodo (https://doi.org/10.5281/zenodo.7415020). For further species level identification (following e.g., Eurola et al. (1992); Laine et al. (2009) and a reference collection at the University of Helsinki), we used a compound light microscope. If the organic remains were unidentifiable for the vegetation type, the percentage of unidentified organic material (UOM) was determined. To present and visualize the hydrological changes based on the analysed vegetation data, we classified the plant macrofossil analysis data into nine functional groups:
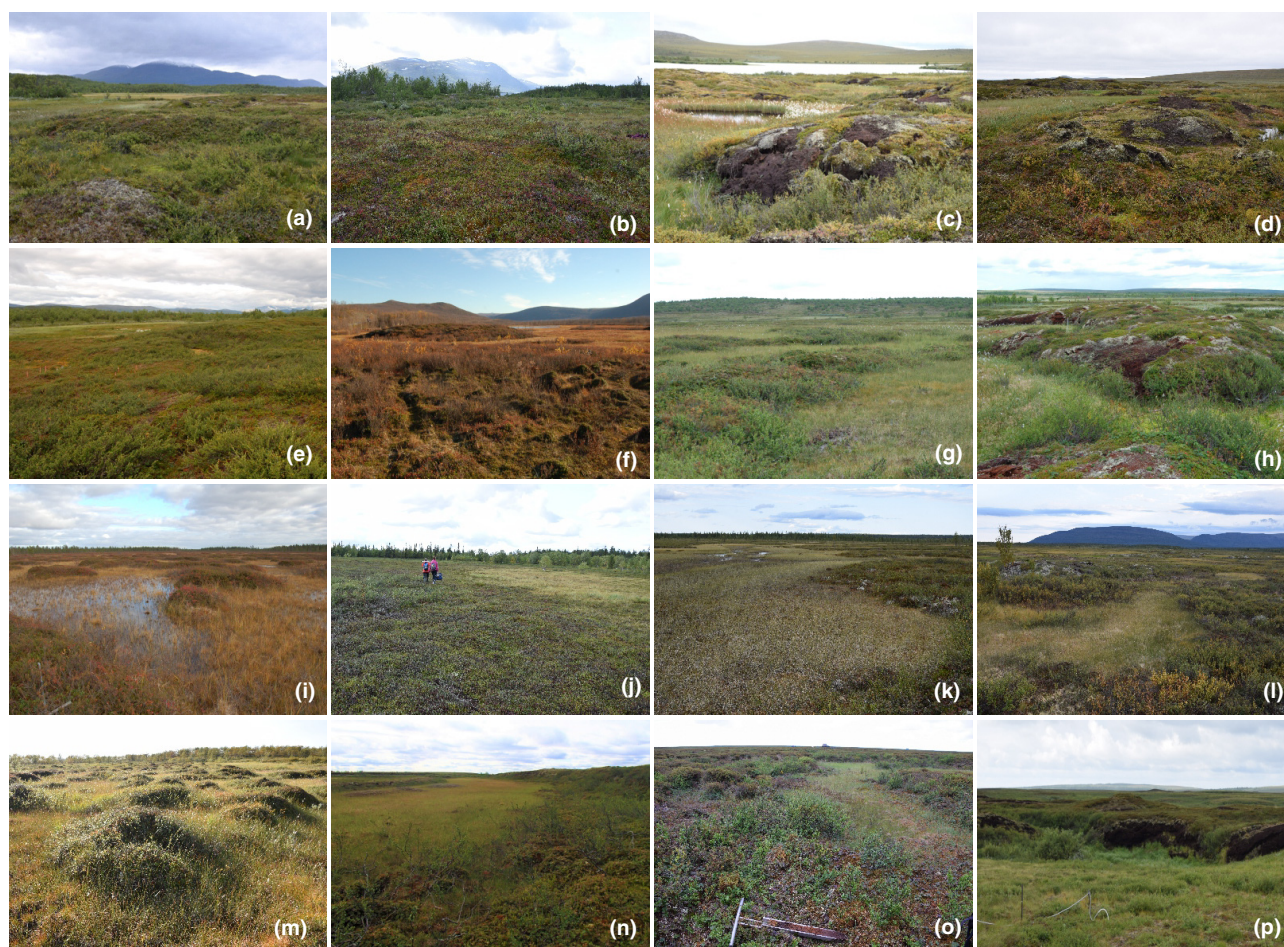

FIGURE 2 Photos illustrating the general appearance of the study peatlands: (a) Abisko, Abi1, (b) Abisko, Abi2, (c) Tavvavuoma, Tav1, (d) Tavvavuoma, Tav2, (e) Kilpisjärvi, Kil, (f) Kilpisjärvi, Iitto, I, (g) Kevo, Kevo2P, (h) Kevo, Kev2, (i) Kaamanen, K, (j) Lovozero, Lov1, (k) Lovozero, Lov2, (l) Lovozero, Lov3, (m) Teriberka, Ter2, (n) Indico, Ind, (o) Rogovoya, Rog and (p) Seida, Sei.

TABLE 2 Grouping of *Sphagnum* mosses and non-*Sphagnum* bryophytes into dry/intermediate and wet categories (e.g., Eurola et al., 1992; Laine et al., 2009). The category indifferent contains also taxa that are found both in wet and intermediate conditions or if the species identification has not been detailed enough, the species were included to this category

Sphagnum mosses		Non-*Sphagnum* bryophytes		
Dry/Intermediate	**Wet**	**Dry/Intermediate**	**Wet**	**Indifferent**
Sect. Acutifolia	Sect. Cuspidata	*Dicranum* sp.	*Warnstorfia* sp.	*Straminergon stramineum*
S. capillifolium	*S. balticum*	*Dicranum elongatum*	*Warnstorfia fluitans*	*Bryum* sp.
S. fuscum	*S. lindbergii*	*Dicranum* cf. *fuscenscens*	*Scorpidium* sp.	cf. *Gymnocolea inflata*
S. russowii	*S. jensenii*	*Dicranum angustum*	*Scorpidium scorpioides*	*Cephalozia* sp.
S. compactum	*S. annulatum*	*Dicranum groenlandicum*	*Exannulata group*	*Aulacomnium palustre*
S. rubellum	*S. riparium*	*Polytrichum* sp.	*Sarmentypnum sarmentosum*	*Marchantiophyta* sp.
S. warnstorfii	*S. majus*	*Polytrichum strictum*	*Calliergon stramineum*	*Hypnum/Hygrohypnum*
S. molle	*S. cuspidatum*	*Polytrichum commune*		*Paludella squarrosa*
cf. *S. subfulvum*	*S. subnitens*	*Pleurozium shreberi*		cf. *Drepanocladus* sp.
cf. *S. tescorum*	Sect. Subsecunda	*Hylocomnium splendens*		
S. angustifolium	*S. platyphyllum/auriculatum/ inundatum*	*Lepidozia reptans*		
S. teres		*Pohlia nutans*		
S. aongstroemii		*Mylia anomala*		
Sect. *Sphagnum*				
S. magellanicum				
S. papillosum				

UOM, herbaceous, non-*Sphagnum* bryophytes (wet, dry/intermediate and indifferent), *Sphagnum* mosses (wet and dry/intermediate), shrubs, and lichens (Table 2. for the detailed classification of the identified mosses). The classification into the functional groups was based on general ecological knowledge and published data (e.g., Laine et al., 2009). To illustrate the overall change in the hydrological conditions interpreted from and reflected by the plant functional types, we grouped the functional types into two categories: wet (herbaceous, non-*Sphagnum* wet bryophytes, and wet *Sphagnum* mosses) and intermediate/dry (dry/intermediate non-*Sphagnum* bryophytes, dry/intermediate *Sphagnum* mosses, shrubs, and lichens). UOM and indifferent non-*Sphagnum* bryophytes were excluded from this division. The wet group was transferred into negative values to insert them in a diagram with a locally estimated scatterplot smoothing (LOESS) curve (span-value of 0.5), created with a function loess () in R version 3.4.3. We used the software C2 (Juggins, 2007), GraphPad Prism, and R to create the diagrams.

To assess the similarity and dissimilarity of vegetation compositions between different selected time slots of 1 CE, 1450 CE, 1850 CE, and present, we applied a nonmetric multidimensional scaling (NMDS). These time slots were selected based on the known climate periods, corresponding to the onset and end of the LIA and from our data the corresponding sample depth was selected to be closest to the selected time slots. NMDS represents the change of

the vegetation compositions through time with a dot for each sample. The closer the dots are to each other in the NMDS ordination space, the more similar the samples are with respect to the vegetation composition data. Bray-Curtis distance was used for testing the dissimilarity in the NMDS. To statistically determine if the data point centroids (centers) differ in the ordination space, we applied function adonis with Vegan package in RStudio Version 1.3.1093.

2.4 | Peat properties and carbon accumulation

To determine apparent C accumulation (ACAR: $g C m^{-2}$ $year^{-1}$) of the peat profiles, dry bulk density ($g cm^{-3}$) was measured for a peat fresh volume of 2–5 cm^3 and C (and nitrogen (N)) content at 4 cm intervals with a LECO TruSpec micro Elemental Determinator, at the University of Helsinki. C to N mass ratios (C/N) were calculated from the C and N content data. Vertical peat growth (accumulation) rates ($mm year^{-1}$) were calculated based on the weighted mean ages of each age-depth model. To calculate ACAR, the dry bulk density of each 1 cm thick subsample was multiplied by its C content and by its peat growth rate (Tolonen & Turunen, 1996). Here we concentrated on the past 2000 years and thus ACAR values do not take into account older sections. To study recent apparent C accumulation rates (RERCA; $g C m^{-2}$ $year^{-1}$), we calculated the cumulative C accumulated (Turunen et al., 2002) for the set periods from 1900 CE, 1950 CE, and

1980 CE to present and calculated the mean ACAR values for the periods of 1900–1950 CE, 1950–1980 CE, and since 1980 CE.

3 | RESULTS AND DISCUSSION

We investigated the responses of plant abundances, vertical peat accumulation, and C dynamics to changes in climate on millennial to centennial and decadal time scales in 16 high-latitude peatlands based on a substantial set of peat records ($n = 33$). The records are taken from two different microforms, intermediate ($n = 25$) surfaces that readily reflect hydrological variations determining vegetation composition (De Vleeschouwer et al., 2010; Väliranta et al., 2007) and dry surfaces ($n = 8$) reflecting permafrost dynamics and potential changes in precipitation/evaporation ratio (Table 1).

3.1 | Vegetation change indicating a shift from wet to intermediate or dry conditions

Vegetation assemblages predominantly indicated changes from wetter habitats to intermediate or dry conditions through time (Figures 3–6; Figures S1–S5). The type, timing, and magnitude of these changes varied. All peat cores collected from currently dry surfaces ($n = 8$) (where no water table (WT) was detectable) suggested that wet conditions had prevailed earlier and a shift from wet to dry conditions occurred between ca. 900 and 1800 CE (Figure 2). The rest of the peat records collected from the intermediate surfaces (WT depths: 12–38 cm) ($n = 25$) revealed more variable dynamics. However, most of them ($n = 23$) indicated a change from wet conditions toward the currently prevailing drier intermediate conditions between ca. 800 CE and the beginning of the 2000's CE (Figure 3). Although the hydrological change suggests a regional drying signal, local-scale peatland dynamics may explain the differences in the timing of the changes. The timing of the past changes varied regionally and locally in both habitat types, but during recent decades, habitat conditions, following the overall regime shift, have stayed relatively stable with intermediate or dry conditions being prevailing (Figures 3 and 4). Obviously, as the coring locations were selected to represent intermediate or dry conditions for their environmental sensitivity, no reverse pattern with a final wet shift toward the present occurred; however, a few cores ($n = 4$) deviated from these general patterns (Figure 3). The ultimate change toward drier conditions generally took place later in the records collected from currently intermediate surfaces than in the dry surfaces (Figure 6). Most striking detected pattern was that in many intermediate microhabitats the abundance of *Sphagnum* has increased during the past ca. 200 years (Figure 4, Figures S1–S5). By and large, when considering the chronological uncertainties associated to the recent decades, our data suggest that for the past 40 years, vegetation compositions of intermediate and dry microhabitats have in general remained very stable suggesting resilience of these microhabitats against recent warming (Figures S1–S5). Our NMDS analysis indicated that the vegetation composition and variation at the intermediate and dry surfaces were statistically significantly different ($p = .001$) from each other when time points of 1 CE, 1450 CE, 1859 CE, and the present were compared (Figure 5). On the other hand, the vegetation composition and variation did not differ between Northern Fennoscandia and Northeast European Russia ($p = .216$) (Figure 5).

The hydrological vegetation signal suggests an overall change from wetter to drier conditions largely after the MCA 1300 CE (Figure 6a). By the end of the LIA, ca. 1850 CE, the overall hydrological signal continues toward drier conditions (Figure 6a, see Table 2 for classification of the taxa). When the intermediate surfaces are inspected separately from the currently dry locations, the overall hydrological signal shifts to drier conditions only at ca. 1600 CE, and the variation in the data is large (Figure 6b). The hydrological signal of the dry surfaces shows a clear change from wetter toward drier conditions around ca. 1300 CE (Figure 6c). The LIA cooling and associated permafrost aggradation likely enhanced the vegetation change toward drier conditions as the surface was uplifted from the surrounding fen (Seppälä, 2011). The timing of the change to vegetation succession toward drier plant communities (Figure 6a–c) is dated to the end of the MCA, possibly suggesting a delayed response of vegetation to the MCA-induced warmer conditions and higher evaporation. Subsequently, MCA warm phase was followed by LIA cooling and permafrost aggradation. However, also the non-permafrost dry-surface locations (K1EP and K3EP) mimicked the vegetation patterns and the inferred hydrological change patterns of the currently dry peat profiles from permafrost peatlands ($n = 6$). The vegetation inferred hydrological change toward drying of the lawn profiles is associated to the post-LIA warming. However, the location-specific variation is large and highlights the differences related to autogenic succession processes (Figures 3 and 4).

3.2 | Spatiotemporal variation in peat properties and carbon accumulation patterns

The spatiotemporal variation in profile basal ages (Figure S6 and Table S1) is prominent, thus only the past two millennia are presented. In this time frame, we did not detect significant differences in vegetation succession patterns between the two study regions, northern Fennoscandia and north European Russia (Figure 5). In addition, we tested if there were regional differences in the average peat accumulation rates between the study regions, but no significant differences emerged ($p = .7$, Mann–Whitney test) nor in ACAR and recent C accumulation (RERCA) (see Section 2) rates (Figure S7). However, the average bulk densities and peat accumulation rates significantly differed between the records collected from the currently intermediate and currently dry surfaces, with the latter showing higher average bulk densities ($p = .002$, Welch's t test) and significantly lower peat accumulation ($p < .0001$, Mann–Whitney test). We acknowledge the difficulty in distinguishing the signal of warming or hydrological changes-induced higher productivity and consequently increased ACAR for the topmost
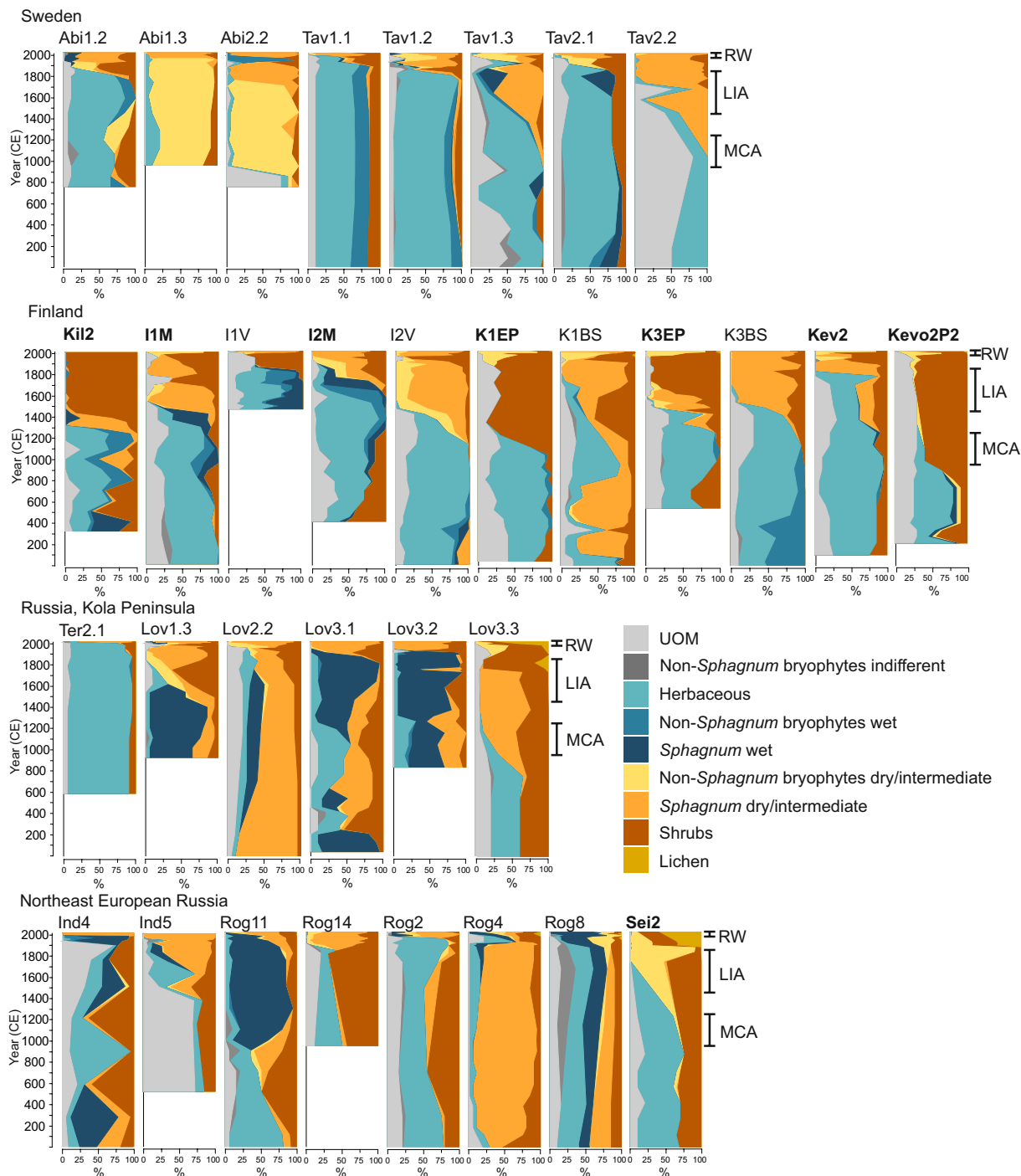
FIGURE 3 Vegetation composition changes over the past 2000 years for individual peat records (see Section 2 for the classification of plant groups and the species in each group and the chronologies). The peat profiles are arranged by country/region from west to east. The site name codes are indicated in the Figure 2 caption. The records collected from currently dry surfaces have names in bold and others represent intermediate conditions (see Section 2). The grey colors for vegetation indicate unidentified organic material (light grey, UOM), indicating high level of peat humification, and non-*Sphagnum* bryophytes (dark grey) that are not sensitive to their habitat wetness conditions. Blue colors indicate, in general, vegetation living in wet habitats and yellowish to brownish colors indicate intermediate to dry conditions. The timing of the recent warming (RW), little ice age (LIA) and medieval climate anomaly are illustrated.

incompletely decomposed young peat layers (Young et al., 2019, 2021) and thus we studied the differences between regions and microhabitats for similar time windows only. Interestingly, RERCA rates between the studied regions and microhabitats did not

statistically differ (Mann–Whitney test), even though the RERCA values for north European Russia and dry habitats were slightly smaller with smaller variation than for northern Fennoscandia and intermediate habitats (Figure S7).
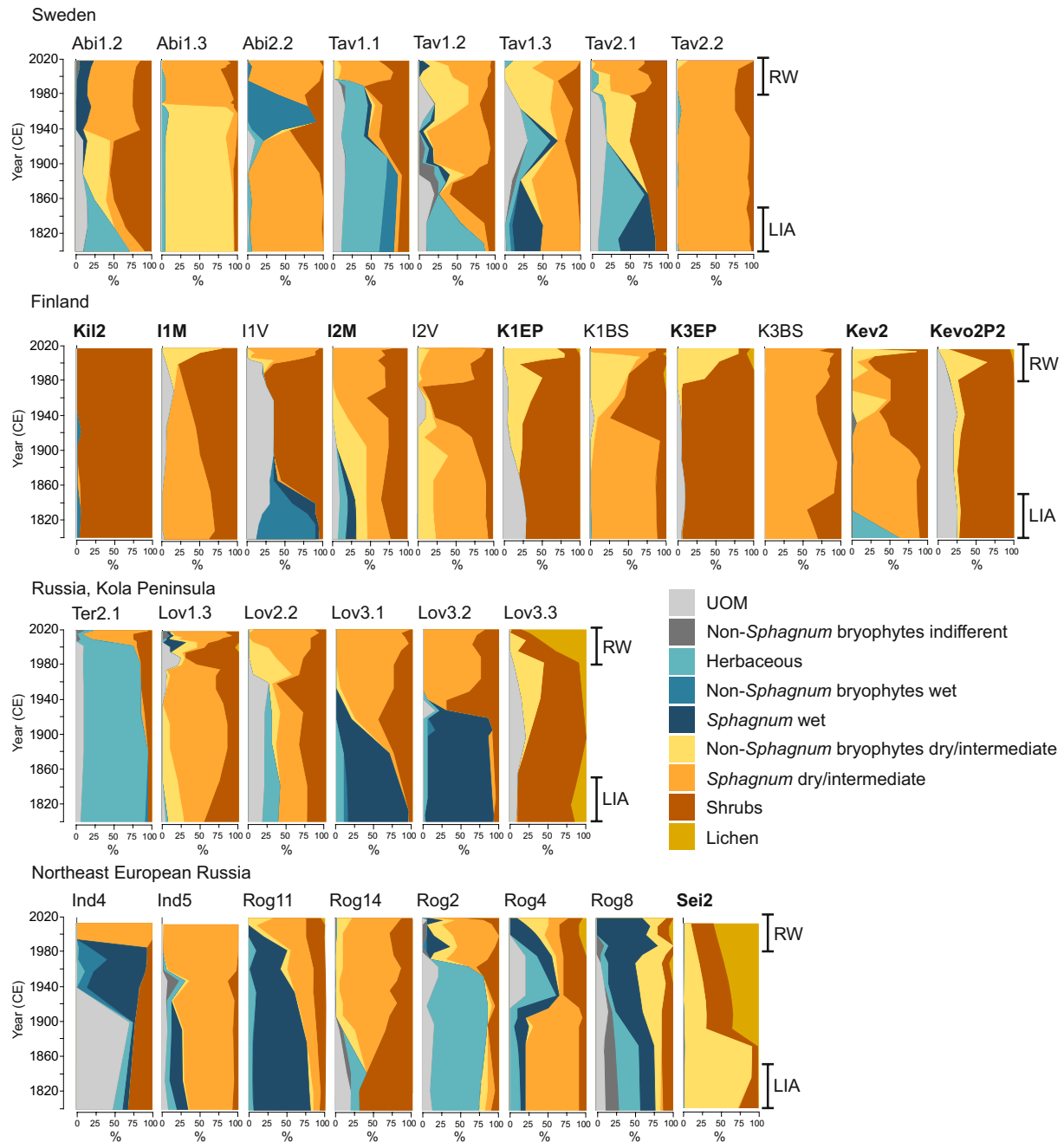
FIGURE 4 Vegetation composition changes over the past 220 years (see Section 2 for the classification of plant groups). The peat profiles are arranged by country/region from west to east. The site name codes are indicated in the Figure 2 caption. The records collected from currently dry surfaces have names in bold and others represent intermediate conditions (see Section 2). Color coding for unidentified organic material (UOM), non-*Sphagnum* bryophytes that are insensitive to their habitat wetness conditions, and plant groups living in wet habitats and in intermediate to dry conditions is similar to Figure 3. The timing of the recent warming (RW) and little ice age (LIA) is illustrated.

3.3 | Resilience of subarctic peatlands to environmental changes and implications for future carbon budgets

The drying of the currently dry habitats during the LIA and up to the early 19th century probably reflects permafrost aggradation. The continuation of dry and intermediate surface conditions, in the present data, since the end of the LIA suggests that peatland

plant communities can remain stable under environmental forcing. Majority of the studied plant communities do not indicate rapid local changes in hydrological conditions over the past ca. 40 years, even though most of the sample cores were collected from intermediate surfaces which are the most sensitive microhabitats reflecting the changes in environmental conditions (De Vleeschouwer et al., 2010; Zhang et al., 2020). In other words, our data suggest that to some extent these ecosystems may remain relatively stable and

FIGURE 5 NMDS ordination. (a) Ellipses indicate the standard deviation from the centroid location of the data points, where the text (Dry1CE, Dry1450CE; Dry1850CE, DryPresent, Lawn1CE, Lawn1450CE, Lawn1850CE or LawnPresent) is located. (b) Locations of plant data in the ordination space. (c) all the data locations behind the ellipses of (a). (d) and (e) show separately the data points from northern Fennoscandia and northeast European Russia. Permanova test showed the significant differences ($p = .001$) between the groups: Dry1CE, Dry1450CE; Dry1850CE, DryPresent, Lawn1CE, Lawn1450CE, Lawn1850CE, and LawnPresent. Also, lawns and dry habitats are different from each other ($p = .001$) and the time slots from 1 CE to present are statistically different from each other ($p = .001$). However, the two regions, northern Fennoscandia and northeast European Russia, do not significantly differ from each other ($p = .216$).
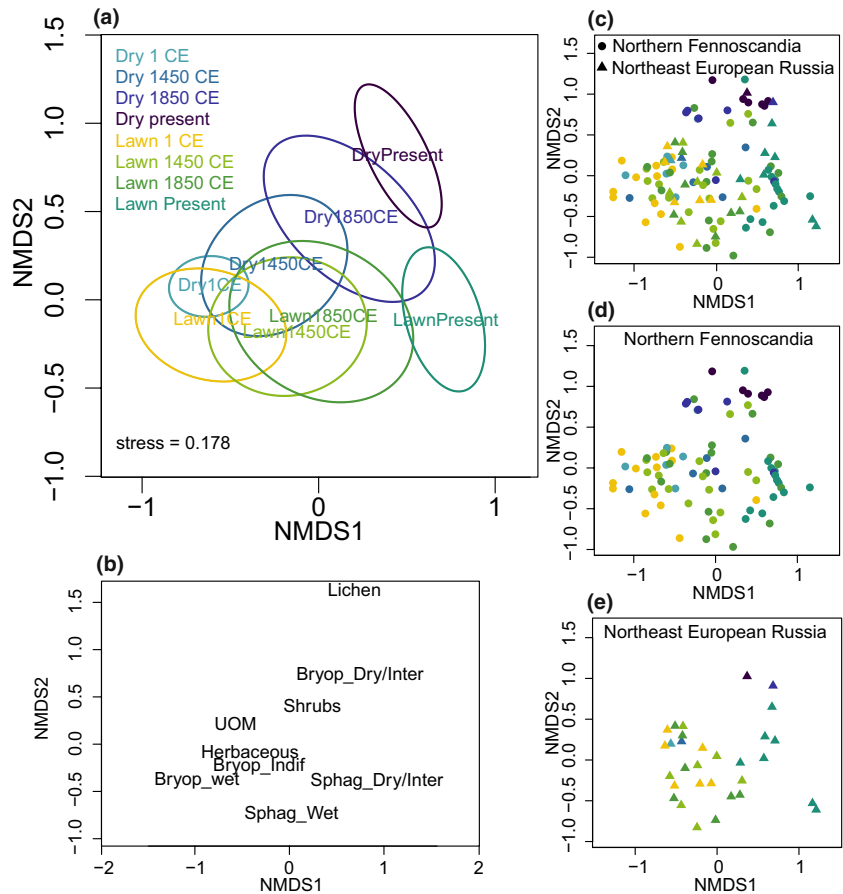
have a strong buffering capacity to changes in climate. Moreover, the increased evapotranspiration may further enhance the drying if permafrost is being lost by gradual thawing and active layer is deepening and the ecosystems may become increasingly suitable for bryophyte establishment whose domination consequently enhances C accumulation (Charman et al., 2013; Laine et al., 2021). Our study sites are located in the sporadic and discontinuous permafrost zone, where permafrost is warming (Biskaborn, 2019) and gradual permafrost thaw and active layer thickening are on-going processes (Hugelius et al., 2020; Swindles et al., 2015). Permafrost collapse and consequent wetting have been widely reported also from the sporadic permafrost zone (Borge et al., 2017; Malmer et al., 2005; Olvmo et al., 2020) and also abrupt thaw has been predicted (Turetsky et al., 2020). The focus of this study was to analyse and discuss widespread vegetation changes and their implications for peat accumulation patterns, and accordingly the carbon balance in permafrost peatlands with currently dry or intermediate surface conditions. Thus, wet surface conditions, possibly a result of ground collapse following permafrost thaw, were not accounted for. However, permafrost thaw does not necessarily trigger a widespread wetting of peatlands and consequent increase in CH_4 emissions if permafrost thaws gradually and the permafrost ice-content is relatively small—or there is a considerable delay in the thaw processes (Hugelius et al., 2020). It should be noted that our records from non-permafrost sites ($n = 7$) mimicked the pattern detected

in permafrost peatland records. This suggests that climate warming, instead of leading to a catastrophic loss of C associated with drying (Ise et al., 2008), could strengthen the northern peatland C sink capacity in general if the observed regime shift from sedges to bryophytes, associated with suitable niche conditions—hydrology in particular—occurs more widely, as also recently reported from northeast Canada (Magnan et al., 2022).

C content and bulk density measurements, ACAR and RERCA do not take into account the autogenic process of long-term decay and thus the ACAR and RERCA values are higher in the top peat layers (Young et al., 2019). Despite this, our observations on C accumulation contradicts some previous studies, where the desiccating permafrost peat is coupled with extremely low C accumulation (Swindles et al., 2015). Various studies suggesting permafrost thaw-induced increased net C emissions do not take into account vegetation changes nor potential benefits on biomass enhancement (Hugelius et al., 2020; Turetsky et al., 2020).

We suggest that the vegetation change from wetter fen conditions to *Sphagnum*-dominated intermediate conditions may increase the C sink capacity of these high-latitude peatland microhabitats in the future, and this development pathway could be further enhanced with climate warming (Gallego-Sala et al., 2018). It is clear that permafrost peatland vegetation dynamics are complex and the short-term response of vegetation and C dynamics to climate change together with autogenic forcing may be spatially markedly variable.
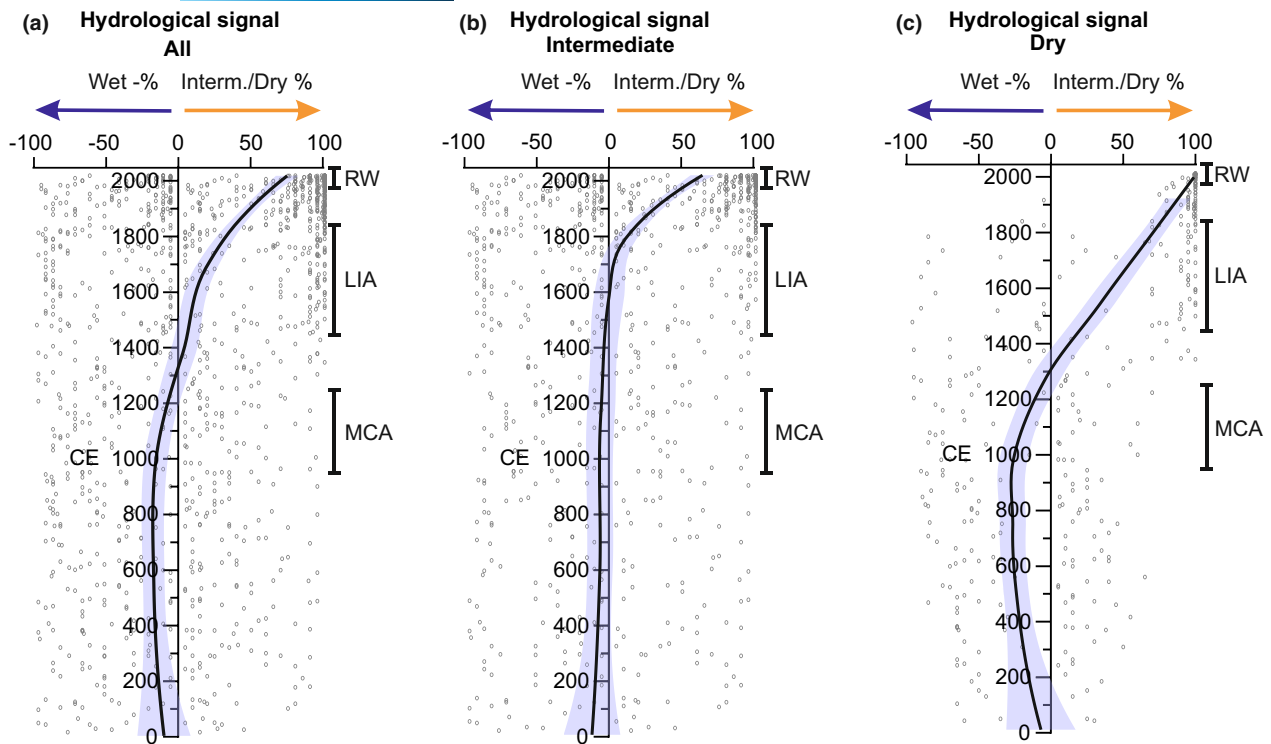
FIGURE 6 The diagrams presenting the hydrological signal (a–c) show the plant abundance data of the records divided to two groups of wet and intermediate/dry indicating vegetation (see Section 2). The negative percentages indicate vegetation living in wet and positive intermediate/dry conditions. The timing of the recent warming (RW), little ice age (LIA), and medieval climate anomaly (MCA) is illustrated. The LOESS curves (in black) show the locally estimated trend of the data points with a 95% confidence interval in light blue shading. In (a) "all" diagrams the data from all of the studied records ($n = 33$) are presented, in (b) "intermediate" diagram the data from the currently intermediate records ($n = 25$) and in (c) "dry" the data from the currently dry records ($n = 8$) are presented.

Hydrology is a stronger driver of vegetation composition, biomass production, and thus vegetation related CO_2 and CH_4 emissions, than temperature (Evans et al., 2021; Laine et al., 2019; Mäkiranta et al., 2018; Peltoniemi et al., 2016). Similarly, vegetation composition and seasonal variations in the thickness of aerobic acrotelm peat layer seem to control decomposition more than temperature per se (Philben et al., 2015). In the north, even though annual precipitation is expected to increase (Bintanja & Andry, 2017) evapotranspiration is expected to increase, making peatlands more prone to drying (Helbig et al., 2020). The impact of increasing evapotranspiration on vegetation compositions may first be less pronounced in vascular plant-dominated fens compared with moss-dominated peatlands such as bogs due to the ability of vascular plants to regulate their ecophysiology through stomatal activity, which buffers them against droughts (Helbig et al., 2020). However, wet fen vegetation communities have been reported to be more sensitive for long-term drying than bogs (Kokkonen et al., 2019).

Future conditions with increased growing season evapotranspiration (Helbig et al., 2020) together with decreased input of water from the mineral catchment soils might promote establishment of *Sphagnum* mosses over fen vegetation (Tahvanainen, 2011) and thus increase C accumulation (Loisel & Yu, 2013), because *Sphagnum* moss litter is more resistant to decay than liverwort,

lichen, or vascular plant litter (Lang et al., 2009). Previous studies showed that between 1970 and 2000 CE permafrost degradation, intensified spring temperatures and earlier snow melt exposed plants to frost drought and triggered a succession where moss and dwarf shrub covered surfaces declined and tall graminoid and lichen cover expanded (Johansson et al., 2006; Malmer et al., 2005). In turn, water level drawdown experiments on high-latitude peatlands have shown that drier conditions result in shrub domination over mosses and forbs, such conditions also sustaining high belowground production (Mäkiranta et al., 2018). However, in the northeast Canada, a regime sift from sedges to *Sphagnum* domination has been documented (Magnan et al., 2022) and centennial peatland drying trend in low latitude Europe (Swindles et al., 2019) and high latitude Eurasian continent is observed from other peatland proxies (testate amoebas) but with more variable signal for North American continent (Zhang et al., 2022). Our results provide valuable information to add on the understanding of global peatland vegetation changes, their response sensitiveness, and complement the hydrological information produced by testate amoebas. Overall, the future trajectory of northern peatland vegetation change and following C dynamics is not yet thoroughly resolved and these dynamics may be accompanied by unpredictable external and sudden forcing events, such as fires and droughts,

which may temporarily and effectively reduce C storage (Fenner & Freeman, 2011; Turetsky et al., 2015).

4 | CONCLUSIONS

Over multiple peatlands across European and Russian sub-Arctic, plant analyses suggest a relatively recent regime shift where sedge-dominated communities were replaced by moss communities namely dominated by *Sphagnum* mosses. Accordingly, the data suggest multi-centennial post medieval climate anomaly drying trend continuing over the recent decades. Accordingly, the habitat change from wet to drier will have an effect on apparent C sink capacity driven by changes in plant composition. Our results suggest that under future climate conditions the long-term C dynamics will be substantially moderated by vegetation, which is regulated by hydrological balance. The resilience of peatland vegetation composition to recent warming also suggests that biological processes should not be overlooked, as vegetation is an important component, which ultimately mediates future C dynamics. Further data on processes linking permafrost peatland vegetation changes, hydrology, and multiannual climate trends are needed to better understand the trajectory of C sequestration and the vegetation succession after gradual and abrupt permafrost thaw.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The raw data used in this study are available in this publication or online through Zenodo https://doi.org/10.5281/zenodo.7415020 (Piilo & Väliranta, 2022).

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REFERENCES

Aquino-López, M. A., Blaauw, M., Christen, J. A., & Sanderson, N. K. (2018). Bayesian analysis of 210 Pb dating. *Journal of Agricultural, Biological, and Environmental Statistics*, *23*, 317–333. https://doi.org/10.1007/s13253-018-0328-7

Aurela, M., Tuovinen, J. P., & Laurila, T. (1998). Carbon dioxide exchange in a subarctic peatland ecosystem in northern Europe measured by the eddy covariance technique. *Journal of Geophysical Research – Atmospheres*, *103*, 11289–11301. https://doi.org/10.1029/98JD00481

Bintanja, R., & Andry, O. (2017). Towards a rain-dominated Arctic. *Nature Climate Change*, *7*, 263–267. https://doi.org/10.1038/nclimate3240

Biskaborn, B. K. (2019). Permafrost is warming at a global scale. *Nature Communications*, *10*, 1–11. https://doi.org/10.1038/s41467-018-08240-4

Borge, A. F., Westermann, S., Solheim, I., & Etzelmüller, B. (2017). Strong degradation of palsas and peat plateaus in northern Norway during the last 60 years. *Cryosphere Discussions*, *11*, 1–16. https://doi.org/10.5194/tc-11-1-2017

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F. W., Brown, R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V. E., Walsh, J. E., Overland, J. E., Wang, M., Corell, R. W., Meier, W. N., Wouters, B., Mernild, S., Mård, J., Pawlak, J., & Olsen, M. S. (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, *14*, 045010. https://doi.org/10.1088/1748-9326/aafc1b

Brown, J., Ferrians, O. J., Heginbottom, J. J. A., & Melnikov, E. S. (1998). *Circum-arctic map of permafrost and ground ice conditions*. National Snow and Ice Data Center/World Data Center for Glaciology Digital Media.

Charman, D. J., Beilman, D. W., Blaauw, M., Booth, R. K., Brewer, S., Chambers, F. M., Christen, J. A., Gallego-Sala, A., Harrison, S. P., Hughes, P. D. M. M., Jackson, S. T., Korhola, A., Mauquoy, D., Mitchell, F. J. G. G., Prentice, I. C., Van Der Linden, M., De Vleeschouwer, F., Yu, Z. C., Alm, J., … Zhao, Y. (2013). Climate-related changes in peatland carbon accumulation during the last millennium. *Biogeosciences*, *10*, 929–944. https://doi.org/10.5194/bg-10-929-2013

Cook, A. E. R., Seager, R., Kushnir, Y., Briffa, K. R., Frank, D., Krusic, P. J., Tegel, W., Van Der Schrier, G., Baillie, M., Baittinger, C., Bleicher, N., Bonde, N., Carrer, M., Cooper, R., Katarina, Č., & Dittmar, C. (2015). Old World megadroughts and pluvials during the Common Era. *Science Advances*, *1*, e1500561. https://doi.org/10.1126/sciadv.1500561

De Vleeschouwer, F., Chambers, F. M., & Swindles, G. T. (2010). Coring and sub-sampling of peatlands for palaeoenvironmental research. *Mires and Peat*, *7*, 1–10. https://doi.org/10.1016/j.ssi.2010.01.014

Estop-Aragonés, C., Cooper, M. D. A., Fisher, J. P., Thierry, A., Garnett, M. H., Charman, D. J., Murton, J. B., Phoenix, G. K., Treharne, R., Sanderson, N. K., Burn, C. R., Kokelj, S. V., Wolfe, S. A., Lewkowicz, A. G., Williams, M., & Hartley, I. P. (2018). Limited release of previously-frozen C and increased new peat formation after thaw in permafrost peatlands. *Soil Biology and Biochemistry*, *118*, 115–129. https://doi.org/10.1016/j.soilbio.2017.12.010

Eurola, S., Bendiksen, K., & Rönkä, A. (1992). Suokasviopas. 2. korjattu painos. In J. Viramo (Ed.), *Oulanka reports*. Oulanka Biological Station.

Evans, C. D., Peacock, M., Baird, A. J., Artz, R. R. E., Burden, A., Callaghan, N., Chapman, P. J., Cooper, H. M., Coyle, M., Craig, E., Cumming, A., Dixon, S., Gauci, V., Grayson, R. P., Helfter, C., Heppell, C. M., Holden, J., Jones, D. L., Kaduk, J., … Morrison, R. (2021). Overriding water table control on managed peatland greenhouse gas emissions. *Nature*, *593*, 548–552. https://doi.org/10.1038/s41586-021-03523-1

Fenner, N., & Freeman, C. (2011). Drought-induced carbon loss in peatlands. *Nature Geoscience*, *4*, 895–900. https://doi.org/10.1038/ngeo1323

Gallego-Sala, A. V., Charman, D. J., Brewer, S., Page, S. E., Colin Prentice, I., Friedlingstein, P., Moreton, S., Amesbury, M. J., Beilman, D. W., Bjamp, S., Blyakharchuk, T., Bochicchio, C., Booth, R. K., Bunbury, J., Camill, P., Carless, D., Chimner, R. A., Clifford, M., Cressey, E., … Zhao, Y. (2018). Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nature Climate Change*, *8*. https://doi.org/10.1038/s41558-018-0271-1

Gong, J., Kellomäki, S., Wang, K., Zhang, C., Shurpali, N., & Martikainen, P. J. (2013). Modeling CO_2 and CH_4 flux changes in pristine peatlands of Finland under changing climate conditions. *Ecological Modelling*, *263*, 64–80. https://doi.org/10.1016/j.ecolmodel.2013.04.018

Helbig, M., Waddington, J. M., Alekseychik, P., Amiro, B. D., Aurela, M., Barr, A. G., Black, T. A., Blanken, P. D., Carey, S. K., Chen, J., Chi, J., Desai, A. R., Dunn, A., Euskirchen, E. S., Flanagan, L. B., Forbrich, I., Friborg, T., Grelle, A., Harder, S., … Zyrianov, V. (2020). Increasing contribution of peatlands to boreal evapotranspiration in a warming climate. *Nature Climate Change*, *10*, 555–560. https://doi.org/10.1038/s41558-020-0763-7

Holmquist, J. R., Finkelstein, S. A., Garneau, M., Massa, C., Yu, Z., & MacDonald, G. M. (2016). A comparison of radiocarbon ages derived from bulk peat and selected plant macrofossils in basal peat cores from circum-arctic peatlands. *Quaternary Geochronology*, *31*, 53–61. https://doi.org/10.1016/j.quageo.2015.10.003

Huang, J., Xie, Y., Guan, X., Li, D., & Ji, F. (2017). The dynamics of the warming hiatus over the northern hemisphere. *Climate Dynamics*, *48*, 429–446. https://doi.org/10.1007/s00382-016-3085-8

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R. B., Jones, M., Macdonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M. B., Treat, C., Turetsky, M., Voigt, C., & Yu, Z. (2020). Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *Proceedings of the National Academy of Sciences of the United States of America*, *1–9*, 20438–20446. https://doi.org/10.1073/pnas.1916387117

Ise, T., Dunn, A. L., Wofsy, S. C., & Moorcroft, P. R. (2008). High sensitivity of peat decomposition to climate change through water-table feedback. *Nature Geoscience*, *1*, 763–766. https://doi.org/10.1038/ngeo331

Johansson, T., Malmer, N., Crill, P. M., Friborg, T., Åkerman, J. H., Mastepanov, M., & Christensen, T. R. (2006). Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. *Global Change Biology*, *12*, 2352–2369. https://doi.org/10.1111/j.1365-2486.2006.01267.x

Jones, M. C., Harden, J., O'Donnell, J., Manies, K., Jorgenson, T., Treat, C., & Ewing, S. (2017). Rapid carbon loss and slow recovery following permafrost thaw in boreal peatlands. *Global Change Biology*, *23*, 1109–1127. https://doi.org/10.1111/gcb.13403

Juggins, S. (2007). *C2 user guide: Software for ecological and palaeoecological data analysis and visualization*. University of Newcastle.

Kelly, T. J., Lawson, I. T., Roucoux, K. H., Baker, T. R., Jones, T. D., & Sanderson, N. K. (2017). The vegetation history of an Amazonian domed peatland. *Palaeogeography Palaeoclimatology Palaeoecology*, *468*, 129–141. https://doi.org/10.1016/j.palaeo.2016.11.039

Kjellman, S. E., Axelsson, P. E., Etzelmüller, B., Westermann, S., & Sannel, A. B. K. (2018). Holocene development of subarctic permafrost peatlands in Finnmark, northern Norway. *Holocene*, *28*, 1855–1869. https://doi.org/10.1177/0959683618798126

Kokkonen, N. A. K., Laine, A. M., Laine, J., Vasander, H., Kurki, K., Gong, J., & Tuittila, E. (2019). Responses of peatland vegetation to 15-year water level drawdown as mediated by fertility level. *Journal of Vegetation Science*, *30*, 1206–1216. https://doi.org/10.1111/jvs.12794

Laine, A. M., Lindholm, T., Nilsson, M., Kutznetsov, O., Jassey, V. E. J., & Tuittila, E.-S. (2021). Functional diversity and trait composition of vascular plant and *Sphagnum* moss communities during peatland succession across land uplift regions. *Journal of Ecology*, *109*, 1774–1789. https://doi.org/10.1111/1365-2745.13601

Laine, A. M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., Minkkinen, K., Fritze, H., & Tuittila, E.-S. (2019). Warming impacts on boreal fen CO_2 exchange under wet and dry conditions. *Global Change Biology*, *1–14*, 1995–2008. https://doi.org/10.1111/gcb.14617

Laine, J., Harju, P., Timonen, T., Laine, A., Tuittila, E., Minkkinen, K., & Vasander, H. (2009). *The intricate beauty of Sphagnum mosses—A Finnish guide to identification*. University of Helsinki Department of Forest Ecology Publications.

Lang, S. I., Cornelissen, J. H. C., Klahn, T., Van Logtestijn, R. S. P., Broekman, R., Schweikert, W., & Aerts, R. (2009). An experimental comparison of chemical traits and litter decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*, *97*, 886–900. https://doi.org/10.1111/j.1365-2745.2009.01538.x

Linderholm, H. W., Nicolle, M., Francus, P., Gajewski, K., Helama, S., Korhola, A., Solomina, O., Yu, Z., Zhang, P., D'Andrea, W. J., Debret, M., Divine, D. V., Gunnarson, B. E., Loader, N. J., Massei, N., Seftigen, K., Thomas, E. K., Werner, J., Andersson, S., … Väliranta, M. (2018). Arctic hydroclimate variability during the last 2000 years: Current understanding and research challenges. *Climate of the Past*, *14*, 473–514. https://doi.org/10.5194/cp-14-473-2018

Loisel, J., Gallego-Sala, A. V., Amesbury, M. J., Magnan, G., Anshari, G., Beilman, D. W., Benavides, J. C., Blewett, J., Camill, P., Charman, D. J., Chawchai, S., Hedgpeth, A., Kleinen, T., Korhola, A., Large, D., Mansilla, C. A., Müller, J., Van Bellen, S., West, J. B., … Wu, J. (2020). Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*, *11*, 70–77. https://doi.org/10.1038/s41558-020-00944-0

Loisel, J., & Yu, Z. (2013). Recent acceleration of carbon accumulation in a boreal peatland, south Central Alaska. *Journal of Geophysical Research: Biogeosciences*, *118*, 41–53. https://doi.org/10.1029/2012JG001978

Maanavilja, L., Riutta, T., Aurela, M., Pulkkinen, M., Laurila, T., & Tuittila, E. S. (2011). Spatial variation in CO_2 exchange at a northern aapa mire. *Biogeochemistry*, *104*, 325–345. https://doi.org/10.1007/s10533-010-9505-7

Magnan, G., Sanderson, N. K., Piilo, S., Pratte, S., Väliranta, M., van Bellen, S., Zhang, H., & Garneau, M. (2022). Widespread recent ecosystem state shifts in high-latitude peatlands of northeastern Canada and implications for carbon sequestration. *Global Change Biology*, *28*, 1919–1934. https://doi.org/10.1111/gcb.16032

Mäkiranta, P., Laiho, R., Mehtätalo, L., Straková, P., Sormunen, J., Minkkinen, K., Penttilä, T., Fritze, H., & Tuittila, E. S. (2018). Responses of phenology and biomass production of boreal fens to

climate warming under different water-table level regimes. *Global Change Biology*, 24, 944–956. https://doi.org/10.1111/gcb.13934

Malmer, N., Johansson, T., Olsrud, M., & Christensen, T. R. (2005). Vegetation, climatic changes and net carbon sequestration in a north-Scandinavian subarctic mire over 30 years. *Global Change Biology*, 11, 1895–1909. https://doi.org/10.1111/j.1365-2486.2005.01042.x

Mann, M. E., Zhang, Z., Rutherford, S., Bradley, R. S., Hughes, M. K., Shindell, D., Ammann, C., Faluvegi, G., & Ni, F. (2009). Global signatures and dynamical origins of the little ice age and medieval climate anomaly. *Science*, 326, 1256–1260. https://doi.org/10.1126/science.1166349

Marshall, G. J., Vignols, R. M., & Rees, W. G. (2016). Climate change in the Kola peninsula, Arctic Russia, during the last 50 years from meteorological observations. *Journal of Climate*, 29, 6823–6840. https://doi.org/10.1175/JCLI-D-16-0179.1

Marushchak, M. E., Pitkämäki, A., Koponen, H., Biasi, C., Seppälä, M., & Martikainen, P. J. (2011). Hot spots for nitrous oxide emissions found in different types of permafrost peatlands. *Global Change Biology*, 17, 2601–2614. https://doi.org/10.1111/j.1365-2486.2011.02442.x

Mauquoy, D., Hughes, P., & Van Geel, B. (2010). A protocol for plant macrofossil analysis of peat deposits. *Mires and Peat*, 7, 1–5.

Oksanen, P. O. (2006). Holocene development of the Vaisjeäggi palsa mire, Finnish Lapland. *Boreas*, 35, 81–95. https://doi.org/10.1111/j.1502-3885.2006.tb01114.x

Oksanen, P. O., Kuhry, P., & Alekseeva, R. N. (2001). Holocene development of the Rogovaya River peat plateau, European Russian Arctic. *The Holocene*, 11, 25–40.

Olvmo, M., Holmer, B., Thorsson, S., Reese, H., & Lindberg, F. (2020). Sub-arctic palsa degradation and the role of climatic drivers in the largest coherent palsa mire complex in Sweden (Vissátvuopmi), 1955–2016. *Scientific Reports*, 10, 8937. https://doi.org/10.1038/s41598-020-65719-1

Peltoniemi, K., Laiho, R., Juottonen, H., Bodrossy, L., Kell, D. K., Minkkinen, K., Mäkiranta, P., Mehtätalo, L., Penttilä, T., Siljanen, H. M. P., Tuittila, E., Tuomivirta, T., & Fritze, H. (2016). Responses of methanogenic and methanotrophic communities to warming in varying moisture regimes of two boreal fens. *Soil Biology and Biochemistry*, 97, 144–156. https://doi.org/10.1016/j.soilbio.2016.03.007

Philben, M., Holmquist, J., Macdonald, G., Duan, D., Kaiser, K., & Benner, R. (2015). Temperature, oxygen, and vegetation controls on decomposition in a James Bay peatland. *Global Biogeochemical Cycles*, 29, 729–743. https://doi.org/10.1002/2014GB004989.Received

Piilo, S. R., Korhola, A., Heiskanen, L., Tuovinen, J. P., Aurela, M., Juutinen, S., Marttila, H., Saari, M., Tuittila, E. S., Turunen, J., & Väliranta, M. M. (2020). Spatially varying peatland initiation, Holocene development, carbon accumulation patterns and radiative forcing within a subarctic fen. *Quaternary Science Reviews*, 248, 106596. https://doi.org/10.1016/j.quascirev.2020.106596

Piilo, S. R., Zhang, H., Garneau, M., Gallego-sala, A., Amesbury, M. J., & Väliranta, M. M. (2019). Recent peat and carbon accumulation following the little ice age in recent peat and carbon accumulation following the little ice age in northwestern Québec, Canada. *Environmental Research Letters*, 14, 75002. https://doi.org/10.1088/1748-9326/ab11ec

Piilo, S., & Väliranta, M. (2022). Plant macrofossil, peat geochemical and chronological data from sub-Arctic European peatlands [Data set]. *Zenodo*, https://doi.org/10.5281/zenodo.7415020

Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J.-P., Karlsson, P., & Ruuhela, R. (2012). *Climatological statistics of Finland 1981–2010*. Reports 2012. Finnish Meteorological Institute.

Post, E., Alley, R., Christensen, T., Macias-Fauria, M., Forbes, B., Gooseff, M., Iler, A., Kerby, J., Laidre, K., Mann, M., Olofsson, J., Stroeve, J., Ulmer, F., Virginia, R., & Wang, M. (2019). The polar regions in a 2°C

warmer world. *Science Advances*, 5, 1–13. https://doi.org/10.1126/sciadv.aaw9883

R Core Team. (2014). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Ronkainen, T., Väliranta, M., McClymont, E., Biasi, C., Salonen, S., Fontana, S., Tuittila, E. S., Väliranta, M., McClymont, E., Biasi, C., Salonen, S., Fontana, S., & Tuittila, E. S. (2015). A combined biogeochemical and palaeobotanical approach to study permafrost environments and past dynamics. *Journal of Quaternary Science*, 30, 189–200. https://doi.org/10.1002/jqs.2763

Sannel, A. B. K., Hempel, L., Kessler, A., & Preskienis, V. (2018). Holocene development and permafrost history in sub-arctic peatlands in Tavvavuoma, northern Sweden. *Boreas*, 47, 454–468. https://doi.org/10.1111/bor.12276

Seppälä, M. (2011). Synthesis of studies of palsa formation underlining the importance of local environmental and physical characteristics. *Quaternary Research*, 75, 366–370. https://doi.org/10.1016/j.yqres.2010.09.007

Sim, T. G., Swindles, G. T., Morris, P. J., Baird, A. J., Cooper, C. L., Gallego-Sala, A. V., Charman, D. J., Roland, T. P., Borken, W., Mullan, D. J., Aquino-López, M. A., & Gałka, M. (2021). Divergent responses of permafrost peatlands to recent climate change. *Environmental Research Letters*, 16, 034001. https://doi.org/10.1088/1748-9326/abe00b

Swindles, G. T., Morris, P. J., Mullan, D., Watson, E. J., Turner, T. E., Roland, T. P., Amesbury, M. J., Kokfelt, U., Schoning, K., Pratte, S., Gallego-Sala, A., Charman, D. J., Sanderson, N., Garneau, M., Carrivick, J. L., Woulds, C., Holden, J., Parry, L., Galloway, J. M., ... Galloway, J. M. (2015). The long-term fate of permafrost peatlands under rapid climate warming. *Scientific Reports*, 5, 1–6. https://doi.org/10.1038/srep17951

Swindles, G. T., Morris, P. J., Mullan, D. J., Payne, R. J., Roland, T. P., Amesbury, M. J., Lamentowicz, M., Turner, T. E., Gallego-sala, A., Sim, T., Barr, I. D., Blaauw, M., Blundell, A., Chambers, F. M., Charman, D. J., Feurdean, A., Galloway, J. M., Gałka, M., Green, S. M., ... Warner, B. (2019). Widespread drying of European peatlands in recent centuries. *Nature Geoscience*, 12, 922–928. https://doi.org/10.1038/s41561-019-0462-z

Tahvanainen, T. (2011). Abrupt ombrotrophication of a boreal aapa mire triggered by hydrological disturbance in the catchment. *Journal of Ecology*, 99, 404–415. https://doi.org/10.1111/j.1365-2745.2010.01778.x

Tolonen, K., & Turunen, J. (1996). Accumulation rates of carbon in mires in Finland and implications for climate change. *The Holocene*, 6, 171–178.

Turetsky, M. R., Abbott, B. W., Jones, M. C., Anthony, K. W., Olefeldt, D., Schuur, E. A. G., Grosse, G., Kuhry, P., Hugelius, G., Koven, C., Lawrence, D. M., Gibson, C., Sannel, A. B. K., & McGuire, A. D. (2020). Carbon release through abrupt permafrost thaw. *Nature Geoscience*, 13, 138–143. https://doi.org/10.1038/s41561-019-0526-0

Turetsky, M. R., Benscoter, B., Page, S., Rein, G., Van Der Werf, G. R., & Watts, A. (2015). Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience*, 8, 11–14. https://doi.org/10.1038/ngeo2325

Turunen, J., Tomppo, E., Tolonen, K., & Reinikainen, A. (2002). Estimating carbon accumulation rates of undrained mires in Finland–application to boreal and subarctic regions. *The Holocene*, 12, 69–80. https://doi.org/10.1191/0959683602hl522rp

Väliranta, M., Korhola, A., Seppa, H., Tuittila, E. S., Sarmaja-Korjonen, K., Laine, J., Alm, J., Seppä, H., Tuittila, E. S., Sarmaja-Korjonen, K., Laine, J., & Alm, J. (2007). High-resolution reconstruction of wetness dynamics in a southern boreal raised bog, Finland, during the late Holocene: A quantitative approach. *Holocene*, 17, 1093–1107. https://doi.org/10.1177/0959683607082550

Waddington, J. M., & Roulet, N. T. (2000). Carbon balance of a boreal patterned peatland. *Global Change Biology*, 6, 87–97. https://doi.org/10.1046/j.1365-2486.2000.00283.x

Wilson, R., Anchukaitis, K., Briffa, K. R., Büntgen, U., Cook, E., D'Arrigo, R., Davi, N., Esper, J., Frank, D., Gunnarson, B., Hegerl, G., Helama, S., Klesse, S., Krusic, P. J., Linderholm, H. W., Myglan, V., Osborn, T. J., Rydval, M., Schneider, L., … Zorita, E. (2016). Last millennium northern hemisphere summer temperatures from tree rings: Part I: The long term context. *Quaternary Science Reviews*, 134, 1–18. https://doi.org/10.1016/j.quascirev.2015.12.005

Xu, J., Morris, P. J., Liu, J., & Holden, J. (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *Catena*, 160, 134–140. https://doi.org/10.1016/j.catena.2017.09.010

Young, D. M., Baird, A. J., Charman, D. J., Evans, C. D., Gallego-Sala, A. V., Gill, P. J., Hughes, P. D. M., Morris, P. J., & Swindles, G. T. (2019). Misinterpreting carbon accumulation rates in records from near-surface peat. *Scientific Reports*, 9, 17939. https://doi.org/10.1038/s41598-019-53879-8

Young, D. M., Baird, A. J., Gallego-Sala, A. V., & Loisel, J. (2021). A cautionary tale about using the apparent carbon accumulation rate (aCAR) obtained from peat cores. *Scientific Reports*, 11, 1–12. https://doi.org/10.1038/s41598-021-88766-8

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., & Hunt, S. J. (2010). Global peatland dynamics since the last glacial maximum. *Geophysical Research Letters*, 37, 1–5. https://doi.org/10.1029/2010GL043584

Zhang, H., Gallego-Sala, A. V., Amesbury, M. J., Charman, D. J., Piilo, S. R., & Väliranta, M. M. (2018). Inconsistent response of Arctic permafrost peatland carbon accumulation to warm climate phases. *Global Biogeochemical Cycles*, 1605–1620, 1605–1620. https://doi.org/10.1029/2018GB005980

Zhang, H., Piilo, S. R., Amesbury, M. J., Charman, D. J., Gallego-Sala, A. V., & Väliranta, M. M. (2018). The role of climate change in regulating Arctic permafrost peatland hydrological and vegetation change over the last millennium. *Quaternary Science Reviews*, 182, 121–130. https://doi.org/10.1016/j.quascirev.2018.01.003

Zhang, H., Väliranta, M., Piilo, S., Amesbury, M. J., Aquino-López, M. A., Roland, T. P., Salminen-Paatero, S., Paatero, J., Lohila, A., & Tuittila, E. (2020). Decreased carbon accumulation feedback driven by climate-induced drying of two southern boreal bogs over recent centuries. *Global Change Biology*, 26, 2435–2448. https://doi.org/10.1111/gcb.15005

Zhang, H., Väliranta, M., Swindles, G. T., Aquino-lópez, M. A., Mullan, D., Tan, N., Amesbury, M., Babeshko, K. V., Bao, K., Bobrov, A., Feurdean, A., Finkelstein, S. A., Garneau, M., Guo, Z., Jones, M. C., Marcisz, K., Mazei, N., Mazei, Y., Payne, R., … Zhao, Y. (2022). Recent climate change has driven divergent hydrological shifts in high-latitude peatlands. *Nature Communications*, 13, 4959. https://doi.org/10.1038/s41467-022-32711-4

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